Fishery Bulletin

Vol. 77, No. 1 January 1979

(Continued on next page)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

Juanita M. Kreps, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46, the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1965 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

[illegible] published quarterly by Scientific Publications Office, National Marine Fisheries Service, [illegible] Seattle, WA 98115. Controlled circulation paid by Finance Department, USPS. [illegible]

[illegible] publication [illegible] entirely reference use. Source is appreciated.

[illegible] the transaction of the public [illegible] This publication has been approved by the Director of the [illegible]

Fishery Bulletin

CONTENTS

Vol. 77, No. 1 January 1979

(Continued on next page)

Seattle, Washington

1979

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington DC 20402.—Subscription price per year $12.00 domestic and $15.00 foreign. Cost per single issue $3.00 domestic and $3.75 foreign.

Notes

Notices

Vol. 76, No. 4 was published on 28 February 1979

DEVELOPMENT AND OCCURRENCE OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES CRAMERI*, *SEBASTES PINNIGER*, AND *SEBASTES HELVOMACULATUS* (FAMILY SCORPAENIDAE) OFF OREGON[1]

SALLY L. RICHARDSON[2] AND WAYNE A. LAROCHE[3]

ABSTRACT

Developmental series of larvae and juveniles of three species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are illustrated and described: *S. crameri* (8.0 to 130.5 mm standard length), *S. pinniger* (7.8 to 181 mm standard length), and *S. helvomaculatus* (7.7 to 183 mm standard length). The descriptions include a literature review, characters used for identification including meristics and supraocular spine patterns, distinguishing features, general development, morphology, fin development, spination, scale formation, and pigmentation. Occurrence in waters off Oregon is discussed.

The approach that was used to identify larval and juvenile specimens of *Sebastes* from plankton, midwater trawl, and bottom trawl collections from Oregon waters is presented, since 36 species reportedly occur there. Developmental terminology is newly defined for *Sebastes*. Larval and juvenile spination is presented schematically and defined.

Larvae and juveniles of the three species described here are compared with other known *Sebastes* larvae and juveniles from the northeast Pacific.

Data gathered during this study extend the southern range limit of *Sebastes emphaeus* to Punta Gordo, Calif.

Rockfish of the genus *Sebastes* are an important group of fishes in the northeast Pacific both in terms of number of species and in commercial and sport fisheries. Sixty-nine species of *Sebastes* occur between the Gulf of California and the Gulf of Alaska (Chen 1971, 1975). In 1975, Pacific trawl landings of *Sebastes* spp. in the United States and Canada, categorized as "Pacific ocean perch" and "other rockfish," were 17,400 metric tons (t) or 23.9% of the total trawl landings (Verhoeven 1976). In California, rockfish compose half the number of sportfish caught (Young 1969).

"Pacific ocean perch" (primarily *Sebastes alutus*) trawl landings in the United States and Canada declined from a peak of 14,000 t in 1965 to 8,500 t in 1975 and "other rockfish" landings subsequently increased from 8,600 t in 1965 to 16,300 t in 1973 and 13,300 t in 1975 (Pacific Marine Fisheries Commission 1964-76; Verhoeven 1976). Because of this shift in composition of trawl landings, knowledge of the biology of the individual species involved, including their early life history, is becoming increasingly important. Such information is relatively scarce, partly because of the difficulty involved in identifying the young stages.

Rockfish larvae, which are extruded live from ovoviviparous females, are pelagic as are young juveniles. The pelagic larvae are very abundant, ranking third or fourth in annual larval fish abundance off California (Ahlstrom 1961, 1965) and second only to osmerid larvae off Oregon (Richardson 1977; Richardson and Pearcy 1977). Juveniles are important as forage items for larger fishes, such as albacore (Powell et al. 1952) and salmon (Whitney 1893; Silliman 1941; Pritchard and Tester 1944; Merkel 1957), and marine birds (Follett and Ainley 1976).

Pelagic larvae and juveniles of relatively few of the 69 northeast Pacific rockfish species have been described. Illustrations or partial descriptions of pigment patterns have been presented for preextrusion or newborn larvae of 47 of these species but only 26 of these were reared to the point of yolk absorption (Table 1). The first larval developmental series of *Sebastes* spp. were presented as two unnamed species (Ahlstrom 1965) the second of

[1]From a final report for NOAA NMFS Contract No. 03-6-208-35343 submitted to Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, on 15 June 1977.

[2]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, P.O. Drawer AG, Ocean Springs, MS 39564.

[3]School of Oceanography, Oregon State University, Corvallis, OR 97331.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

which is now known to be *S. paucispinis* (Moser 1967; Moser et al. 1977). Complete development series from newly hatched larvae to benthic juveniles have only been described for *S. cortezi*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, *S. paucispinis*, and *Sebastes* sp. — Gulf of California Type A (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978).

This paper is a contribution to the knowledge of the early life history of northeast Pacific rockfishes. Developmental series of three species, *S. crameri*, *S. pinniger*, and *S. helvomaculatus*, are described for the first time. The first two species are important contributors to Oregon trawl landings (Niska 1976). Information on occurrence of larvae and juveniles of these three species off Oregon is also given. Because of the large species complex of *Sebastes* in the northeast Pacific and the difficulty in identifying young rockfish, e.g., adult keys cannot be used, the approach that was used to identify the specimens in this study is presented as part of the methodology.

MATERIALS AND METHODS

Collections

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. The collections were obtained with 70 cm bongo nets, neuston nets, meter nets, Isaacs-Kidd midwater trawls, beam trawls, and otter trawls off the Oregon coast since 1961 during all months of the year. Samples were taken along the entire coast, but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1′ N). All material had been preserved in either 5 or 10% Formalin[1] and most had been transferred to 30 or 40% isopropyl alcohol. Over 12,000 *Sebastes* larvae and juveniles were sorted from the available collections.

Approach to Identification

Geographic ranges of all known northeast Pacific species (excluding the new species being described by Lea and Fitch (Chen 1975), presumably from California) were recorded from the literature (Appendix Table 1). Additional range information gathered during this study extends the southern range of *S. emphaeus* through Oregon to Punta Gordo, Calif. (lat. 40°12.9′ N, long. 124°23.7′ W, depth 97 m). Adults of only 36 of these species are reported to occur off Oregon. The occurrence of two of these, *S. eos* and *S. rosaceus*, is questionable north of northern California (Chen 1971). Although ocean currents could potentially carry larvae and juveniles of additional species into Oregon waters, it is unlikely that large numbers of young of other species would be taken in an area where the adults do not occur. Following this assumption, tables of morphological characters were prepared for these 36 potential species. The most useful characters for identifying young rockfish were shape of the upper profile of the head (interorbital space) and presence or absence of specific head spines, particularly the supraocular (Appendix Table 2); number, including range and usual (most commonly occurring) number of dorsal fin rays, anal fin rays, and pectoral fin rays (Appendix Table 3); total number of gill rakers on the first gill arch (Appendix Table 4); number of lateral line pores (Appendix Table 5); number of diagonal scale rows below the lateral line (Appendix Table 6). Proportions of body parts related to standard length such as length of upper jaw, head length, length of longest dorsal spine, and body depth at pelvic fin insertion were compiled but were not particularly useful. Additional information which was sometimes helpful included records from trawl surveys off Oregon (Demory et al. 1976) and commercial catch trends in Oregon (Niska 1976) which gave indications of species common in trawlable habitats in the area. Pigment banding patterns of adults were also useful.

Initially, counts were made on each juvenile to be identified along with notes on additional, potentially useful characters. Data for each specimen were then screened through each of the appendix tables, and the species which did not agree were eliminated as potential candidates. This approach, together with some additional data from the literature as noted in the text, lead to positive identification for the species included in this paper.

Developmental series were established backwards from juveniles primarily on the basis of pigmentation, particularly that of the pectoral and pelvic fins and that on the dorsal and ventral body margins, general body shape (e.g., short and stubby, slender and elongate), and constancy in number of dorsal, anal, and pectoral fin rays which could be counted back to postflexion, sometimes

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

flexion, larvae. Developmental series could not be carried back to newly extruded larvae in the plankton samples with certainty. Pigmentation is the primary character used to distinguish small larvae prior to development of fin rays and head spines. Pigment patterns of newborn larvae are often similar among a number of species and these patterns may change considerably by the time the yolk is absorbed (Westrheim 1975; Moser et al. 1977). Preextrusion and newborn larvae have been described for 29 of the 36 species of *Sebastes* off Oregon, but larvae reared to yolk absorption have only been described for 15 (Table 1). The number of species which have patterns similar to those that have been described is unknown. Rearing larvae of the remaining species to yolk absorption will be necessary to provide an adequate foundation for identification of small larvae in plankton samples. We had no opportunity to rear larvae from known parents.

Meristics[5]

Counts were made on unstained material as not enough specimens were available to make complete stained series for developmental ossification studies. [One to several pelagic juveniles of *S. crameri*, *S. pinniger*, and *S. helvomaculatus* were stained with alizarin red S (Taylor 1967) for examination of general bone structure, spination, and secondary caudal rays.] Fin spines and rays were only counted when they appeared to be fully formed structures under magnification, which may approximate initial ossification. Bases of fin rays, visible prior to actual ray formation, were not counted. In *Sebastes*, the 13th dorsal spine and the 3d anal spine form first as soft rays which then transform to spines beginning at the basal portion and continuing distally. These were considered to be "prespines" until spine formation was complete.

Counts were made of dorsal fin spines and rays, anal fin spines and rays, pectoral fin rays, pelvic fin rays, principal caudal fin rays, gill rakers on the upper and lower limb of the first gill arch, lateral line pores, and diagonal scale rows below the lateral line. In some cases India ink was applied to the right side of a fish to increase visibility of the latter two features.

[5]The term "meristic" is used here to refer to all countable characters.

Morphometrics

Measurements of various body parts of selected specimens were made to the nearest 10th or 100th of a millimeter using an ocular micrometer in a stereomicroscope as follows:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle (SL of 30.3 mm on *S. crameri*, 16.8 mm on *S. pinniger*, 41.6 mm on *S. helvomaculatus*).

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine, posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series)

Length of angle gill raker = distance from tip of gill raker to point of articulation with gill arch.

TABLE 1.—Summary of data on preextrusion larvae (P) or newborn, reared larvae (L) of northeast Pacific species of *Sebastes*. Asterisk indicates figure is included.

Species	Eigenmann (1892)	Wales (1952)	Morris (1956)	DeLacy et al. (1964)	Ahlstrom (1965)	Moser (1967)	Waldron (1968)	Westrheim et al. (text footnote 7)	Westrheim et al. (text footnote 9)	Efremenko and Lisovenko (1970)	Harling et al. (text footnote 10)	Moser (1972)	Westrheim (1975)	Moser et al. (1977)	Moser and Ahlstrom (1978)
S. aleutianus								P*		P*			P		
S. alutus				P*				P*		P*			P		
S. atrovirens															
S. auriculatus	(P*)			P*									P	L*	
S. aurora															
S. babcocki				[1]P*				[1]P*		[1]P*			P		
S. borealis															
S. brevispinis				P*						P*			P	P	
S. carnatus						L*								L*	
S. caurinus				P*									P	L*	
S. chlorostictus						L*								L*	
S. chrysomelas															
S. ciliatus											P*		P		
S. constellatus						L*								L*	
S. cortezi															
S. crameri								P*					P		
S. dalli						L*								L*	
S. diploproa				P*					P*				P	P	
S. elongatus						L*			P*				P	L*	
S. emphaeus															
S. ensifer						L*								L*	
S. entomelas											P*		P		
S. eos						L*								L*	
S. exsul															
S. flavidus				P*									P	P	
S. gilli														L*	
S. goodei			L*										P	L*	
S. helvomaculatus									P*				P		
S. hopkinsi						L								L*	
S. jordani			L*										P	L*	
S. lentiginosus															
S. levis						L*								L*	
S. macdonaldi						L*						L*		L*	
S. maliger				P*					P*				P	P	
S. melanops															
S. melanostomus														L*	L
S. miniatus														L*	
S. mystinus		P*							P*						
S. nebulosus															
S. nigrocinctus															
S. notius															
S. ovalis						L*								L*	
S. paucispinis			L*		L	L*							P	L*	
S. pedunculatus															
S. phillipsi															
S. pinniger							L*						P	L*	
S. polyspinis															
S. proriger									F				P		
S. rastrelliger															
S. reedi								P*					P		
S. rosaceus						L*								L*	
S. rosenblatti														L*	
S. ruberrimus				P*					P*		P*		P		
S. rubrivinctus	F			(3)				(3)		(3)					
S. rufinanus															
S. rufus														P	
S. saxicola			L*					P*					P	L*	
S. semicinctus						L*								L*	
S. serranoides														P	
S. serriceps														L*	
S. simulator															
S. sinensis															
S. spinorbis															
S. umbrosus						L*								L*	
S. variegatus											P*		P		
S. varispinis															
S. wilsoni														P	
S. zacentrus									P*	P*	P*		P		
S. new sp. (Lea and Fitch)															

[1]Described as *S. rubrivinctus* but northern occurrence indicates it must be *S. babcocki*.
[2]Described as *S. rhodochloris*.
[3]These descriptions of *S. rubrivinctus* must be *S. babcocki* due to the northern occurrence of specimens.

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise.

Developmental Terminology

Terminology for development of *Sebastes* spp. used in this paper is as follows:

Preflexion larva = prior to notochord flexion.

Flexion larva = undergoing notochord flexion from time urostyle begins to slant upward until urostyle is in final upturned position and caudal fin is formed.

Postflexion larva = from completion of notochord flexion (urostyle may still extend beyond the base of the caudal fin) to onset of transformation of 13th dorsal spine and 3d anal spine from soft ray to spine, and to the associated onset of development of juvenile pigment pattern (usually addition of pigment to the dorsum).

Transforming larva = from onset to completion of transformation of 13th dorsal spine and 3d anal spine from soft ray to fully developed spine. Also from the onset of development of juvenile pigment pattern to development of distinctive juvenile pigmentation, often in the form of melanistic saddles over the dorsum.

Pelagic juvenile = from completion of formation of 13th dorsal and 3d anal spine (and thus attainment of adult complement of actual fin spines and rays) and development of juvenile pigmentation until no longer captured pelagically.

Benthic juvenile = from time of first capture on bottom and usual associated decrease in intensity of melanistic pigmentation to attainment of sexual maturity.

Spination (Figure 1, Table 2)

Difficulties arise in naming all the spines found in the head region of larvae and juveniles of *Sebastes* because not all are found in adults. Further complications arise because the names traditionally used for a number of the head spines do not reflect the bone from which the spine originates. For these reasons we include a composite diagram of spines which may occur during the larval and juvenile periods. The terminology is a combination and modification of that used by Phillips (1957), Chen (1971), Moser (1972), and Moser and Ahlstrom (1978). Most names used in this paper are the same as those used for adult rockfishes to avoid confusion, even though the bones from which the spines originate are not indicated by the name. Exceptions are as follows. The two spines found on the opercular margin are here called the subopercular and the interopercular according to the bones from which they originate. The superior posttemporal (supracleithral of adults), inferior posttemporal (not found in adults), and supracleithral (cleithral of adults) are so-called because of their origin. This is done to avoid confusion with a spine present on the posterior margin of the cleithrum, which is here called the cleithral spine. Use of the term infraorbital

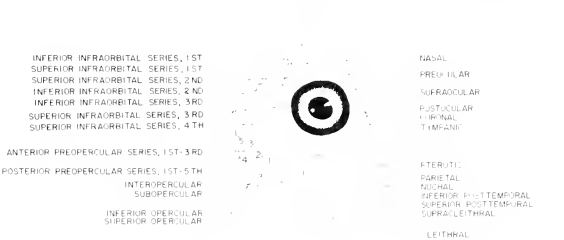


FIGURE 1.—Composite diagram of spines present in the head region of larval and juvenile *Sebastes* species including names used in this paper. Refer to Table 2 for corresponding names used for adults and bones from which spines originate.

TABLE 2.—Names of head region spines of larval and juvenile *Sebastes* spp. used in this paper with corresponding names used for adults and bones from which the spines originate. Spines listed in the first column are shown in Figure 1 clockwise beginning with the nasal

Name used in this paper	Name used in adults[1]	Bone from which spine(s) originates[2]
Nasal	Nasal	Nasal
Preocular	Preocular	Prefrontal
Supraocular	Supraocular	Frontal
Postocular	Postocular	Frontal
Coronal	Coronal	Frontal
Tympanic	Tympanic	Frontal
Pterotic	Pterotic	Pterotic
Parietal	Parietal	Parietal
Nuchal	Nuchal	Parietal
Inferior posttemporal	—	Posttemporal
Superior posttemporal	Supracleithral	Posttemporal
Supracleithral	Cleithral	Supracleithrum
Cleithral	—	Cleithrum
Superior opercular	Opercular	Operde
Inferior opercular	Opercular	Operde
Subopercular	Gill cover spine	Subopercle
Interopercular	Gill cover spine	Interopercle
Posterior preopercular series 1st-5th	Preopercular	Preopercle
Anterior preopercular series 1st-3d	—	Preopercle
Superior infraorbital series 4th	—	Infraorbital 3 (2d suborbital)
Superior infraorbital series	—	Infraorbital 2 (1st suborbital)
Inferior infraorbital series 3d	—	Infraorbital 1 (preorbital)
Inferior infraorbital series 2d	Lachrymal projection (suborbital spine)	Infraorbital 1 (preorbital)
Superior infraorbital series 2d	—	Infraorbital 1 (preorbital)
Superior infraorbital series 1st	—	Infraorbital 1 (preorbital)
Inferior infraorbital series 1st	Lachrymal projection (suborbital spine)	Infraorbital 1 (preorbital)

[1]After Phillips (1957) and Chen (1971).
[2]After Matsubara (1943) and Weitzman (1962).

follows Weitzman (1962) as recommended by Poss.[6]

SEBASTES CRAMERI (JORDAN) (Figures 2, 3, 4)

Literature.—Pigment patterns of preextrusion larvae of *S. crameri* were described by Westrheim et al.,[7] including one figure, and Westrheim (1975). Preextrusion larvae (mean total length = 5.7 mm) have a row of 10 to 23 melanophores (45% of 60 larvae had > 16 melanophores) along the ventral body midline which stops short of the anus by four myomeres. Melanophore(s) are also usually present on the ventral finfold in the hypural region. The gut is pigmented. No pigment occurs on the head, nape, or dorsal body midline, however, Westrheim (1975) reported that *S. crameri* larvae, along with several other species, reared for several days develop pigment spots on the head, nape, and or lower jaw.

Identification (Table 3, Appendix Tables 2-6).—Eighty-one specimens of *S. crameri*, ranging from 8.0 to 130.5 mm, were identified. Juveniles were identified using the following combination of characters recorded from specimens in our collections:

Gill rakers = 30-34
Lateral line pores = 43-50
Pectoral fin rays = 18-20, usually 19
Anal fin soft rays = 7
Dorsal fin soft rays = 13-15
Supraocular spine = present
Interorbital space = flat to convex.

No other species on our list of potential species agrees with all these characters. In addition, the characteristic pigment banding of adults was obvious on larger juveniles. Larvae and juveniles were relatively abundant in our collections and adults are known to be abundant in terms of biomass in trawl catches off the Oregon coast (Demory et al. 1976; Niska 1976). The developmental series was linked together primarily on the basis of pigmentation and also body shape and time of occurrence. Identification of most of the smaller specimens was further substantiated by meristics, particularly the constancy in number of anal and pectoral fin rays (Table 3).

[6]S. G. Poss, Ph.D. Candidate, Department of Zoology, University of Michigan, Ann Arbor, MI 48109, pers. commun. July 1977.
[7]Westrheim, S. J., W. R. Harling, and D. Davenport. 1968. Preliminary report on the maturity, spawning season and larval identification of rockfishes (*Sebastes* spp.) collected off British Columbia in 1967. Fish. Res. Board Can. Manuscr. Rep. 951, 23 p.

FIGURE 2.—Planktonic larvae (9.0, 12.6, 14.7 mm) of *Sebastes crameri*.

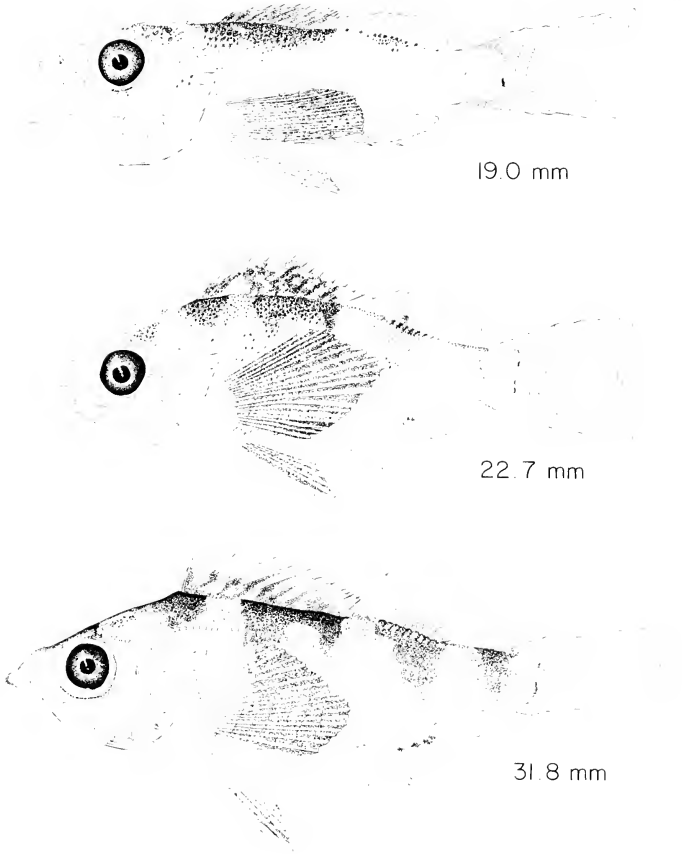


FIGURE 3.—Transforming specimen (19.0 mm) and pelagic juveniles (22.7, 31.8 mm) of *Sebastes crameri*

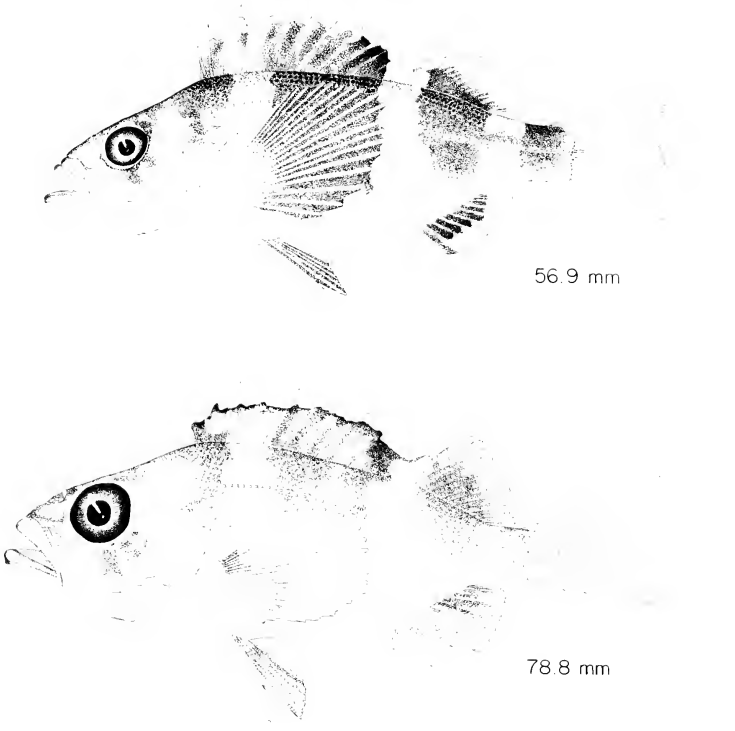


FIGURE 4.—Pelagic juvenile (56.9 mm) and benthic juvenile (78.8 mm) of *Sebastes crameri*

Distinguishing Features.—Characters useful to distinguish the smallest identified larvae (8.0 mm) are the heavily pigmented pectoral and pelvic fins, the presence of a heavy nape pigment patch from which some melanophores extend down and over the gut externally on the body wall, the absence of dorsal midline pigment other than at the nape, the presence of ventral midline pigment as <11 distinct melanophores of which the anterior ones are embedded and only the posteriormost ones remain on the ventral body surface and pigment at the tip of the lower jaw. The presence of pigment on the first dorsal fin in larvae as small as 11 mm is also a useful character. Meristics, presence of a supraocular spine, flat to convex shape of the interorbital space, heavily pigmented

TABLE 3 — Meristics from larvae and juveniles of *Sebastes crameri* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
8.0	(3)	(3)	—	19	(2)	(2)	—	—	—	—	—
8.0	(3)	(3)	19	19	(2)	(2)	—	—	—	—	—
9.0	III + I,13-14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
9.0	I,14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
9.3	I,14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
10.6	VI + I,13	I,7	19	19	I,5	I,5	—	—	—	—	—
10.6	VIII + I,14	II,7	19	19	I,5	I,5	—	—	—	—	—
10.7	IX + I,13	II,7	—	19	I,5	I,5	—	—	—	—	—
12.2	X + I,14	III,7	19	19	I,5	I,5	—	19 + 8	27	—	—	—
12.6	XI + II,13	III,7	19	19	I,5	I,5	—	19 + 8	27	—	—	—
12.8	XI + II,14	III,7	19	19	I,5	I,5	—	—	—	—	—	—
13.6	XIII,13	III,7	19	19	I,5	I,5	—	18 + 8	26	—	—	—
13.8	XIII,14	III,7	19	20	I,5	I,5	—	20 + 8	28	—	—	—
14.4	XIII,14	III,7	19	19	I,5	I,5	—	20 + 8	28	—	—	—
14.7	XIII,14	III,7	20	19	I,5	I,5	—	21 + 9	30	—	—	—
15.4	XIII,14	III,7	18	18	I,5	I,5	—	—	—	—	—	—
†16.0	XIII,14	III,7	19	19	I,5	I,5	—	21 + 8	29	—	—	—
†16.3	XIII,14	III,7	19	19	I,5	I,5	—	22 + 8	30	—	—	—
†17.3	XIII,13	III,7	19	19	I,5	I,5	—	21 + 9	30	—	—	—
†17.4	XIII,13	III,7	19	19	I,5	I,5	—	22 + 9	31	—	—	—
†18.2	XIII,14	III,7	19	19	I,5	I,5	—	20 + 9	29	—	—	—
†18.4	XIII,13	III,7	20	19	I,5	I,5	—	22 + 9	31	—	—	—
†18.6	XIII,14	III,7	20	20	I,5	I,5	—	22 + 8	30	—	—	—
†19.0	XIII,14	III,7	19	20	I,5	I,5	—	22 + 10	32	—	—	—
†20.0	XIII,14	III,7	19	19	I,5	I,5	21 + 9	30	22 + 9	31	—	—
†20.3	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	22 + 9	31	—	—
†21.0	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	21 + 9	30	—	—
*22.7	XIII,13	III,7	20	20	I,5	I,5	22 + 9	31	22 + 9	31	—	—
*23.5	XIII,13	III,7	19	19	I,5	I,5	23 + 9	32	22 + 10	32	—	—
*24.2	XIII,14	III,7	19	19	I,5	I,5	23 + 9	32	22 + 9	31	—	—
*25.6	XIII,15	III,7	19	20	I,5	I,5	22 + 9	31	23 + 9	32	—	—
†28.6	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	23 + 10	33	—	—
†30.0	XIII,13	III,7	19	19	I,5	I,5	22 + 9	31	23 + 9	32	48	47
†31.8	XIII,13	III,7	19	19	I,5	I,5	23 + 10	33	22 + 10	32	46	—
†35.7	XIII,14	III,7	19	19	I,5	I,5	23 + 9	32	23 + 9	32	45	43
†38.2	XIII,14	III,7	19	19	I,5	I,5	23 + 10	33	23 + 9	32	—	—
†36.9	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	22 + 9	31	45	46
†46.8	XIII,13	III,7	19	19	I,5	I,5	24 + 9	33	23 + 9	32	48	—
†49.2	XIII,14	III,7	19	19	I,5	I,5	23 + 10	33	24 + 10	34	43	46
†58.9	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	22 + 9	31	—	45
†63.0	XIII,14	III,7	19	19	I,5	I,5	23 + 9	32	23 + 9	32	45	46
†63.2	XIII,13	III,7	—	19	I,5	I,5	22 + 9	31	23 + 9	32	—	46
†65.0	XIII,14	III,7	19	20	I,5	I,5	24 + 9	33	23 + 9	32	49	50
†67.6	XIII,14	III,7	19	19	I,5	I,5	22 + 10	32	23 + 10	33	47	48
†78.8	XIII,14	III,7	19	19	I,5	I,5	22 + 9	31	22 + 9	31	48	44
†96.1	XIII,13	III,7	19	18	I,5	I,5	23 + 9	32	23 + 9	32	46	46
†41.8	XIII,14	III,7	19	19	I,5	I,5	22 + 10	32	22 + 10	32	47	45
†94.4	XIII,14	III,7	19	19	I,5	I,5	22 + 8	30	23 + 9	32	44	47
†94.7	XIII,14	III,7	19	20	I,5	I,5	23 + 10	33	23 + 9	32	47	46
†96.2	XIII,13	III,7	19	18	I,5	I,5	22 + 9	31	22 + 9	31	47	45
†96.6	XIII,13	III,7	19	19	I,5	I,5	24 + 9	33	22 + 9	31	47	47
†124.7	XIII,14	III,7	19	19	I,5	I,5	23 + 9	32	23 + 9	32	45	44
†207.6	XIII,13	III,7	20	19	I,5	I,5	23 + 10	33	23 + 9	32	46	47

Forming.
Not formed.
Anteriormost dorsal- or anal spine appears as a soft ray.
*Transforming.
†Pelagic juvenile.
‡Benthic juvenile.

pectoral and pelvic fins and pigment banding pattern on the body serve to distinguish juveniles.

General Development — The smallest specimens (8.0-9.0 mm) of *S. crameri* in the series are undergoing the final stages of notochord flexion, which is completed by the time larvae are 10 mm. Transformation from postflexion larvae to pelagic juveniles is rather gradual beginning when larvae are about 16 mm. Body characterized by addition of pigment beneath the second dorsal fin and along with initiation of structural changes of the "prespines" in the dorsal and anal fins. Transformation is complete in 22 mm specimens; and the juvenile pigment pattern is obvious. Transition from pelagic to benthic habitat probably occurs when fish are 40 to 60 mm. The largest pelagic juvenile, captured in a neuston net was 96.2 mm and the

smallest juvenile taken in a bottom trawl was 46.8 mm.

Morphology (Tables 4, 5).—Measurements of various body parts were made on 53 selected specimens of *S. crameri*, ranging from 8.0 to 130.5 mm long, to examine developmental morphology. Relative body depth at the pectoral fin base and at the anus increases somewhat, 32 to 34% SL and 24 to 28% SL, respectively, during development from flexion larvae to benthic juveniles. A more marked change occurs in snout to anus distance which increases from 54 to 65% SL. The distance from the snout to the pelvic fin base increases slightly.

Head length decreases somewhat during development from 39 to 36% SL, while major decreases occur in eye diameter (40-33% HL), upper jaw length (56-41% HL), and interorbital distance (36-23% HL). Snout length first increases slightly and then decreases with respect to head length. The length of the angle gill raker increases from 9 to 16% HL.

Fin Development (Tables 3, 4, 5).—Pectoral fins are formed in 8 mm larvae of *S. crameri* and the adult complement of 18 to 20 (usually 19) fin rays (or ray elements) are countable in 9 mm specimens. The fins become more elongate with development, increasing from 17% SL in flexion larvae to a maximum of 32% SL in pelagic juveniles. Depth of the pectoral fin base decreases from 13 to 10% SL.

Pelvic fin buds are present on 8 mm larvae and the forming spines and rays (I, 5) can be counted in 9 mm larvae although they are not fully developed until the larvae reach about 10 mm. Length of the pelvic fins increased from 7 to 21% SL during the larval and juvenile periods. Length of the pelvic spine, which is less than the longest ray, increases from 5% SL in flexion larvae to 19% during transformation, and then decreases to an average of 13% in benthic juveniles.

In 8.0 mm larvae the adult complement of 8 + 7 principal caudal rays can be counted although notochord flexion does not appear to be complete until larvae are >9.3 mm. Counts of superior and inferior secondary caudal rays made on one stained juvenile, 38.2 mm, were 12 and 13, respectively.

Bases of some dorsal and anal fin rays and spines are visible on 8 mm larvae. Development of the second dorsal and anal soft rays occurs simultaneously with the central rays forming first and the posteriormost rays last. Developing soft ray elements are visible and adult complements can be counted on 9 mm larvae although rays do not appear fully formed until larvae are ~10 mm. Dorsal spines begin to form slightly after initiation of soft ray formation at ≈9 mm. The third, fourth, and fifth dorsal spines develop first. The 12th spine is not formed until larvae are >13 mm long. The second anal spine is formed at 10.6 mm and the first is formed by 12 mm. The transition of dorsal and anal fin "prespines" to spines is complete at around 22 mm. The longest dorsal spine increases from 22 to 45% HL during the pelvic phase, and decreases to 37% in benthic juveniles. The longest dorsal ray increases from 26 to 41-43% HL during development. The longest anal spine increases from 16 to 37 or 38% HL.

Spination (Tables 4, 6).—Spines visible on the left side of the head of an 8.0 mm larva of *S. crameri* consist of the parietal; the second, third, and fourth preopercular spines of the posterior series; the first, second, and third preopercular spines of the anterior series; the postocular; and the pterotic. Another more developed 8.0 mm specimen has a developing nuchal spine bump; the inferior posttemporal; the first spine of the inferior infraorbital series, and the first spine on the superior infraorbital series.

The parietal spine is relatively short, averaging 6.5 to 6.6% HL in larvae and decreasing to 3.0% HL in pelagic juveniles. The nuchal spine increases in length from 1% HL in flexion larvae to 4% in postflexion and transforming specimens then decreases to 3% in pelagic juveniles. Parietal and nuchal spines begin to fuse near their bases at 10.7 mm, gradually fusing towards the tips until in specimens >38 mm the parietal tip is no longer visible. In benthic juveniles the nuchal and parietal spines are fused and their relative lengths are ≈2% HL; however, increased pigment and musculature allowed measurement only from tip to body junction. The parietal spine and ridge are not serrated in larvae <9 mm. Serrations first appear at the center of the parietal ridge at 9 mm and persist until ≈39 mm.

The posterior series of preopercular spines are among the most prominent in the larvae. The first through fifth spines of the series are present in larvae >10 mm. The third spine of the series is the largest, averaging 17 or 18% HL in larvae and then decreasing to 7% HL in benthic juveniles. Spines in the posterior preopercular series never

TABLE 4.—Body proportions of larvae and juveniles of *Sebastes crameri*, *S. pinniger*, and *S. helvomaculatus*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens measured may be derived from Tables 5, 8, and 11.)

Item	*Sebastes crameri*	*Sebastes pinniger*	*Sebastes helvomaculatus*
Body depth at pectoral fin base SL			
Flexion	31.8 ± 2.05 (29.0-33.8)	40.3 ± 0.92 (39.7-41.0)	33.3 ± 1.44 (32.5-35.0)
Postflexion	31.7 ± 1.26 (30.3-34.9)	38.1 ± 2.51 (33.7-42.0)	33.4 ± 0.46 (33.0-33.9)
Transforming	32.4 ± 1.74 (29.5-35.6)	35.9 ± 1.36 (33.3-38.3)	32.6 ± 1.79 (30.6-35.8)
Pelagic Juvenile	32.7 ± 1.89 (30.3-37.4)	33.0 ± 1.88 (29.8-37.0)	31.2 ± 1.58 (28.4-32.9)
Benthic Juvenile	34.4 ± 1.96 (30.1-36.5)	34.9 ± 2.15 (32.7-37.0)	33.4 ± 1.63 (32.3-34.6)
Body depth at anus SL			
Flexion	23.6 ± 0.67 (22.6-24.4)	27.6 ± 0.92 (26.9-28.2)	20.7 ± 0.61 (20.0-21.2)
Postflexion	24.9 ± 1.19 (22.6-26.5)	28.5 ± 1.92 (24.7-30.6)	24.5 ± 2.56 (21.6-26.3)
Transforming	26.7 ± 1.34 (24.7-29.4)	27.6 ± 1.63 (24.8-30.9)	24.7 ± 1.22 (23.1-26.9)
Pelagic Juvenile	26.8 ± 1.15 (25.2-29.2)	26.0 ± 1.11 (23.9-28.0)	23.2 ± 1.24 (21.2-25.0)
Benthic Juvenile	27.7 ± 1.56 (25.1-30.7)	29.8 ± 3.68 (27.3-34.0)	25.4 ± 2.33 (23.7-27.0)
Snout to anus length SL			
Flexion	54.0 ± 1.28 (52.5-55.9)	58.8 ± 1.63 (57.7-60.0)	56.1 ± 1.28 (55.0-57.5)
Postflexion	60.5 ± 3.25 (55.1-65.1)	59.6 ± 3.42 (51.7-62.6)	59.1 ± 0.50 (58.6-59.6)
Transforming	61.0 ± 3.26 (54.3-65.0)	60.6 ± 1.84 (58.1-63.1)	61.7 ± 1.86 (59.2-64.5)
Pelagic Juvenile	61.6 ± 2.63 (57.9-64.3)	61.4 ± 3.50 (56.0-67.4)	62.8 ± 2.46 (59.8-66.0)
Benthic Juvenile	65.0 ± 1.81 (61.5-68.7)	64.2 ± 3.27 (60.6-67.0)	63.8 ± 1.06 (63.0-64.5)
Snout to pelvic fin origin SL			
Flexion	37.6 ± 1.56 (35.0-38.9)	41.1 ± 3.61 (38.5-43.6)	40.5 ± 1.27 (39.0-41.2)
Postflexion	40.8 ± 2.02 (38.1-44.3)	40.7 ± 3.03 (34.7-44.9)	40.9 ± 0.45 (40.4-41.3)
Transforming	39.8 ± 3.49 (34.1-46.5)	41.9 ± 2.74 (38.7-46.2)	42.8 ± 3.13 (38.0-47.3)
Pelagic Juvenile	38.9 ± 3.23 (34.0-44.5)	39.9 ± 3.83 (32.9-45.5)	42.8 ± 3.16 (39.3-48.2)
Benthic Juvenile	40.5 ± 1.86 (37.3-43.1)	42.7 ± 2.86 (41.0-46.0)	40.0 ± 0.92 (39.4-40.7)
Head length SL			
Flexion	39.0 ± 1.55 (37.5-41.1)	43.0 ± 0.92 (42.3-43.6)	41.4 ± 1.27 (40.0-42.5)
Postflexion	38.9 ± 1.90 (36.8-43.4)	42.4 ± 2.58 (38.2-47.7)	42.0 ± 2.03 (40.4-44.3)
Transforming	36.6 ± 2.43 (32.8-38.7)	40.5 ± 1.39 (38.0-42.6)	40.8 ± 1.92 (36.4-43.0)
Pelagic Juvenile	35.8 ± 1.82 (32.3-38.3)	37.5 ± 2.52 (33.3-42.1)	40.1 ± 1.48 (37.5-41.9)
Benthic Juvenile	36.4 ± 2.75 (31.8-39.9)	36.6 ± 0.51 (36.0-37.0)	37.6 ± 0.57 (37.2-38.0)
Eye diameter HL			
Flexion	40.2 ± 1.82 (37.8-42.9)	37.3 ± 1.27 (36.4-38.2)	38.8 ± 1.63 (29.4-31.2)
Postflexion	38.2 ± 1.87 (33.9-40.0)	39.3 ± 1.89 (37.5-41.3)	36.3 ± 0.36 (35.9-36.6)
Transforming	36.9 ± 2.47 (33.3-42.1)	37.5 ± 1.35 (34.2-38.7)	35.5 ± 2.38 (32.0-38.8)
Pelagic Juvenile	30.4 ± 2.60 (26.6-35.0)	34.2 ± 2.77 (30.8-42.3)	33.6 ± 1.76 (30.8-36.9)
Benthic Juvenile	31.6 ± 2.05 (28.9-35.6)	26.8 ± 3.22 (24.0-30.3)	31.6 ± 5.30 (27.8-35.3)
Upper jaw length HL			
Flexion	46.5 ± 4.35 (40.5-50.0)	47.8 ± 0.99 (47.1-48.5)	45.0 ± 3.29 (41.2-46.9)
Postflexion	43.6 ± 2.45 (40.0-46.3)	46.1 ± 3.73 (41.2-52.4)	44.0 ± 3.00 (41.0-47.0)
Transforming	43.8 ± 5.55 (34.2-50.9)	42.1 ± 3.64 (35.6-47.0)	45.7 ± 4.23 (39.7-53.1)
Pelagic Juvenile	41.3 ± 4.66 (33.9-47.5)	41.3 ± 3.14 (34.6-47.4)	45.1 ± 2.60 (42.0-47.6)
Benthic Juvenile	41.2 ± 2.44 (37.8-45.6)	44.9 ± 2.15 (42.7-47.0)	52.1 ± 0.78 (51.5-52.6)
Snout length HL			
Flexion	29.1 ± 1.38 (27.0-30.7)	26.9 ± 0.28 (26.7-27.1)	32.3 ± 2.20 (30.0-34.4)
Postflexion	30.0 ± 1.65 (26.1-31.7)	28.7 ± 3.45 (23.8-34.6)	33.0 ± 1.18 (31.7-34.1)
Transforming	31.2 ± 2.69 (27.0-35.6)	30.2 ± 3.31 (25.8-36.5)	32.4 ± 3.72 (25.0-37.9)
Pelagic Juvenile	28.2 ± 2.97 (24.6-32.1)	27.3 ± 3.68 (21.7-32.5)	31.7 ± 2.49 (26.7-34.1)
Benthic Juvenile	26.3 ± 2.43 (22.4-31.2)	28.8 ± 0.72 (28.0-29.4)	26.7 ± 0.42 (26.4-27.0)
Interorbital distance HL			
Flexion	35.6 ± 1.95 (32.4-37.1)	37.3 ± 1.27 (36.4-38.2)	30.6 ± 1.04 (29.4-31.2)
Postflexion	33.0 ± 1.94 (29.3-36.0)	34.2 ± 2.26 (30.4-38.2)	31.4 ± 0.55 (30.8-31.8)
Transforming	31.2 ± 3.39 (25.9-36.8)	30.0 ± 1.82 (26.3-32.3)	27.0 ± 2.89 (23.3-30.6)
Pelagic Juvenile	25.9 ± 2.48 (23.0-30.0)	24.4 ± 3.31 (19.5-30.8)	21.5 ± 3.83 (13.3-25.6)
Benthic Juvenile	21.6 ± 2.18 (18.0-26.8)	19.8 ± 1.37 (18.3-21.0)	14.6 ± 2.47 (12.9-16.4)
Angle gill raker length HL			
Flexion	8.6 ± 0.00 (8.6)	—	—
Postflexion	11.4 ± 1.77 (8.6-14.4)	10.6 ± 1.42 (8.3-12.3)	13.4 ± 0.95 (12.3-14.1)
Transforming	13.1 ± 1.13 (11.1-15.1)	13.0 ± 0.72 (11.5-14.5)	15.1 ± 1.46 (12.9-18.0)
Pelagic Juvenile	13.9 ± 0.82 (13.3-15.1)	14.1 ± 1.21 (11.7-16.5)	14.2 ± 1.90 (12.7-15.7)
Benthic Juvenile	15.8 ± 1.06 (13.7-17.4)	14.9 ± 1.10 (13.8-16.0)	10.6 ± 0.50 (10.3-11.0)
Longest dorsal spine length[1] HL			
Flexion	—	—	—
Postflexion	21.6 ± 2.26 (19.4-24.1)	20.1 ± 6.05 (13.0-28.8)	19.0 ± 0.64 (18.6-19.5)
Transforming	34.3 ± 7.13 (26.2-45.1)	32.4 ± 5.49 (23.6-40.6)	29.2 ± 6.08 (22.4-37.5)
Pelagic Juvenile	44.7 ± 1.55 (42.0-46.2)	38.0 ± 3.79 (33.1-46.2)	30.9 ± 2.93 (28.0-35.7)
Benthic Juvenile	36.9 ± 4.32 (31.7-44.3)	35.6 ± 4.74 (32.0-41.0)	37.0 ± 4.88 (33.6-40.5)
Longest dorsal ray length[1] HL			
Flexion	—	—	22.8 ± 7.39 (15.9-30.6)
Postflexion	26.2 ± 6.96 (14.6-33.3)	31.5 ± 4.26 (23.8-38.0)	26.4 ± 5.14 (20.5-29.5)
Transforming	41.4 ± 2.32 (39.3-43.9)	38.5 ± 3.60 (30.8-42.9)	36.1 ± 3.08 (32.5-41.7)
Pelagic Juvenile	42.0 ± 2.97 (38.1-46.7)	41.6 ± 3.46 (35.4-48.7)	35.1 ± 2.53 (32.0-38.1)
Benthic Juvenile	43.1 ± 4.74 (37.6-48.1)	42.6 ± 3.83 (40.0-47.0)	42.8 ± 3.89 (40.0-45.5)
Longest anal spine length[1] HL			
Flexion	—	—	—
Postflexion	15.6 ± 3.16 (9.6-18.5)	18.7 ± 2.52 (14.6-21.3)	16.0 ± 1.91 (14.6-17.3)
Transforming	28.1 ± 3.46 (23.0-32.0)	28.5 ± 5.65 (20.0-38.6)	27.3 ± 4.46 (22.4-36.1)

TABLE 4.—Continued

Item	*Sebastes crameri*	*Sebastes pinniger*	*Sebastes helvomaculatus*
Pelagic Juvenile	37.8–4.36(31.2-43.5)	37.4–4.07(30.8-44.0)	32.4–5.70(26.8-38.1)
Benthic Juvenile	36.5–4.34(30.6-44.3)	34.5–2.50(32.0-37.0)	48.8–4.67(45.5-52.1)
Pectoral fin length SL			
Flexion	17.1–1.52(15.0-18.9)	25.0–2.69(23.1-26.9)	23.6–2.11(21.2-25.0)
Postflexion	21.1–2.26(17.0-23.5)	24.7–2.64(20.2-28.5)	24.4–0.57(23.9-25.0)
Transforming	27.1–1.54(24.7-29.5)	27.0–2.42(22.7-31.5)	26.0–1.45(24.3-28.3)
Pelagic Juvenile	32.1–1.73(30.2-35.3)	26.2–1.36(24.0-28.5)	26.6–0.28(26.1-26.9)
Benthic Juvenile	29.5–3.61(25.0-38.9)	24.3–1.21(22.9-25.0)	27.0–0.85(26.4-27.6)
Pectoral fin base depth SL			
Flexion	12.6–1.27(10.8-13.8)	14.8–0.92(14.1-15.4)	12.5–0.00(12.5)
Postflexion	11.1–0.39(10.4-11.8)	12.6–0.83(11.4-13.6)	11.5–0.84(11.0-12.5)
Transforming	10.4–0.61(9.5-11.7)	10.7–0.59(9.7-11.5)	9.9–0.64(9.0-10.8)
Pelagic Juvenile	9.6–0.51(8.5-10.2)	9.1–0.64(8.2-10.1)	9.0–0.33(8.2-9.1)
Benthic Juvenile	10.2–0.53(8.8-10.9)	8.9–0.23(8.6-9.0)	9.3–0.71(8.6-9.8)
Pelvic fin length SL			
Flexion	7.3–1.81(5.2-9.8)	13.8–2.19(12.3-15.4)	13.5–1.32(12.5-15.0)
Postflexion	15.3–1.46(12.3-16.9)	17.2–4.12(10.0-22.8)	15.5–0.70(14.8-16.2)
Transforming	20.6–1.01(18.3-22.1)	22.7–1.59(20.8-25.3)	19.3–1.62(16.7-21.6)
Pelagic Juvenile	20.9–0.60(20.1-21.9)	21.7–1.29(19.4-23.7)	19.2–1.36(17.3-21.4)
Benthic Juvenile	20.7–0.97(18.5-22.2)	21.3–2.08(19.0-23.0)	22.7–0.99(22.0-23.4)
Pelvic spine length SL			
Flexion	4.7–1.42(3.4-6.2)	5.1–0.00(5.1)	8.3–0.15(8.2-8.5)
Postflexion	11.4–2.20(8.4-14.6)	12.1–2.99(8.2-15.0)	12.3–2.26(10.2-14.7)
Transforming	18.8–1.65(14.5-20.1)	19.5–1.38(17.6-21.7)	17.6–1.02(15.8-19.1)
Pelagic Juvenile	19.0–1.35(16.2-20.7)	17.9–2.10(14.5-22.1)	16.4–1.99(13.5-18.9)
Benthic Juvenile	13.9–1.34(12.3-17.1)	12.5–0.50(12.0-13.0)	14.9–0.71(14.4-15.4)
Parietal spine length HL			
Flexion	6.5–1.01(5.4-7.4)	24.4–0.35(24.2-24.4)	27.4–4.19(22.9-31.2)
Postflexion	6.6–1.06(5.2-8.5)	19.5–7.17(8.8-23.5)	18.5–2.24(15.9-20.0)
Transforming	6.0–1.24(3.7-7.4)	10.2–3.07(3.9-12.9)	12.6–2.39(9.0-16.3)
Pelagic Juvenile	2.9–0.98(1.8-4.2)	7.1–2.66(5.4-10.2)	5.6–3.31(1.1-9.5)
Benthic Juvenile	—	—	3.1–0.00(3.1)
Nuchal spine length HL			
Flexion	1.1–0.00(1.1)	—	1.8–0.85(1.2-2.4)
Postflexion	4.1–0.73(3.4-5.8)	4.4–1.63(2.5-6.9)	4.3–1.51(2.6-5.0)
Transforming	4.4–0.88(3.1-6.0)	4.8–1.57(2.3-7.2)	4.6–0.78(3.0-4.9)
Pelagic Juvenile	3.2–1.03(2.0-5.0)	3.1–0.96(1.9-5.4)	3.5–1.13(1.7-5.2)
Benthic Juvenile	1.7–0.64(0.7-2.8)	1.4–0.64(1.0-2.1)	—
Preopercular spine length HL			
Flexion	17.6–3.84(12.0-20.5)	34.4–2.83(32.4-36.4)	27.4–4.19(22.9-31.2)
Postflexion	17.0–1.09(15.5-18.5)	31.8–4.86(25.0-39.0)	31.2–0.64(30.8-31.7)
Transforming	18.3–1.53(16.0-19.7)	23.6–2.09(21.2-29.1)	20.2–3.58(16.2-26.5)
Pelagic Juvenile	12.0–2.85(8.6-16.2)	12.8–3.96(9.1-22.2)	11.8–6.29(2.5-15.9)
Benthic Juvenile	7.2–2.72(3.1-11.4)	4.8–1.39(4.0-6.4)	1.6–1.34(0.6-2.5)

[1]Usually third or fourth in larvae; fifth or sixth in juveniles.
[2]Usually midfin.
[3]The second spine.

develop strong serrations. Spines in the anterior preopercular series are much shorter than those in the posterior series. The second or middle spine is present only in larvae prior to completion of notochord flexion, ~10 mm. Its appearance as a spine changes to a small bump which then fuses with the ridges connecting it to the third preopercular spine of the posterior series. The first and third anterior spines are present on larvae through pelagic juveniles of ~23 mm and then are no longer visible.

The superior and inferior opercular spines and the interopercular spine appear by the time the larvae reach 12 mm, although percursor bumps may be seen as early as 9 mm. These spines persist into the juvenile stage. The subopercular spine is present in juveniles ~78 mm.

Around the eye, the ridge anterior to the postocular spine becomes serrated at 10.6 mm. These serrations disappear at the time of supraocular spine formation, >21 mm. The preocular spine begins to appear in transforming specimens ~16 mm and is strongly formed by the time fish are 20 mm. Beneath the eye the second spine of the inferior infraorbital series forms in larvae ~10 mm. The fourth spine of the superior infraorbital series develops under the posterior third of the eye on larvae ~13.6 mm and it persists through the juvenile stage as do the two inferior infraorbital spines. The second and third superior and third inferior infraorbital spines never develop. Tiny serrations appear along a ridge between the first and fourth superior infraorbital spines in specimens 14.4 to 38.2 mm. The first spine of the superior infraorbital series disappears in specimens >50 mm. The nasal spine develops in larvae of ≈10 mm and persists in juveniles.

TABLE 5 —Measurements (millimeters) of larvae and juveniles of *Sebastes crameri* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at dorsal fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle spine length	Longest dorsal spine length	Longest dorsal ray length	Longest anal spine length[1]
8.0	9.4	4.2	3.0	0.88	1.5	1.2	1.1	2.7	1.9	1.2	1.1	(4)	0.52	2.8	0.20	(4)	0.56	—	(5)	(4)	(4)
8.0	9.7	4.3	3.0	0.92	1.5	1.2	1.1	2.7	1.9	1.4	1.1	(4)	0.52	3.0	—	—	0.36	—	(5)	(4)	(4)
9.0	11.2	4.9	3.7	1.0	1.5	1.4	1.2	2.8	2.2	1.6	1.1	0.56	0.76	3.4	0.20	0.04	0.76	—	(5)	(4)	(4)
9.0	10.7	4.8	3.5	1.0	1.7	1.5	1.3	2.8	2.1	1.7	1.1	0.40	0.88	3.5	0.26	(4)	0.68	—	(5)	(4)	(4)
9.3	11.4	5.2	3.7	1.1	1.6	1.5	1.3	2.7	2.1	1.5	1.0	0.32	0.48	3.6	—	—	—	0.32	(5)	(4)	(4)
10.6	12.8	6.3	4.1	1.3	1.9	1.6	1.4	3.3	2.4	1.8	1.2	0.72	1.3	4.2	0.28	—	—	0.36	(4)	0.60	(4)
10.6	13.0	6.9	4.6	1.4	2.1	1.7	1.5	3.7	2.8	1.9	1.2	1.1	—	4.7	—	—	—	0.50	(4)	0.88	0.44
10.7	13.4	—	—	—	—	—	—	3.4	2.6	—	—	1.2	1.5	—	0.28	—	—	—	0.60	1.2	—
12.2	15.0	7.3	4.6	1.2	2.0	1.8	1.5	3.7	3.0	2.5	1.4	1.5	1.8	4.8	—	0.20	0.80	0.50	0.92	1.4	0.76
12.6	15.8	7.2	4.8	1.4	2.0	1.9	1.6	3.9	3.0	2.8	1.4	1.6	2.0	4.8	0.32	0.28	0.80	0.50	1.1	1.5	0.80
12.8	15.8	7.5	5.0	1.6	2.0	2.0	1.7	4.2	3.3	2.8	1.4	1.3	2.1	5.4	—	0.20	0.84	0.50	—	1.1	0.60
13.6	16.0	7.5	5.0	1.5	2.0	2.0	1.8	4.3	3.4	3.2	1.5	—	2.3	5.2	0.36	0.20	—	0.60	—	—	0.92
13.8	16.0	8.3	5.2	1.6	2.2	2.0	1.8	4.4	3.5	3.0	1.5	1.6	2.0	5.6	0.30	0.20	—	0.64	—	—	—
14.4	17.3	9.3	5.4	1.6	2.5	2.0	1.8	4.5	3.7	3.1	1.7	2.1	2.2	6.0	0.46	0.20	1.0	0.78	—	1.8	1.0
14.7	17.6	9.2	5.8	1.7	2.6	2.2	1.7	4.5	3.9	—	1.6	1.9	2.4	6.2	0.36	0.20	—	0.82	1.4	1.9	1.0
15.4	18.1	9.7	6.2	1.9	2.8	2.1	1.9	4.9	4.2	3.5	—	1.6	2.6	6.5	0.32	0.24	0.96	0.66	1.2	1.6	1.0
[6]16.0	20.0	9.5	6.1	2.0	—	2.3	2.1	5.2	4.3	4.1	1.7	—	3.4	6.2	0.44	—	—	0.72	1.6	2.4	1.4
[6]16.3	20.3	10.3	6.3	1.7	3.0	2.3	2.0	5.8	4.8	—	1.9	3.1	3.6	6.3	0.42	0.28	1.2	0.86	2.2	—	—
[6]17.3	20.5	10.0	6.7	2.2	3.0	2.4	2.0	5.8	4.7	5.1	1.8	2.8	3.4	7.1	0.46	0.28	—	0.88	2.0	—	1.7
[6]17.4	21.8	10.7	5.7	1.9	2.9	2.4	2.1	5.8	4.6	4.8	1.9	3.2	3.6	6.7	0.42	0.34	—	0.86	—	2.5	1.5
[6]18.2	21.6	10.7	6.2	1.8	2.9	2.4	2.2	6.0	5.1	—	2.0	3.2	3.8	6.2	0.40	0.30	1.2	0.84	2.2	—	—
18.4	23.4	11.0	6.6	2.0	3.2	2.6	2.1	6.3	5.1	4.7	1.9	3.7	—	6.7	0.40	0.28	1.1	0.92	—	—	2.1
[6]18.6	22.7	10.1	6.4	2.0	2.8	2.4	1.8	5.8	4.8	4.6	1.9	2.7	3.4	7.1	—	0.36	1.2	0.88	—	2.2	2.0
19.0	24.0	12.2	7.3	2.6	2.5	2.6	2.0	5.8	4.7	5.2	1.9	3.4	3.9	8.1	0.42	0.34	—	0.94	—	3.0	2.0
[6]20.0	24.8	13.0	8.1	2.7	3.4	2.7	2.1	5.9	5.1	5.5	2.0	3.9	4.2	9.3	0.34	0.28	—	0.90	—	—	2.0
[6]20.2	24.5	13.0	7.1	2.1	3.2	2.5	2.2	6.4	5.2	5.5	2.0	3.7	4.2	7.9	0.38	0.22	1.4	0.90	3.2	—	2.2
[6]21.0	25.3	13.1	7.5	2.2	2.6	2.6	2.3	6.7	5.5	6.0	2.0	4.0	4.4	9.2	0.28	0.30	1.2	0.90	—	—	2.4
[6]22.7	28.3	13.3	8.0	2.3	3.3	2.8	2.3	7.5	6.0	6.9	2.3	4.2	4.8	8.3	—	0.34	—	1.1	3.7	—	2.5
[6]23.5	28.3	13.6	8.0	2.0	3.8	2.7	2.4	7.6	6.4	7.3	2.4	—	5.0	8.0	0.34	0.40	1.3	1.2	3.7	3.4	3.0
[6]24.2	28.6	15.5	8.8	2.6	4.1	2.7	2.4	8.1	6.6	7.3	2.4	5.0	5.2	9.9	0.36	—	—	1.1	—	—	3.5
[6]25.6	32.3	16.3	9.8	3.1	3.9	2.7	2.6	8.2	7.0	8.4	2.4	5.3	5.6	11.4	0.30	0.38	1.5	1.3	—	3.8	—
[6]28.6	34.7	17.1	9.8	3.1	3.7	3.0	2.7	8.9	7.2	8.9	2.7	5.5	5.8	12.2	0.26	0.20	1.2	1.3	—	4.3	3.6
[6]30.0	35.2	17.6	11.2	2.8	3.8	3.4	2.7	9.1	7.6	9.3	2.8	5.8	6.2	11.7	0.20	0.28	1.1	1.5	4.7	—	—
[6]31.8	39.8	19.4	11.8	2.9	5.2	3.5	2.8	10.2	8.3	10.7	2.7	6.0	6.4	11.2	0.26	0.46	1.6	1.6	5.3	4.5	4.0
[6]35.7	45.1	22.9	13.1	3.4	5.4	3.7	3.2	11.7	9.6	12.6	3.5	6.8	7.4	13.9	0.26	0.34	1.4	1.9	6.0	5.6	5.5
[6]38.2	46.1	24.3	13.9	3.8	5.8	3.7	3.2	14.3	10.3	13.0	3.8	7.0	—	14.9	Joined	0.34	1.2	2.1	6.2	5.7	—
[6]56.9	68.7	36.6	18.4	5.9	7.2	5.7	4.3	18.7	16.6	17.8	5.7	9.2	11.6	21.6	Joined	0.48	1.7	2.6	8.0	8.6	8.0
[6]46.8	60.9	31.2	14.9	3.4	6.8	4.6	4.0	14.1	12.0	18.2	4.1	8.0	10.3	17.9	Joined	0.40	1.7	2.6	6.6	7.9	6.6
[6]49.2	60.7	32.0	16.3	4.7	7.0	5.8	4.0	15.0	12.8	16.0	4.8	7.1	10.5	19.2	Joined	0.34	1.7	2.6	6.5	7.6	—
[6]58.9	73.0	39.4	21.9	5.8	8.1	6.6	4.8	19.5	16.6	18.1	6.0	8.4	10.9	25.0	Joined	0.44	2.1	3.0	7.9	9.2	7.4
[6]63.0	76.2	41.8	20.8	6.5	9.3	7.2	4.6	20.5	15.8	19.4	5.9	9.0	12.5	26.4	Joined	0.56	1.7	3.5	8.0	10.0	8.0
[6]63.2	77.6	40.0	21.3	6.0	9.4	7.4	5.1	22.7	18.4	20.0	6.6	9.6	13.3	24.9	Joined	0.60	2.3	3.2	9.3	10.2	8.4
[6]65.0	80.6	40.0	22.6	6.6	8.9	6.6	4.9	22.9	18.4	21.4	6.7	—	14.4	27.4	Joined	0.38	2.1	3.8	8.5	10.7	9.5
[6]76.8	82.8	42.8	22.4	6.2	9.4	7.4	4.9	23.0	19.0	21.6	6.8	10.2	14.1	26.6	Joined	0.38	2.2	3.6	9.8	10.2	9.8
[6]78.6	96.6	51.5	30.3	8.7	13.0	9.8	5.9	27.6	25.7	21.8	7.7	9.6	15.8	32.3	Joined	0.40	2.1	4.8	9.6	12.5	9.8
[6]86.1	105.3	55.0	33.9	8.9	14.2	9.8	7.7	31.4	25.9	22.9	9.3	12.6	18.2	35.2	Joined	0.46	1.7	5.3	12.0	15.8	12.0
[6]91.8	112.3	63.1	36.6	9.3	14.2	11.2	6.6	30.9	25.0	23.8	9.3	11.5	18.4	36.8	Joined	0.60	1.8	5.9	11.7	14.1	11.7
[6]94.4	113.9	60.8	33.9	9.3	12.8	11.2	7.1	33.0	25.0	24.5	9.7	12.3	18.7	35.2	Joined	0.40	1.8	5.7	11.8	12.8	11.7
[6]94.7	114.7	61.5	36.2	8.6	15.2	11.2	7.5	33.6	26.4	23.7	9.8	11.8	20.0	40.2	Joined	0.44	1.9	5.1	12.5	14.4	12.6
[6]96.2	118.3	63.4	35.7	8.4	14.4	11.0	7.7	34.7	27.7	28.2	10.0	13.4	20.5	41.5	Joined	0.50	2.0	5.7	13.8	14.4	13.6
[6]105.6	128.2	67.0	41.2	10.7	16.3	12.8	8.5	38.0	32.4	28.8	10.7	13.6	20.8	45.2	Joined	0.44	2.0	6.8	13.1	15.7	12.6
[6]125.7	154.5	80.0	48.5	12.3	20.0	15.2	9.1	44.9	35.2	33.3	13.6	15.5	25.6	47.6	Joined	0.50	2.0	7.2	17.3	19.0	16.0
[6]130.5	160.9	86.6	51.0	13.3	19.7	14.9	10.4	46.6	35.6	37.3	14.2	18.4	28.0	52.2	Joined	0.36	1.6	7.4	16.3	19.2	17.6

[1]Usually third or fourth in larvae, fifth or sixth in juveniles
[2]Usually ninth
[3]The second spine
[4]Not formed
[5]Transforming
[6]Pelagic juvenile
[7]Benthic juvenile

The tympanic spine, sometimes bifid, appears on specimens ~25 mm. This spine forms at the anterior edge of a foramen of the cephalic lateral line system. The pterotic spine is present in flexion larvae and disappears in juveniles ~50 mm. The supracleithral spine develops in larvae of ~11 mm and the superior posttemporal spine can be seen on specimens ~18 mm. These latter three spines persist in juveniles, however, the inferior posttemporal becomes reduced in larger juveniles. A cleithral spine develops dorsal to the pectoral fin base immediately posterior to the opercular margin on juveniles ~30 mm.

Scale Formation.—Lateral line pores are visible on transforming specimens >18.2 mm. Developing scales are first visible on unstained specimens ≈20 mm on the posterodorsal region of the head and anterodorsal region of the trunk above the gut cavity. Scale development proceeds posteriorly with the body being covered by 29 mm.

Pigmentation.—Melanistic pigment on 8.0 mm specimens of *S. crameri* (similar to the 9 mm specimen illustrated) is present on the head over the brain. Melanophores line the inside tip of the lower jaw and may also be present along the anteroventral margin of the maxillary. In the abdominal region internal melanophores are densely concentrated on the dorsal surface of the gut and more sparsely distributed laterally and ventrally. Additional external melanophores are present on the body wall over the gut cavity. A heavy concentration of external melanophores and some in-

TABLE 6.—Development of spines in the head region of *Sebastes crameri* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and – denotes spine absent

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
8.0	+		+	+	+	+	+	+	+	–	+	+	–				+
8.0	+	+	+	+	–	+	+	+	+	–	+	+	–				+
9.0	+	+	+	+	+	–	+	+	+	–	–	–					+
9.0	+		+	+	+	–	+	+	+	–	–	–				–	+
9.3	+	+	–	(1)	+		+	+	+	–	+	–					+
10.6	+	+	+	–	–	+	+	+	+	–	+	+	–				+
10.6	+	+	+	–	+	+	+	+	+	–	+	+	+				+
12.2	+	+	–	–	+	+	+	+	+	–	+	+	+				+
12.6	+	+	+	–	–	+	+	+	+	–	+	+	+				+
12.8	+	+	+	–	–	+	+	+	+	–	+	+	+	–			+
13.6	+	+	+	–	–	+	+	+	+	–	+	+	+				+
13.8	+	+	+	–	+	+	+	+	+	–	+	+	+			–	+
14.4	+	+	+	–	+	+	+	+	+	–	+	+	+				+
14.7	+	+	+	–	+	+	+	+	+	–	+	+	+	–			+
15.4	+	+	+	–	+	+	+	+	+	–	+	+	+				+
[2]16.0	+		+	–	+	+	+	+	+	–	+	+	+				+
[2]16.3	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]17.3	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]17.4	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]18.2	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]18.4	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]18.6	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]19.0	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)		+
[2]20.0	+	+	+	–	+	+	+	+	+	–	+	+	+		(1)	–	+
[2]20.3	+	+	+	–	+	+	+	+	+	–	+	+	+		+	–	+
[2]21.0	+	+	+	–	+	+	+	+	+	–	+	+	+			(1)	+
[2]22.7	+	+	+	–	+	+	+	+	+	–	+	+	+			(1)	+
[2]23.5	+	+	(1)	–	(1)	+	+	+	+	–	+	+	+			(1)	+
[2]24.2	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[2]25.6	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[2]28.6	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[2]30.0	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[2]31.8	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[3]35.7	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[3]38.2	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[3]56.9	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]46.8	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]49.2	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]58.9	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]63.0	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]63.2	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]65.0	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]67.6	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]79.8	+	+	–	–	–	+	+	+	+	–	+	+	+	–		+	+
[4]86.1	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]91.8	+	+	–	–	–	+	+	+	+	–	+	+	+	–		+	+
[4]94.4	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]94.7	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]96.2	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]105.6	+	+	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]125.7	+[5]	+[5]	–	–	–	+	+	+	+	–	+	+	+			+	+
[4]130.5	+[5]	+[5]	–	–	–	+	+	+	+	–	+	+	+			+	+

[1]Bump indicates beginning of spine formation
[2]Transforming
[3]Pelagic juvenile
[4]Benthic juvenile
[5]Parietal and nuchal spines fused
[6]Spine is bifid

TABLE 6.—Continued

Standard length (mm)	Infraorbitals													
	Interior			Superior							Posttemporal			
	1st	2d	3d	1st	2d	3d	4th	Nasal	Coronal	Tympanic	Pterotic	Superior	Interior	Supracleithral	Cleithral
8.0	-			-				-			-		-		
8.0	-			-				-			-		-		
9.0	-			-							-		-		
9.0				-							-		-		
9.3				-						-	-		-		
10.6	-			-				(1)			-		-		
10.6	-	-		-				(1)			-		-	+	
12.2	-	-		-				-			-		-	+	
12.6	-	-		-				+			-		-	+	
12.8	-	-		-				+			-		-	+	
13.6	-	-		-				+			-		-	+	
13.8	-	-		-			(1)	-			-		-	+	
14.4	-	-		-			-	-			+		-	+	
14.7	-	-		-			-	-			+		-	+	
15.4	-	-		-			-	-			+		-	+	
16.0	-	-		-			-	-			+		-	+	
16.3	-	-		-			-	-			+		-	+	
17.3	-	-		-			-	-			+		-	+	
17.4	-	-		-			-	-			+		-	+	
18.2	-	-		-			-	-			+		-	+	
18.4	-	-		-			-	-			+	-	-	+	
18.6	-	-		-			-	-			+	-	-	+	
19.0	-	-		-			-	-			+	-	-	+	
20.0	-	-		-			-	-			+	+	-	+	
20.3	-	-		-			-	-			+	(1)	-	+	
21.0	-	-		-			-	-			+	+	-	+	
22.7	-	-		-			-	-			+	-	-	+	
23.5	-	-		-			-	-			+	-	-	+	
24.2	-	-		-			-	-		-	+	-	-	+	
25.6	-	-		-			-	-		+	+	-	-	+	
28.6	-	-		-			-	-		+	+	-	-	+	
30.0	-	-		-			-	-		-	+	-	-	+	
31.8	-	-		-			-	-		-[b]	+	-	-	+	-
35.7	-	-		-			-	-		-[b]	+	-	-	+	-
38.2	-	-		-			-	-		-	+	-	-	+	-
56.9	-	-		-			-	-		-	+	-	-	+	-
46.8	-	-		-			-	-		-	+	-	-	+	-
49.2	-	-		-			-	-		-[b]	+	-	-	+	-
58.9	-	-		-			-	-		-	+	-	-	+	-
63.0	-	-		-			-	-		-	+	-	-	+	-
63.2	-	-		-			-	-		-	+	-	-	+	-
65.0	-	-		-			-	-		-[b]	+	-	-	+	-
67.6	-	-		-			-	-		-	+	-	-	+	-
78.8	-	-		-			-	-		-[b]	+	-	-	+	-
86.1	-	-		-			-	-		-	+	-	-	+	-
91.8	-	-		-			-	-		-[b]	+	-	-	+	-
94.4	-	-		-			-	-		-	+	-	-	+	-
94.7	-	-		-			-	-		-	+	-	-	+	-
96.2	-	-		-			-	-		-	+	-	-	+	-
105.6	-	-		-			-	-		-	+	-	-	+	-
125.7	-	-		-			-	-		-	+	-	-	+	-
130.5	-	-		-			-	-		-	+	-	-	+	-

ternal pigment is present in the nape region although the dorsal midline is pigmentless. A few large stellate melanophores extend laterally from the nape to the gut cavity. A series of 10 or 11 distinct melanophores is visible along the ventral midline of the tail, the anterior five of which are embedded in musculature dorsal to the developing anal fin. A few small melanophores may be present on the notochord tip. The pectoral fins are distinctively and heavily pigmented. A dense concentration of melanophores occurs on the proximal surface of the fin base but the distal surface is unpigmented. Elongate melanophores line the inner and outer surfaces of the fin blades creating a striated appearance. The developing pelvic fins are also pigmented.

As larvae develop, pigment increases on the head over the brain. Melanophores persist along the tip of the lower jaw and the anteroventral margin of the maxillary. Several melanophores develop around the bases of the posttemporal and supracleithral spines in larvae ~10.5 mm and on the dorsal part of the operculum anterior to the opercular spines in larvae ~13.5 mm.

Pigmentation within the gut cavity remains intense through larval development and external melanophores remain scattered on the body wall over the gut. In larvae ~10.5 mm, as dorsal fin

spines develop, melanophores are added to the nape patch along the dorsal midline and posteriorly along the dorsolateral body surface. The large stellate melanophores extending from the nape patch to the gut disappear by 12 mm. A few external melanophores appear along the anterior margin of the middle of the cleithrum beneath the gill cover in 12 or 13 mm larvae.

In the tail region the ventral midline melanophores gradually become embedded, anterior ones first, and are obscured by overlying musculature by the time larvae are 13 mm long. A melanophore is sometimes present near the tip of the notochord.

The pigmentation of the paired fins increases in intensity throughout the larval period, although the distal base of the pectoral fin remains unpigmented. As the pelvic fins develop, melanophores line the rays giving a striated appearance similar to that of the pectoral fins.

Melanophores appear on the anterior portion of the spinous dorsal fin by the time larvae are 11 mm long, and the anterior two-thirds of the fin remains rather heavily pigmented throughout larval development. The soft dorsal and anal fins remain unpigmented.

One to several internal, vertically elongate melanophores appear at the base of the caudal fin posterior to the hypural elements on most larvae >9 mm long, but the fin base is never completely lined with pigment.

During the transformation period, 16 to 21 mm, pelagic juvenile pigmentation begins to develop. On the head, pigment increases around the posttemporal spines and joins with the nape pigment. Internal and external melanophores are added on the dorsal part of the opercle forming a patch which expands ventrally on specimens >19 mm. Scattered melanophores appear along the dorsal surface of the snout and the anterior portion of the upper lip (internal and external) on specimens >18.5 mm long. Pigment increases around the orbit, lining the dorsal, posterior, and ventral margin of the orbit by 19 mm. In the abdominal region, an increase in musculature over the gut cavity obscures the internal gut pigment although scattered external melanophores persist. The nape patch extends anteriorly joining the head pigment, laterally toward the body midline, and posteriorly to the 12th dorsal spine. Two saddles of intensified melanistic pigment begin to develop beneath the first dorsal fin late in the transformation period. An anterior saddle joins the head pigment and another saddle located midfin expands ventrolaterally. Melanophores are added dorsally and ventrally along the anterior margin of the cleithrum beneath the gill cover, eventually appearing as a line of pigment. In the tail region, melanophores appear beneath the middle of the second dorsal fin in 16 mm specimens. They expand anteriorly to join the pigment beneath the spinous dorsal, posteriorly over the caudal peduncle, and laterally towards the body midline appearing as a saddle by 20 mm. Some melanophores at the base of the second dorsal fin become concentrated along muscles surrounding the dorsal pterygiophores giving the appearance of vertical lines of pigment by 20 mm. An additional melanophore may appear at the point of articulation of each dorsal soft ray 4 through 10 beginning on 18 mm specimens. Pigment is added internally and externally along the lateral midline of the caudal peduncle. On the first dorsal fin pigmentation increases extending posteriorly to the 11th or 12th dorsal spine.

In pelagic juveniles >22 mm long, small melanophores appear over the surface of the head. Melanophores almost entirely ring the orbit by 31 mm. Pigment increases on the snout and upper and lower jaws. The two pigment saddles beneath the first dorsal fin become more pronounced and extend more ventrolaterally. A third saddle forms beneath the first dorsal fin posterior to the first two in specimens about 22 to 25 mm long. In the tail region, the saddle beneath the second dorsal fin extends to the lateral midline by 24 mm and eventually reaches the ventral body margin in a 57 mm specimen. The number of melanophores increases on the caudal peduncle until dorsal and lateral pigment are joined forming a fifth pigment saddle in juveniles about 25 mm long. This fifth saddle eventually extends to the ventral body margin as does the saddle beneath the spinous dorsal fin. An increase in the number of melanophores occurs along the lateral midline of the caudal peduncle giving the appearance of a distinguishable, but not heavy, line of pigment. Small melanophores are added between saddles 3 and 4 and 4 and 5, along the myosepta first. The pectoral and pelvic fins remain heavily pigmented, although the amount of pigment on the base of the rayed portion of the pectoral fin decreases. Pigmentation on the spinous dorsal fin decreases in intensity between spines III and V, and between spines VIII and IX, corresponding to areas between the first, second, and third pigment saddles on the body. On specimens >38 mm long, pigment on the dorsal fin

above the third saddle darkens into a distinct black blotch. Melanophores are added to the basal half of the second dorsal fin above the fourth saddle, appearing continuous with it on specimens ·29 mm long. Melanophores are also added to the basal half of the anal fin eventually extending from the second anal spine to the posteriormost anal fin ray on all specimens ·38 mm. Specimens ·36 mm have a melanophore at the point of articulation of each soft anal fin ray, although these melanophores soon become obscured by musculature and scales. Three to seven small external melanophores are added near the bases of the caudal fin rays forming an indistinct line.

Benthic juveniles ·60 mm long retain essentially the same melanistic pigment pattern as pelagic juveniles except the intensity decreases resulting in a somewhat faded appearance. Additional light scatterings of melanophores appear in the lower jaw and gular region, second dorsal and anal fins, and body in general. Two bars of pigment radiate ventrally from the posteroventral margin of the eye. The basic banding pattern and black blotch at the base of the dorsal fin remain evident in the largest juvenile, 130 mm, examined. This is the same banding pattern apparent in adults, however, the black blotch on the spinous dorsal fin disappears.

In life (Moser*) a juvenile (122 mm) is reddish-brown dorsally, with white on the belly and five brownish bars on the body. The first four bars extend ventrally to slightly below the lateral line and dorsally onto the dorsal fins as diffuse dark areas. The head is reddish-brown and pale below eye level, with three brownish transverse bars: one at the anterior level of the orbit, one at the posterior level of the orbit, and one between and posterior to the parietal ridges. A large spot is on the opercle dorsally, and the axillary region has a dusky blotch. Except for the dark bars, the first and second dorsal fins are dusky at the base, grading to pale orange or yellowish with vermillion or deep red at the margin. The basal half of the anal and pelvic fins is whitish and the distal half grades from reddish to dark orange-red at the tips. The outer pelvic ray has a milky white lateral margin. The pectorals and caudal fins are pale orange, the pectorals with dark orange-red tips and the caudal with a faint dusky band on its posterior half.

Occurrence (Figures 5, 6).—*Sebastes crameri* ranges from Santa Catalina Island off southern California to the Bering Sea (Miller and Lea 1972). Off Oregon, Washington, and British Columbia it is primarily an outer shelf-upper slope species generally occuring in depths of 150 to 300 m (Snytko and Fadeev 1974). Distinct population clumps have been found off the Oregon coast between lat. 44°30′ and 45°20′ N (Snytko and Fadeev 1974). Most of our collections containing young *S. crameri* were taken along a transect off Newport (lat. 44°39.1′ N) off the central Oregon coast. The smallest larvae and the greatest numbers of larvae and pelagic juveniles were taken at stations 83 and 93 km offshore (water depths 700-1,300 m). The nearest inshore station on this transect at

*H. G. Moser, Fishery Biologist (Research), Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. 1977.

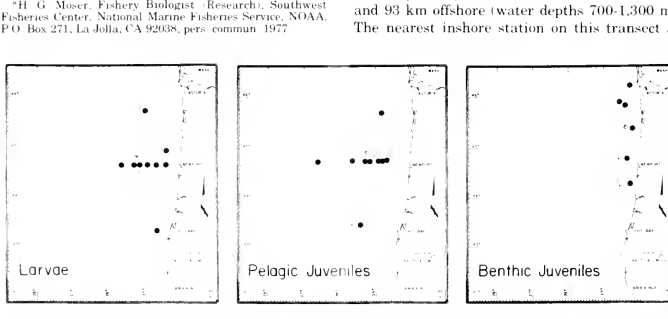


FIGURE 5.—Number of specimens and location of capture of larvae and juveniles of *Sebastes crameri* off Oregon (1961-75) described in this paper.

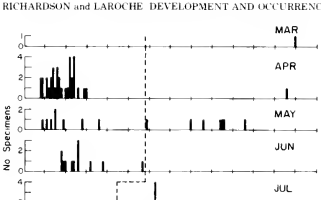


FIGURE 6.—Seasonal occurrence of larvae and juveniles of *Sebastes crameri* off Oregon. Data from 1961 to 1975 combined. Dashed line separates pelagic and benthic stages.

which a larva (15.7 mm) was taken was 28 km (depth 95 m). The farthest offshore occurrence on this transect was a 26 mm pelagic juvenile 194 km offshore. Benthic juveniles were generally taken nearer to shore than larvae or pelagic juveniles at depths of 55 to 200 m. Most pelagic specimens came from Isaacs-Kidd midwater trawls towed obliquely through the water column. Four specimens, 17.7, 24.0, 38.2, and 56.9 mm, were collected in a neuston net in June, 56 to 65 km off Newport.

Spawning times reported for *S. crameri* are November through March off California (Phillips 1964) and primarily February off Oregon, Washington, and British Columbia (Westrheim 1975; Westrheim et al. see footnote 7). However, mature females with ovaries containing embryos have been collected in February, March, April, and June (Westrheim et al.,[9] see footnote 7; Harling et al.[10]). Pelagic specimens in our collections were taken primarily in April, May, and June although two postflexion larvae were taken in August. Larvae under 10 mm were only taken in April and May. No specimens were taken September through February. Because of a lack of information on larval growth, parturition time cannot be inferred. The wide range of lengths of pelagic specimens, 8 to 30 mm in April, 9 to 36 mm in May, 18 to 57 mm in July, indicates spawning may be variable and protracted. Benthic juveniles were taken March through July.

In trawl surveys off Oregon, adults ranked second in biomass only to *S. diploproa* of all rockfishes collected over the continental slope and fifth or sixth on the continental shelf (Demory et al. 1976). Snytko and Fadeev (1974) reported it to be one of the most abundant trawl-caught rockfish species over the slope together with *S. alutus*, *S. saxicola*, and *S. diploproa*. This species was one of the three major contributors to the 1963-71 Oregon landings of the Pacific ocean perch fishery exceeding *S. alutus* in 1971 (Niska 1976). Although little can be said about the actual abundance of larvae and juveniles off Oregon because of the various kinds of samples examined and irregular nature of the sampling effort, they were one of the more common kinds relative to the other species of *Sebastes* in the samples.

SEBASTES PINNIGER (GILL) (Figures 7, 8, 9)

Literature.—Pigmentation of preextrusion larvae of *S. pinniger* was listed in tabular form by Westrheim (1975). Newborn to 2-wk-old larvae were described by Waldron (1968) and the older larva was redrawn by Moser et al. (1977). Mean length of larvae at hatching is 3.6 mm SL. Newborn larvae have an irregular double row of pigment (usually <16 melanophores) along the ventral midline between the 18th and 22d myomere and some pigment above the yolk sac near the anus. After 2 wk additional melanophores are present at the tip of the lower jaw, on the ventral part of the yolk sac, on the pectoral fins, along the dorsal midline in an irregular double row between the 19th and 21st myomeres, and in the hypural region. The ventral midline melanophores may extend as far forward as the 14th myomere.

Identification (Table 7, Appendix Tables 2-6).—A total of 269 specimens of *S. pinniger*, 7.9 to 181 mm long, were identified. Juveniles were identified using the following combination of characters compiled from specimens in our collections:

Gill rakers = 40-45, left arch; 38-46, right arch
Lateral line pores = 40-45
Pectoral fin rays = 16-18, usually 17

[9]Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1968. Preliminary report on maturity, spawning season, and larval identification of rockfishes (*Sebastodes*) collected off British Columbia in 1968. Fish. Res. Board Can., Manuscr. Rep. 1005, 28 p.

[10]Harling, W. R., M. S. Smith, and N. A. Webb. 1971. Preliminary report on maturity, spawning season, and larval identification of rockfishes (Scorpaenidae) collected during 1970. Fish. Res. Board Can. Manuscr. Rep. 1137, 26 p.

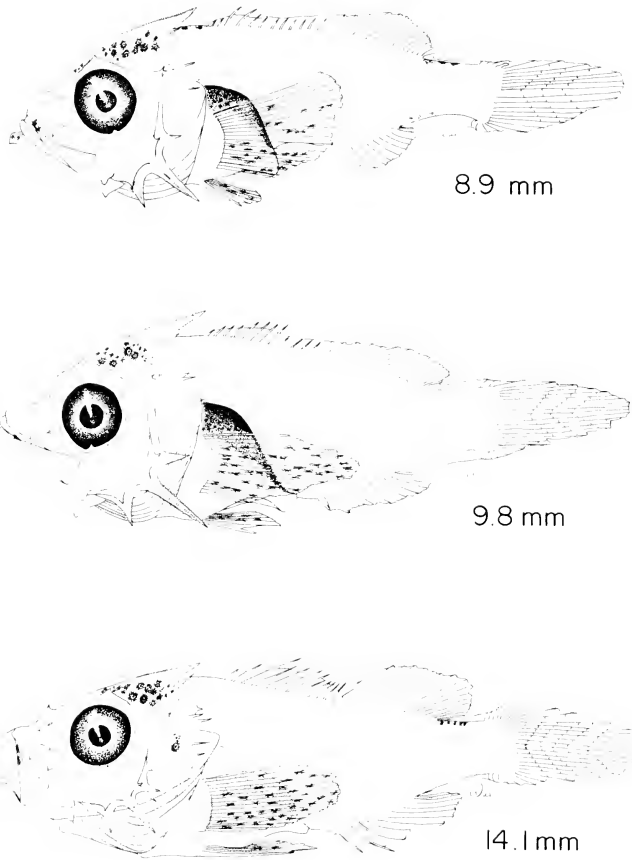


FIGURE 7.—Planktonic larvae (8.9, 9.8 mm) and transforming specimen (14.1 mm) of *Sebastes pinniger*.

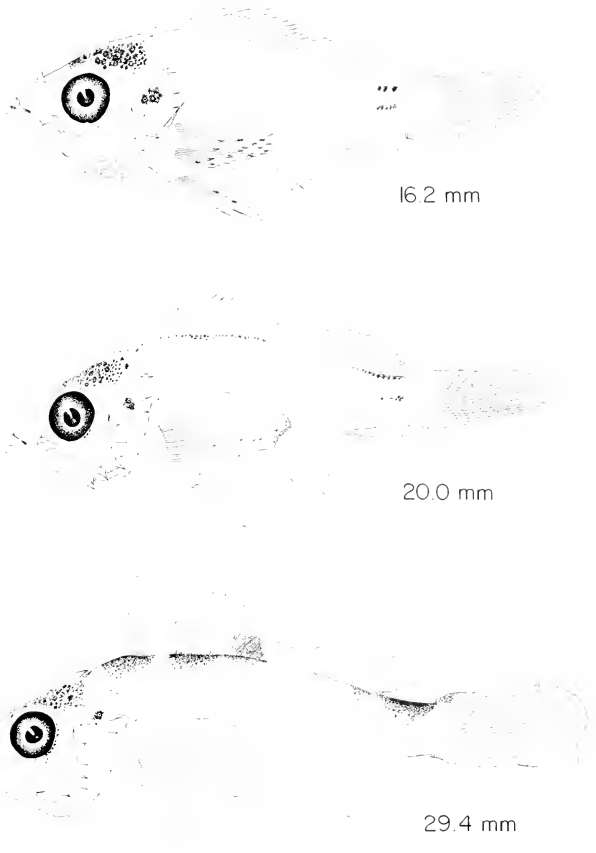


FIGURE 8.—Transforming specimen (16.2 mm) and pelagic juveniles (20.0, 29.4 mm) of *Sebastes pinniger*

FIGURE 9.—Pelagic juvenile (40.0 mm) and benthic juvenile (59.4 mm) of *Sebastes pinniger*.

Anal fin soft rays = 7
Dorsal fin soft rays = 13-15, usually 14 or 15
Supraocular spine = present
Interorbital space = flat to convex.

Large juveniles (>26 mm SL) have the black blotch at the base of the posterior half of the spinous dorsal fin characteristic of adults. Other *Sebastes* juveniles which have a black blotch, e.g., *S. melanops*, *S. flavidus*, *S. crameri*, do not agree with the characters given above. Of the *Sebastes* species occurring off Oregon, *S. pinniger* has the best fit to all these characters. *Sebastes miniatus* and *S. emphaeus* also agree with many of the counts. However, juvenile *S. miniatus* and *S. emphaeus* lack a black blotch at the posterior base of the spinous dorsal fin. *Sebastes miniatus* usually has 18 rather than 17 pectoral rays, and *S. emphaeus* lacks supraocular spines. The larvae and juveniles in the series in question were among the most abundant in our collections. Adult *S. pinniger* are known to be abundant in trawlable areas offshore whereas *S. miniatus* are not commonly taken (Demory et al. 1976; Niska 1976). *Sebastes emphaeus*, although not previously reported from Oregon, is well represented in our samples. Pigment pattern, general body shape, time of occurrence, and constancy in number of anal fin soft rays and pectoral rays helped link the developmental series together.

TABLE 7.—Meristics from larvae and juveniles of *Sebastes pinniger* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
7.8	[1]	[1]	—	17	[4]	[4]	—	—	—	—	—
7.8	[1]	[2]	17	—	[4]	[4]	—	—	—	—	—
8.8	VIII–I 14	III 7	17	17	I 5	I 5	—	—	—	—	—
8.9	IX–I 15	III 7	17	17	I 5	I 5	—	—	—	—	—
9.3	XIII 14	III 7	18	17	I 5	I 5	—	—	—	—	—
9.8	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
10.7	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
10.7	XIII 15	III 7	17	17	I 5	I 5	—	—	—	—	—
10.9	XIII 15	III 7	17	17	I 5	I 5	—	—	—	—	—
12.3	XIII 15	III 7	17	17	I 5	I 5	—	—	—	—	—
12.3	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
12.8	XIII 15	III 7	17	17	I 5	I 5	—	—	—	—	—
13.0	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
14.1	XIII 14	III 7	17	17	I 5	I 5	—	27 - 12 or 13 39 or 40	—	—	—
14.2	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
15.2	XIII 15	III 7	17	17	I 5	I 5	—	—	—	—	—
16.0	XIII 14	III 7	17	17	I 5	I 5	—	28 - 13 41	—	—	—
16.0	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
16.2	XIII 15	III 7	17	17	I 5	I 5	—	27 - 13 40	—	—	—
16.8	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
17.8	XIII 15	III 7	18	18	I 5	I 5	—	27 - 12 39	—	—	—
18.4	XIII 14	III 7	17	17	I 5	I 5	—	—	—	—	—
18.6	XIII 15	III 7	17	18	I 5	I 5	27 - 14 41	28 - 14 42	—	—	—
18.9	XIII 15	III 7	17	17	I 5	I 5	29 - 13 42	28 - 13 41	—	—	—
19.4	XIII 15	III 7	17	17	I 5	I 5	27 - 13 40	26 - 12 38	—	—	—
19.5	XIII 14	III 7	18	18	I 5	I 5	27 - 13 40	27 - 12 39	—	—	—
20.0	XIII 14	III 7	17	17	I 5	I 5	27 - 14 41	28 - 13 41	44	—	—
20.8	XIII 14	III 7	17	17	I 5	I 5	28 - 13 41	28 - 13 41	—	—	—
22.4	XIII 14	III 7	17	18	I 5	I 5	28 - 13 41	29 - 13 42	—	44	—
23.4	XIII 14	III 7	17	17	I 5	I 5	29 - 13 42	28 - 14 42	44	—	—
26.4	XIII 14	III 7	17	17	5	I 5	29 - 15 44	29 - 14 43	43	40	—
26.4	XIII 14	III 7	17	17	I 5	I 5	28 - 14 42	27 - 13 41	—	—	—
26.6	XIII 15	III 7	17	17	I 5	I 5	28 - 13 41	28 - 14 43	—	—	—
28.6	XIII 14	III 7	17	17	I 5	I 5	28 - 13 41	29 - 14 43	42	44-45	—
28.8	XIII 15	III 7	17	17	I 5	I 5	29 - 13 42	28 - 13 41	—	—	—
29.4	XIII 14	III 7	17	17	I 5	I 5	28 - 13 41	28 - 14 42	44	—	—
30.4	XIII 13	III 7	1	1	I 5	I 5	28 - 13 41	28 - 13 41	44	—	—
30.9	XIII 14	III 7	1	18	7	I 5	31 - 14 45	31 - 15 46	—	—	—
34.1	XIII 14	III 7	17	17	I 5	I 5	29 - 14 43	29 - 14 43	44	44	—
38.0	XIII 14	III 7	17	18	I 5	I 5	28 - 14 42	29 - 14 43	—	42	—
38.7	XIII 15	III 7	17	17	I 5	I 5	27 - 13 40	29 - 14 42	42	44	—
39.2	XIII 14	III 7	17	17	I 5	I 5	29 - 14 43	29 - 15 43	41	41	—
40.0	XIII 14	III 7	17	17	I 5	I 5	28 - 14 42	29 - 13 41	40	—	—
41.0	XIII 14	III 7	17	17	I 5	I 5	30 - 14 44	30 - 14 44	—	43	—
42.4	XIII 15	III 7	1	17	I 5	I 5	29 - 14 43	29 - 14 43	—	40	—
59.4	XIII 14	III 7	17	18	I 5	I 5	29 - 14 43	29 - 14 43	—	43	51
117.7	XIII 14	III 7	17	17	I 5	I 5	29 - 14 43	29 - 13 42	45	44	—
181	XIII 15	III 7	17	17	I 5	I 5	30 - 14 44	28 - 14 42	43	43	50

[1] Forming
[2] Not formed
[3] Posteriormost dorsal or anal spine appears as a soft ray
[4] Transforming
[5] Pelagic juvenile
[6] Benthic juvenile

Distinguishing Features.—Characters useful in distinguishing the smallest larvae (7.8 mm) of *S. pinniger* identified from our collections are the presence of remnants of both dorsal and ventral midline melanophores the anterior of which are internal, the lightly pigmented pectoral fins, melanophores at the tip of the lower jaw and on the anteroventral margin of the maxillary, the presence of one or two large external stellate melanophores on the dorsum just posterior to the parietal spines, the relatively deep body (40% SL), long parietal spines (24% HL), and long pectoral fins (25% SL). Later stage larvae are characterized by their relative lack of pigment on the trunk except over the gut, together with the relatively deep body and long parietal and third posterior preopercular spines. Meristics, presence of the supraocular spine, flat to convex shape of the interorbital space, and dark blotch at the base of the spinous dorsal serve to distinguish the juveniles.

General Development.—The smallest larvae of *S. pinniger* identified, 7.8 mm, are in the final stage of notochord flexion. By the time larvae are 8.8 mm long, flexion is complete. Transformation to pelagic juvenile begins in larvae ~12.5 mm long with the initiation of spine formation in the dorsal and anal fin "prespines" and the appearance of a patch of melanophores on the dorsum immediately posterior to the second dorsal fin. Transformation of the "prespines" to spines is complete in specimens ~18.6 mm and some pigment has been added beneath the first dorsal fin marking the beginning of pelagic juvenile pigmentation. The dorsal pigmentation becomes more pronounced during the pelagic juvenile period which lasts until ~40 to 50 mm. The largest pelagic juvenile taken was 42.4 mm and the smallest benthic juvenile was 59.4 mm.

Morphology (Tables 4, 8).—Forty-eight specimens of *S. pinniger*, 7.8 to 181.0 mm long, were measured for developmental morphology. Larvae appear quite deep bodied, but body depth at the pectoral fin base decreases considerably during the pelagic period from 40 to 33% SL. In comparison, body depth at the anus SL changes relatively little, decreasing slightly then increasing. Snout to anus length increases from 59 to 64% SL while snout to pelvic fin distance increases to a lesser degree.

Head length decreases from 43 to 37% SL during development as more marked changes occur in eye diameter, decreasing from 37-39 to 27% HL, and interorbital distance, decreasing from 37 to 20% HL. Upper jaw length HL first decreases and then increases while snout length HL increases then decreases. The length of the angle gill raker increases with respect to head length from 11 to 14 or 15%.

Larvae and young juveniles up to 24 mm have a prominent symphyseal knob directed anteroventrally. It becomes less obvious with development and is barely noticeable by the time juveniles are 29 mm long.

Fin Development (Tables 4, 7, 8).—Pectoral fins are present and the adult complement of 16 to 18 (usually 17) rays can be counted in 7.8 mm larvae of *S. pinniger*, although the ventral rays are not fully formed until ~8 mm. The pectoral fins are relatively long in flexion and postflexion larvae averaging 25% SL and they maintain this approximate proportion through development. Depth of the pectoral fin base decreases from 15 to 9% SL.

Developing pelvic fins are visible on 7.8 mm larvae and the adult complement of 1, 5 is countable in postflexion larvae of 8.8 mm. The pelvic fins are rather long, averaging 14% SL in flexion larvae and increasing to a maximum of 23% SL in transforming specimens. Length of the pelvic spine, always less than the fin itself, increases from 5% SL in flexion larvae to 20% in transforming specimens then decreases to 13% in benthic juveniles.

The adult complement of principal caudal rays can be counted in 7.8 mm larvae, before the completion of notochord flexion at 8.8 mm. Counts of secondary caudal rays were 11 superior and 12 inferior rays on each of two stained juveniles, 29.5 and 33.4 mm.

Bases of some of the dorsal and anal fin ray and spine elements are visible on the 7.8 mm larvae. The adult complement of ray and spine elements is present in postflexion larvae ~9 mm and the rays and spines (with "prespines") appear fully formed by 9.3 mm. Transformation of "prespines" to spines is completed by 18.5 mm. The longest dorsal spine increases from 20 to 38% HL during the pelagic period. The longest dorsal ray increases from 32 to 42 or 43%. The longest anal spine increases from 19 to 37% HL during pelagic development.

Spination (Tables 4, 9).—Spines present on the left side of the head of the two smallest specimens of *S. pinniger*, 7.8 mm, include the parietal; the nuchal; the first and third anterior preopercular; the second, third, and fourth posterior preopercular; the postocular, the pterotic, the inferior posttemporal; the first spine of the inferior infraorbital series; and the first spine of the superior infraorbital series.

The parietal spine and ridge are heavily and relatively deeply serrated in small larvae and the spine is relatively long, averaging 24% HL in flexion larvae. Its relative length decreases with development to 20% HL in flexion larvae, 10% in transforming specimens, and 7% in early pelagic juveniles, ~20 mm. The much smaller nuchal spine averages 4 or 5% HL in postflexion and transforming larvae, decreasing to 1% in benthic juveniles. The parietal and nuchal spines fuse together, beginning in pelagic juveniles ~20 mm until only the nuchal tip is visible in juveniles ~40 mm. Serrations along the parietal ridge can be seen on specimens up to 39 mm.

TABLE 8.—Measurements (millimeters) of larvae and juvenles of *Sebastes pinniger* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine number	Preopercular spine length	Angle	Gill raker length	Longest dorsal spine length	Longest dorsal ray length[2]	Longest anal length[2]
7.8	9.8	4.6	3.3	0.88	1.6	1.2	1.2	3.2	2.1	2.1	1.1	0.40	1.2	3.4	0.80	(4)	1.2	—	(5)	(5)	(5)	(5)	(5)
7.8	9.5	4.5	3.4	0.92	1.6	1.3	1.3	3.1	2.2	1.8	1.2	(5)	0.96	3.0	0.84	(4)	1.1	—	(5)	(5)	(5)	(5)	(5)
8.8	11.2	5.5	4.2	1.0	2.2	1.5	1.4	3.7	2.5	2.1	1.2	0.72	0.88	3.6	—	—	1.2	—	—	1.0	(5)		
8.9	11.1	4.6	3.4	0.92	1.4	1.4	1.3	3.0	2.2	1.8	1.2	0.88	1.1	3.4	0.76	0.16	1.2	—	0.46	1.1	(5)		
9.3	11.5	5.6	4.0	1.3	1.9	1.5	1.4	3.5	2.6	2.1	1.2	1.2	1.4	3.8	0.94	0.10	1.4	—	0.52	1.1	(5)		
9.8	12.3	5.8	4.1	1.2	1.9	1.6	1.5	3.8	3.0	2.7	1.2	—	1.7	3.4	0.96	0.18	1.6	0.34	—	1.3	0.60		
10.7	14.1	6.5	4.7	1.3	2.2	1.9	1.6	4.3	3.2	2.7	1.4	—	1.9	4.8	—	—	—	0.54	1.1	1.5	1.0		
10.7	13.4	6.3	4.6	1.6	2.0	1.9	1.4	3.9	2.9	2.7	1.3	1.6	2.3	4.7	—	—	1.2	0.48	1.0	1.4	0.88		
10.9	12.8	6.3	4.5	1.2	2.2	1.8	1.5	4.3	3.3	—	1.4	1.6	2.0	4.4	—	—	1.5	0.44	0.92	1.4	0.84		
12.3	15.5	7.7	5.0	1.3	2.1	1.9	1.7	4.4	3.4	3.0	1.4	—	2.4	4.9	0.44	0.18	1.6	0.56	—	1.9	1.0		
12.3	15.4	7.6	5.2	1.6	—	2.1	1.7	4.8	3.7	3.5	1.4	—	2.8	5.2	—	0.36	1.3	0.64	1.5	1.9	—		
12.8	15.7	8.0	5.2	1.9	2.1	2.0	1.6	4.5	3.4	2.9	1.3	2.4	2.7	5.9	0.66	0.18	1.3	0.70	1.5	1.6	1.3		
13.0	15.2	8.2	5.5	1.7	2.1	2.1	1.6	4.8	3.5	3.5	1.5	—	2.7	5.9	0.60	0.30	1.6	0.68	1.3	2.0	1.1		
14.1	17.1	8.5	5.9	2.1	2.1	2.2	1.7	4.9	3.5	—	1.5	2.6	3.0	6.0	0.68	0.32	1.3	0.68	—	—	1.5		
14.2	16.8	8.6	5.7	1.6	—	2.2	1.8	5.1	3.9	—	1.6	2.5	3.0	5.8	—	0.36	1.3	0.72	1.7	2.2	1.5		
15.2	19.2	9.1	6.2	1.9	2.8	2.3	2.0	5.4	4.3	4.3	1.7	3.1	3.7	6.2	0.80	0.40	1.5	0.84	1.9	2.4	1.8		
16.0	20.0	9.4	6.2	1.7	2.6	2.4	2.0	5.9	4.5	4.5	1.8	—	3.8	6.2	—	0.28	1.4	0.80	2.4	—	2.0		
16.0	20.8	9.3	6.6	1.7	3.1	2.5	2.0	5.7	4.5	4.5	1.6	—	—	6.2	0.26	0.18	1.4	0.88	—	2.4	1.7		
16.2	20.6	10.2	6.9	1.9	3.2	2.6	2.0	6.2	5.0	5.1	1.8	—	4.1	6.7	—	0.50	1.6	0.90	2.8	2.9	—		
16.8	19.7	10.1	6.7	2.1	2.8	2.5	1.9	6.3	4.7	4.5	1.6	—	—	6.5	—	0.34	1.6	0.88	2.2	2.5	—		
17.6	20.8	10.7	7.0	2.2	2.8	2.7	2.0	6.4	5.2	4.8	1.8	3.6	4.1	7.6	—	—	1.6	0.90	—	2.8	—		
18.4	21.8	10.7	7.0	1.9	2.8	2.5	2.2	6.4	5.1	4.9	2.0	4.0	4.4	7.5	0.72	0.16	1.6	0.94	—	3.0	2.7		
18.6	22.9	11.7	7.6	2.3	3.3	2.6	2.0	6.2	4.7	5.0	1.8	3.6	4.2	8.6	0.70	0.32	—	1.1	2.6	3.2	2.6		
18.9	23.5	11.7	7.7	2.4	3.3	2.7	2.1	6.4	4.8	—	1.9	3.6	4.1	8.4	—	—	1.6	0.9	—	—	2.4		
19.4	23.4	11.2	8.0	1.9	3.4	2.7	2.2	6.6	5.4	5.2	1.9	4.2	4.6	7.6	0.46	0.30	1.7	1.1	—	3.1	2.6		
19.5	24.6	11.5	8.2	2.2	3.5	2.8	2.2	6.7	5.2	—	2.0	4.3	4.6	8.6	0.84	0.44	1.4	1.0	3.0	—	2.7		
20.0	25.4	11.5	7.4	1.8	3.4	2.8	2.2	7.4	5.6	5.7	2.0	—	4.6	8.0	0.40	0.30	—	1.1	—	3.2	2.8		
20.8	24.8	12.6	8.0	2.6	3.1	2.8	2.1	7.0	5.3	5.9	2.0	3.9	4.2	8.5	Joined	0.32	1.2	1.2	—	—	2.7		
22.4	26.7	13.0	8.4	2.0	3.4	3.0	2.3	7.7	5.9	6.0	2.2	4.5	5.2	8.0	Joined	0.26	1.4	1.2	—	—	3.2		
23.4	28.8	13.1	7.8	2.1	3.7	3.3	2.4	8.0	6.3	6.1	2.1	4.7	5.1	7.7	Joined	0.28	—	1.2	3.6	3.8	3.3		
26.4	33.4	15.2	9.1	2.1	4.2	3.5	2.6	8.9	7.0	7.3	2.5	—	6.0	9.9	Joined	0.40	1.4	1.5	—	4.0	4.0		
26.4	31.2	17.3	10.4	3.4	4.0	3.4	2.4	8.9	7.0	7.2	2.4	4.6	5.5	12.0	Joined	0.20	1.2	1.5	—	—	3.2		
26.6	32.0	17.0	10.6	2.6	4.2	3.4	2.2	8.9	7.1	7.1	2.4	4.8	6.1	10.9	Joined	0.40	—	1.4	—	—	3.6		
28.6	38.1	17.9	10.7	3.0	4.0	3.5	2.7	9.2	7.3	7.6	2.6	—	6.4	11.4	Joined	0.28	1.3	1.5	—	4.2	4.1		
28.8	36.3	19.2	10.6	3.4	4.3	3.7	2.6	9.6	7.6	7.6	2.6	5.2	6.2	13.1	Joined	0.30	1.2	1.5	4.0	4.1	4.4		
29.4	37.1	17.9	10.7	2.6	4.1	3.7	2.7	10.5	8.0	7.5	2.8	5.2	6.6	10.7	Joined	0.28	1.2	1.6	4.4	4.4	4.4		
30.4	38.1	20.5	11.5	3.7	4.9	3.7	2.6	10.1	7.5	7.7	2.5	5.2	6.5	13.4	Joined	—	1.2	1.6	4.4	4.4	4.4		
30.9	38.6	20.8	13.0	4.1	4.5	4.0	2.7	10.4	8.1	8.6	2.8	5.5	7.2	13.4	Joined	—	1.2	1.6	4.6	4.6	—		
34.1	42.6	22.7	12.5	3.9	5.3	4.0	2.7	11.0	8.3	—	2.8	5.7	6.6	15.5	Joined	0.34	1.5	1.6	4.4	4.8	4.8		
38.0	46.6	22.5	13.8	3.0	5.7	4.7	3.0	11.5	9.1	9.3	3.1	—	7.7	14.1	Joined	0.30	1.3	1.9	4.9	5.7	5.3		
38.7	46.4	23.4	13.3	3.9	6.0	4.5	2.9	12.0	9.8	9.6	3.4	6.6	7.6	14.2	Joined	0.46	1.4	2.1	5.4	—	—		
39.2	48.8	23.5	13.9	3.2	5.9	4.5	3.0	11.7	10.1	10.2	3.3	5.7	8.0	14.6	Joined	0.30	1.3	1.9	—	6.1	5.3		
40.0	49.1	23.5	14.9	3.6	6.0	4.7	3.3	12.5	10.4	9.6	3.6	6.5	8.8	15.5	Joined	0.30	1.4	2.1	5.3	6.6	6.3		
41.0	50.4	25.0	14.7	4.3	5.9	4.6	3.1	12.2	9.8	10.4	3.4	6.3	8.4	17.8	Joined	0.30	1.5	2.1	5.6	6.6	5.5		
42.4	51.7	26.4	15.4	4.3	5.7	4.9	3.0	13.0	11.0	10.2	3.7	6.4	8.7	16.5	Joined	0.40	1.4	2.1	5.1	6.3	5.2		
59.4	71.0	36.0	21.8	6.4	9.3	6.6	4.0	19.4	16.2	13.6	5.1	7.4	11.3	24.4	Joined	0.46	1.4	3.0	7.4	8.9	7.5		
117.7	141.8	78.3	43.8	12.5	19.5	11.2	8.6	41.6	33.2	29.4	10.1	14.8	25.5	48.3	Joined	0.64	1.7	6.6	13.8	17.4	14.2		
9.1	22.4	11.7	6.5	4.0	1.8	1.5	1.3	6.7	2.2	6.1	5.5	4.5	1.3	2.1	8.3	8.5	0.7	2.3	1.0	6.2	7.0	3.9	2.3

[1]Usually third or fourth in larvae, fifth or sixth in juveniles
[2]Usually midfin
[3]The second spine
[4]Bump
[5]Not formed
[6]Forming
[7]Transforming
[8]Pelagic juvenile
[9]Benthic juvenile

The posterior series of preopercular spines are prominent in *S. pinniger* larvae. The heavily serrated third spine is relatively long averaging 32 to 34% HL in flexion and postflexion larvae. Its relative length then decreses to 5% in benthic juveniles. All five spines of the series are present in larvae >10 mm. Serrations are visible on the second, third, and fourth spines until ≈29 mm. The first posterior preopercular spine is sometimes bifid in pelagic juveniles. The smaller first and third spines of the anterior preopercular series are also conspicuous on small larvae, but decrease in prominence until they are no longer visible in pelagic juveniles >26 mm. The second anterior preopercular spine never becomes apparent.

The superior opercular spine is present on larvae by 9 mm and the inferior opercular spine appears later in larvae ≈12 or 13 mm. Both spines are present on juveniles. An interopercular spine develops on the edge of the gill cover, usually in larvae >10 mm. A subopercular spine was not present on any of the specimens examined.

The ridge anterior to the postocular spine is heavily serrated and remains so until preocular spine formation. The preocular appears first as a bump in transforming larvae ≈16.0 mm long and develops into a spine in pelagic juveniles >19 mm.

Development of the supraocular follows a similar pattern appearing at about the same time as the preocular. Beneath the eye the fourth spine of the superior infraorbital series is present in larvae >9 mm and the third spine of this series is present in all larvae >13 mm. The second superior infraorbital spine never forms. All three superior infraorbital spines disappear by 43 mm. The second spine of the inferior infraorbital series is present on specimens >10 mm and the two spines in this series persist in juveniles. The third inferior infraorbital spine never develops. The nasal spine develops

TABLE 9.—Development of spines in the head region of *Sebastes pinniger* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and − denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Opercular Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
7.8	-	-	+	+	+	-	-	+	-								+
7.8	-	-	+	+	+	-	-	+	-								+
8.8	-	-	-	-	+	-	+	+	-	+							+
8.9	-	-	-	-	+	-	+	+	-	+						-	+
9.3	-	-	-	-	+	-	+	+	-	+						-	+
9.8	-	-	-	-	+	-	+	+	-	+						-	+
10.7	-	-	-	+	+	-	+	+	+	+			+			-	+
10.7	-	-	-	-	+	-	+	+	-	+			-			-	+
10.9	-	-	-	-	+	-	+	+	-	+							+
12.3	-	-	-	+	+	-	+	+	-	+			+				+
12.3	-	-	-	-	+	-	+	+	-	+			+				+
[1]12.8	-	-	-	-	+	-	+	+	-	+			+			+	+
[1]13.0	-	-	-	-	+	-	+	+	-	+			+			+	+
[1]14.1	-	-	-	-	+	-	+	+	-	+			+		-		+
[1]14.2	-	-	-	-	+	-	+	+	-	+			+				+
[1]15.2	-	-	-	-	+	-	+	+	-	+			+				+
[1]16.0	-	-	-	-	+	-	+	+	-	+			+				+
[1]16.0			-	-	+				-	+			+		(2)	-	+
[1]16.2		-	-	-	+	-			-	+			+		(2)	(2)	+
[1]16.8	-		+	-	+		-		-	+			+			-	+
[1]17.8				-	+				-	+			+		(2)	-	+
[1]18.4	-	-	-	-	+				-	+			+		(2)	-	+
[1]18.6		-	-	-	+	[3]	-		-	+			+		(2)	(2)	(2)
[1]18.9					+	-	-		-	+			+		(2)	(2)	(2)
[1]19.4	-	-	-	-	+				-	+			+		-	-	+
19.5				-	+				-	+			+			-	+
20.0	-	-		-	+	-			-	+			+			-	+
20.8	-	-		-	+				-	+			+			-	+
22.4		-		-	+				-	+			+			-	+
23.4				-	+				-	+			+			-	+
26.4	-	-	-		+				-	+			+			-	+
26.4					+				-	+			+			-	+
26.6					+				-	+			+			-	+
28.6					+				-	+			+			-	+
28.6		-			+				-	+			+			-	+
29.4		-			+				-	+			+			-	+
30.4					+				-	+			+			-	+
30.9					+				-	+			+			-	+
34.1					+	[4]	-		-	+			+			-	+
38.0					+	[4]	-		-	+			+			-	+
48.7					+	[4]			-	+			+			-	+
49.2					+	[4]	-		-	+			+			-	+
50.0					+	[4]				+			+			-	+
51.0					+	-				+			+			-	+
52.4					+	-				+			+			-	+
[5]53.4					+	-				+			+			-	+
117.7					+	-	-			+			+			-	+
[6]61					+	[4]				+			+			-	+

[1]Transforming.
[2]Bump indicates beginning of spine formation.
[3]Pelagic juvenile.
[4]Spine is bifid.
[5]Parietal and nuchal spines fused.
[6]Benthic juvenile.
[7]Spine has become rounded, no sharp tip.

TABLE 9.—Continued.

Standard length (mm)	Infraorbitals							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supracleithral	Cleithral
	Inferior			Superior											
	1st	2d	3d	1st	2d	3d	4th					Superior	Inferior		
7.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
7.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.9	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
9.3	+	–	–	+	–	–	+	(2)	–	–	+	–	+	–	–
9.8	+	–	–	+	–	–	+	(2)	–	–	+	–	+	+	–
10.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
10.7	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
10.9	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.3	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
12.3	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
14.1	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
14.2	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
15.2	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
16.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
16.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
16.2	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
16.8	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
17.8	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
18.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
18.6	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
18.9	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
19.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
19.5	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
20.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
20.8	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
22.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
23.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
26.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
26.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
26.6	+	+	–	+	–	(–)	(–)	+	–	–	+	+ 4	+	+	–
28.6	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
28.8	+	+	–	?	–	?	?	+	–	–	+	–	+	+	–
29.4	+	+	–	(2)	–	(2)	–	–	–	–	+	+ 4	+	+	–
30.4	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
30.9	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
34.1	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
38.0	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
38.7	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
39.2	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
40.0	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
41.0	+	+	–	–	–	–	–	+	–	–	+	–	+	+	–
42.4	+	+	–	–	–	–	–	+	–	+	+	–	+	+	–
59.4	+	+	–	–	–	–	–	+	–	+	+	–	+	+	–
117.7	+	+	–	–	–	–	–	+	–	–	(2)	–	+	+	–
181	+	+	–	–	–	–	–	+	–	+	+	–	+	+	–

first as a bump in larvae >9 mm and is present in juveniles.

The tympanic spine appears on specimens >35 mm SL. This spine forms at the anterior edge of a foramen of the cephalic lateral line system. The pterotic spine, present in the smallest larvae, disappears in benthic juveniles. The supracleithral spine develops posterior to the inferior posttemporal on larvae >9.5 mm and the superior posttemporal spine is present dorsal to these in specimens >14 or 15 mm. This latter spine is occasionally bifid. The inferior posttemporal disappears in benthic juveniles. Posterior to the opercle the cleithral spine is visible in pelagic juveniles of 19.5 mm and persists in benthic juveniles.

Scale Formation.—Lateral line pores are visible on specimens >17 mm. Scale formation has begun on juveniles >23 mm.

Pigmentation.—The smallest larvae of *S. pinniger* examined, 7.8 mm (similar to the 8.9 mm specimen illustrated), have pigment on the head over the brain. Melanophores line the inner tip of the lower jaw and a few are present along the anteroventral margin of the maxillary. In the abdominal region, an internal melanistic shield covers the dorsal half of the gut, appearing darkest on the dorsal surface. A few additional melanophores are present along the ventral midline of the gut cavity. Two or three large stellate melanophores are

on the dorsum immediately posterior to the parietal spines. In the tail region several embedded melanophores, sometimes fused, are on the dorsal and ventral body midlines near the caudal peduncle. These midline melanophores are present in the same region as the midline pigment shown on Waldron's (1968) reared 2-wk-old larva. The pectoral fin blades are lightly pigmented with elongate melanophores. Melanophores are also present on the inner side of the pectoral fin base but not on the outer side. The pelvic fins also have a light scattering of melanophores. The caudal fin base is unpigmented.

During larval development, pigment increases on the head over the brain. Occasionally one or two melanophores are present on the snout. Melanophores lining the inner tip of the lower jaw and those on the anteroventral margin of the maxillary remain throughout the larval period.

The melanistic shield over the gut intensifies laterally and melanophores on the ventral midline disappear. The two to three stellate melanophores on the dorsum posterior to the parietal spines disappear by the time larvae are 9 mm long.

In the tail region, the dorsal and ventral midline melanophores near the caudal peduncle are no longer visible on larvae >9 mm.

The rayed portions of the pectoral and pelvic fins remain lightly pigmented during the larval period but melanophores are no longer present on the inner side of the pectoral fin base in larvae >10 mm.

During the transformation period, 12.8 to 18.6 mm, the amount of pigment increases gradually. In the head region, internal pigment is added to the opercle dorsally until a patch of 6 to 10 melanophores is visible on specimens >16 mm. Internal gut pigmentation decreases in intensity due to overgrowth by musculature. A few melanophores sometimes appear on the nape and beneath spines V to XI of the first doral fin, although not consistently until late in the transformation period in specimens >17 mm. The most prominent addition of pigment occurs dorsally in the tail region just posterior to the soft dorsal fin. Melanophores are added along the dorsolateral surface of the caudal peduncle. Directly below these melanophores, three or four internal and one to four external melanophores are added along the lateral midline in specimens >15 mm. The amount of pigment on the pectoral and pelvic fins decreases during this period.

During the pelagic juvenile period, 18.9 to 42.4 mm, new pigment is added over the dorsal surface of the head, interorbital, snout, premaxillary (specimen >26 mm), and on the lower jaw (specimen >35 mm). The opercular patch enlarges. Around the eye, melanophores are added first on the posteroventral margin of the orbit in specimens 19 to 23 mm, and eventually line the orbit. A radiating bar of melanophores begins to extend from the posteroventral margin of the orbit on specimens >28 mm, extending onto the preopercle on specimens >30 mm. In the abdominal region, melanophores are added dorsolaterally to the nape and beneath spines V to X of the first dorsal fin forming two pigment patches connected by a dorsal row of melanophores by 23 mm. The nape patch expands forming a saddle (first in position) extending from the parietal spine to the third dorsal spine and ventrally to the superior posttemporal spine by 28 mm. Two saddles (second and third) develop from the pigment patch beneath the spinous dorsal fin, midfin beneath spines IV to VI and posteriorly beneath spines VIII to XI. These two saddles are separated by a relatively unpigmented area on the dorsum. As they extend more ventrolaterally, they fuse together in two places just above and below the lateral line creating a second, circular, less pigmented area on specimens >39 mm. These two saddles eventually extend to the dorsal portion of the gut cavity by 42 mm. A single external melanophore may occur on the midanterior margin of the cleithrum beneath the gill cover. In the tail region, the dorsal patch of pigment on the caudal peduncle extends to the lateral line forming another saddle by 23 mm which reaches the ventral body margin by 27 mm. Beneath the second dorsal fin melanophores increase in number and become concentrated along the muscles surrounding the dorsal pterygiophores appearing as vertical lines of pigment by 23 mm. Melanophores also develop at the point of articulation of all but the anteriormost three or four dorsal soft rays. A melanistic saddle (fourth in position) develops beneath soft dorsal rays 3 to 12 or 13 extending ventrolaterally to the body midline by 34 mm and three-fourths the distance to the ventral margin by 42 mm. The pectoral and pelvic fins are no longer pigmented in specimens >21 mm. Pigment develops on the first dorsal fin membrane between spines IX and XI in juveniles >26 mm, eventually forming the "black blotch" characteristic of larger juveniles and adults. Melanistic bars form on the first dorsal fin between spines I to III

and V to VIII above the first and second saddles. By 39 mm the outer half of the fin is completely pigmented, while two unpigmented areas remain on the proximal half of the fin between the two pigment bars. Melanophores are added on the second dorsal fin above the fourth saddle until the proximal one-fourth of the fin between rays 2 and 13 or 14 is pigmented. The base of the caudal fin never becomes outlined with melanophores, but some melanophores develop on the dorsal secondary caudal rays.

Recently preserved pelagic juveniles of *S. pinniger*, 32 to 35 mm, are covered with orange chromatophores which are lost during prolonged preservation. They are present on the dorsal part of the head, on the snout, around the orbit, and on the opercle. On the body they are concentrated along the myosepta and lateral midline, with greater numbers on the dorsal half of the body but also extending to the ventral margin. Orange chromatophores are also concentrated on the spinous dorsal fin, along the basal one-fourth of the caudal fin, and the anal fin membrane around the anal spines.

A general increase in melanistic pigmentation occurs in benthic juveniles >59 mm. On the head, the two pigment bars beneath the orbit remain distinct and extend over the operculum. Pigment increases between the saddles obscuring the pattern seen on pelagic juveniles. Melanophores are added to both the inner and outer surfaces of the pectoral fin base and on the basal one-third of the pectoral fin blade. The pelvic fin remains unpigmented. The addition of melanophores to the spinous dorsal fin obscures the pattern seen on pelagic juveniles although the black blotch remains intense and distinct. The entire caudal fin is lightly pigmented with more intense pigment occurring over the bases of the primary rays and all upper secondary rays.

Occurrence (Figures 10, 11).—Adults of *S. pinniger* occur between Cape Colnett, Baja California, and southeast Alaska (lat. 56° N, long. 134° W) (Hart 1973). Off Oregon they are most common on the continental shelf between 100 and 200 m (Snytko and Fadeev 1974). A major population concentration has been found between lat. 44°30′ and 45° N off Oregon (Snytko and Fadeev 1974).

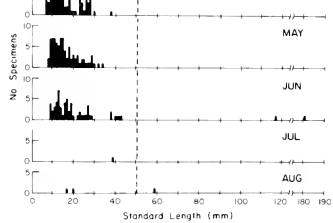


FIGURE 11.—Seasonal occurrence of larvae and juveniles of *Sebastes pinniger* off Oregon. Data from 1964 to 1975 combined. Dashed line separates pelagic and benthic stages.

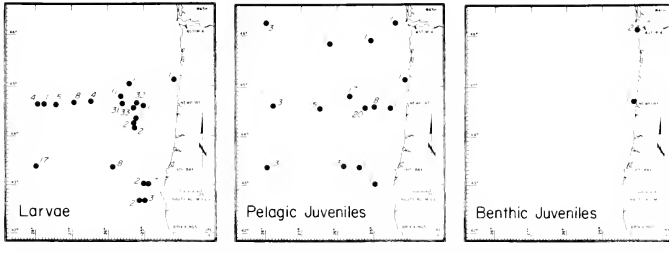


FIGURE 10.—Number of specimens and location of capture of larvae and juveniles of *Sebastes pinniger* off Oregon (1964-75) described in this paper.

Larvae, including transforming specimens, of *S. pinniger* in our collections were captured at a wide range of stations from 13 to 306 km offshore. The largest numbers and smallest larvae (< 8.8 mm) were taken at stations 83 to 120 km off Newport beyond the continental shelf break. This may partly be a reflection of increased sampling effort in that area. Pelagic juveniles occurred at a similar wide range of stations, mostly beyond the continental shelf. Interestingly, 30 specimens, ranging in length from 8.9 to 18.6 mm were captured 306 km off Coos Bay, Oreg., well beyond the continental shelf. Perhaps this wide ranging offshore occurrence of larvae and pelagic juveniles is related to their morphology. The larvae are quite stubby and deep bodied with particularly long head spines, features which could contribute to increased flotation and dispersal by currents. Most specimens were captured in oblique midwater trawl and bongo net tows. Three benthic juveniles were taken close to the coast in depths of 30 to 35 m.

Reported spawning times for *S. pinniger* are November to March off California (Phillips 1964) and January to March off Oregon, Washington, and British Columbia (Westrheim 1975). Larvae < 10 mm were taken March through June, and larger pelagic specimens were taken March through August. The wide range in lengths, 9 to 25 mm in March, 7 to 38 mm in April, 8 to 34 mm in May, 9 to 43 mm in June, may be indicative of protracted and variable spawning. Benthic juveniles were taken in June and August.

Sebastes pinniger is one of the most abundant trawl-caught rockfish species on the continental shelf off Oregon together with *S. flavidus* and *S. entomelas* (Snytko and Fadeev 1974). In trawl surveys off Oregon it ranked either first or second only to *S. entomelas* in biomass over the shelf (Demory et al. 1976). It was one of the major contributors to "other rockfish" landings in Oregon during 1963-71 (Niska 1976). Larvae and juveniles were the most numerous in available collections of the three species described in this paper.

SEBASTES HELVOMACULATUS AYRES (Figures 12, 13)

Literature.—Westrheim et al. (see footnote 9) presented a schematic illustration of a preextrusion larva of *S. helvomaculatus* and described the pigment pattern in a tabular form. The latter table was also in Westrheim (1975). Preextrusion larvae (mean total length = 4.1 mm) have a ventral midline row of usually <16 (83% of 120 larvae) melanophores which stop short of the anus usually by as much as four myomeres. Pigment is absent from the dorsal midline, the head, nape, and lower jaw, and is usually not in the hypural region. The illustration shows some melanophores over the hindgut and ventrally beneath the yolk sac. Westrheim (1975) added that larvae of *S. helvomaculatus*, along with 10 other species which had been reared for several days, develop pigment spots on the head, nape, and/or lower jaw.

Identification (Table 10, Appendix Tables 2-6).—Twenty-six specimens of *S. helvomaculatus*, 7.7 to 183 mm long, were identified. Juveniles were identified using the following combination of characters obtained from specimens examined in this study:

Gill rakers = 28-31
Lateral line pores = 35-43
Pectoral fin rays = 15-17, usually 16
Anal fin soft rays = 5-6, usually 6
Dorsal fin soft rays = 12-14, usually 13
Supraocular spine = present
Interorbital space = concave.

Of the *Sebastes* species occurring off Oregon, *S. helvomaculatus* has the best fit to the above characters. *Sebastes aurora* and *S. elongatus* also agree with many of these characters, but *S. aurora* was eliminated since it has 24 to 28 gill rakers and *S. elongatus* was eliminated since it does not have a supraocular spine. Larval and juvenile specimens of *S. elongatus* identified from our collections are noticeably more slender than specimens of *S. helvomaculatus* and also are pigmented differently. Pigment pattern, body shape, time of occurrence, and constancy in number of anal fin soft rays and pectoral fin rays helped link together the developmental series.

Distinguishing Features.—Characters useful in distinguishing the smallest larva of *S. helvomaculatus* identified, 7.7 mm, are the pigmented fringes of the pectoral and pelvic fins; the general lack of body pigment; melanophores inside the tip of the lower jaw; narrow interorbital distance (31% HL); long, deeply serrated, parietal spines (27% HL); and relatively long pectoral fins

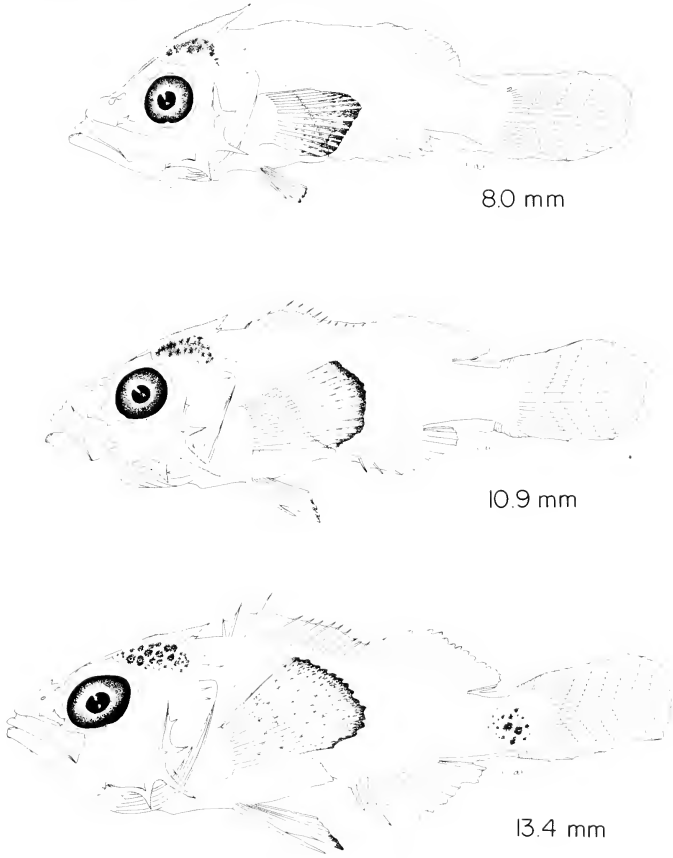


FIGURE 12.—Planktonic larvae (8.0, 10.9 mm) and transforming specimen (13.4 mm) of *Sebastes helvomaculatus*.

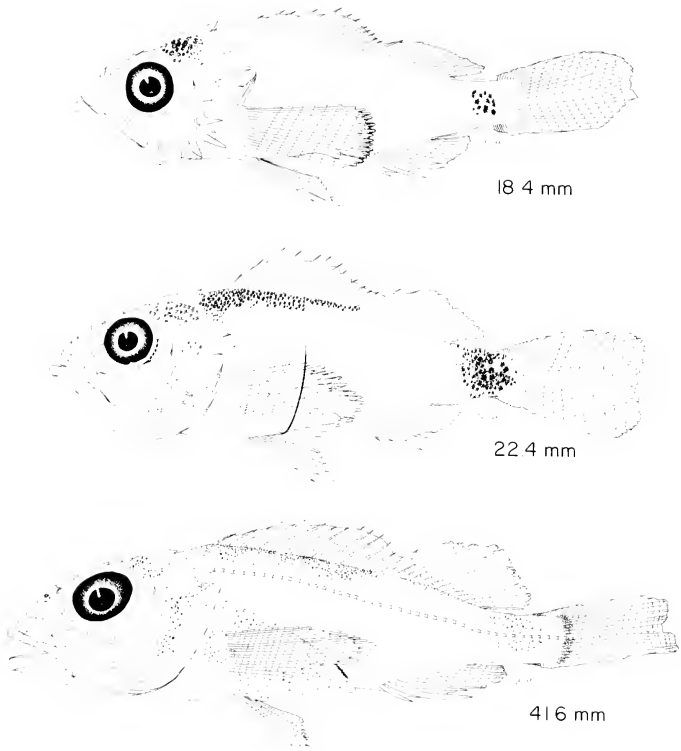


FIGURE 13.—Transforming specimen (18.4 mm) and pelagic juveniles (22.4, 41.6 mm) of *Sebastes helvomaculatus*.

(24% SL). Later stage larvae change very little in appearance from the smallest larva, except for an increase of dorsolateral internal gut pigment. A distinctive pigment patch appears on the caudal peduncle during the period of transformation from larva to pelagic juvenile. Meristics, presence of a supraocular spine, the concave shape and narrow width of the interorbital space, the patch of melanophores on the caudal peduncle, and the single melanistic pigment saddle extending pos-

TABLE 10.—Meristics from larvae and juveniles of *Sebastes helvomaculatus* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
7.7	—	—	16	16	I,(1)	I,(1)	—	—	—	—	—
8.0	—	III?,7	16	16	I,(1)	I,(1)	—	—	—	—	—
8.0	—	III?,7	16	16	I,(1)	I,(1)	—	—	—	—	—
8.8	—	III?,6	16	16	I,5	I,5	—	—	—	—	—
9.9	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
10.9	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
[3]12.0	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
[3]12.0	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
[3]13.4	XIII?,13	III?,7	16	16	I,5	I,5	—	—	—	—	—
[3]13.4	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
[3]13.6	XIII?,13	III?,6	16	16	I,5	I,5	—	—	—	—	—
[3]17.8	XIII?,12	III?,6	16	16	I,5	I,5	21+9=30	22+9=31	≈42	—	—
[3]17.9	XIII?,12	III?,6	16	16	I,5	I,5	21+9=30	21+9=30	—	—	—
[3]18.4	XIII?,13	III?,6	16	16	I,5	I,5	21+9=30	20+8=28	—	—	—
[3]18.4	XIII?,12	III?,6	16	16	I,5	I,5	21+9=30	21+9=30	42	—	—
[3]18.6	XIII?,13	III,6	16	17	I,5	I,5	19+8=27	19+8=27	—	—	—
[4]19.8	XIII,13	III,6	16	16	I,5	I,5	21+8=29	21+8=29	≈40	—	—
[4]20.3	XIII,14	III,6	16	16	I,5	I,5	21+9=30	20+8=28	≈39	—	—
[4]21.6	XIII,13	III,6	16	16	I,5	I,5	21+8=29	21+8=29	≈39	—	—
[4]22.1	XIII,14	III,6	16	16	I,5	I,5	20+9=29	20+8=28	≈40	40	—
[4]22.2	XIII,13	III,6	16	16	I,5	I,5	20+8=28	20+8=28	≈38	38	—
[4]22.4	XIII,13	III,6	16	15	I,5	I,5	21+9=30	21+9=30	≈41	41	—
[4]23.8	XIII,12	III,5	16	16	I,5	I,5	20+9=29	20+9=29	≈43	≈43	—
[4]41.6	XIII,13	III,6	16	16	I,5	I,5	22+9=31	22+8=30	39	38	—
[5]136.4	XIII,13	III,6	16	15	I,5	I,3	21+9=30	21+9=30	35	35	—
[5]183	XIII,14	III,6	17	16	I,5	I,5	22+9=31	22+9=31	40	39	≈43

[1]Not formed
[2]Posterior dorsal or anal spine appears as a soft ray
[3]Transforming
[4]Pelagic juvenile
[5]Benthic juvenile

teriorly from the nape to dorsal spine XI and ventrally about one-half the distance to the lateral line, all serve to distinguish pelagic juveniles.

General Development.—The smallest larva of *S. helvomaculatus* identified, 7.7 mm, is in the final stage of notochord flexion, which is completed by 8.8 mm. Transformation to pelagic juvenile begins in larvae ≈12 mm long with the initiation of spine formation in the dorsal and anal fin "prespines" and the appearance of a lateral pigment patch on the caudal peduncle. Transformation of the "prespines" to spines is completed in specimens >19 mm at which time some pigment appears beneath the spinous dorsal fin and pigment is added to the dorsal margin of the caudal peduncle pigment patch marking the beginning of pelagic juveniles pigmentation. More pigment is added beneath the first dorsal fin during the pelagic juvenile period although the saddle never becomes pronounced. Additional small external melanophores cover most of the fish by the end of the pelagic juvenile period, which probably lasts until ≈40-60 mm. The largest pelagic juvenile examined was 41.6 mm and the smallest benthic juvenile was 136.4 mm.

Morphology (Tables 4, 11).—Twenty-six specimens of *S. helvomaculatus*, 7.7 to 183 mm long, were measured for developmental morphology. Relative body depth/SL changes little at the pectoral fin base, decreasing slightly then increasing while it generally increases at the anus. Snout to anus distance increases from 56 to 63 or 64% SL and the snout to pelvic fin distance increases somewhat then decreases.

Head length increases slightly (41-42%) then decreases (38%) with respect to standard length. Eye diameter decreases (39-32% HL), as do the interorbital distance (31-15% HL) and snout length (32 or 33-27% HL). Upper jaw length increases from 44-46 to 52% HL. The length of the angle gill raker first increases (13-15% HL) then decreases (11%).

Larvae and juveniles <24 mm have a weak symphyseal knob which becomes less obvious with development.

Fin Development (Tables 4, 10, 11).—The adult complement of 15 to 18 (usually 16) pectoral fin rays can be counted on the smallest larva, 7.7 mm, of *S. helvomaculatus* although the ventralmost rays are not fully developed. Pectoral fins are

TABLE 11.—Measurements (millimeters) of larvae and juveniles of *Sebastes helvomaculatus* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle spine length	Longest dorsal spine length	Longest dorsal ray length	Longest anal spine length	Longest anal ray length
7.7	9.5	4.3	3.2	1.1	1.5	1.2	1.0	2.5	1.6	1.9	0.96	0.64	1.0	3.0	1.0	0	1.0	—	(4)	(5)	(4)	
8.0	9.8	4.4	3.2	0.96	1.5	1.3	1.0	2.8	1.7	2.0	1.0	0.68	1.2	3.3	0.90	0.04	0.90	—	(4)	(5)	(4)	
8.0	9.9	4.6	3.4	1.1	1.4	1.3	1.0	2.6	1.6	1.7	1.0	0.66	1.0	3.3	0.78	0.08	0.78	—	(4)	(5)	(4)	
8.8	10.9	5.2	3.9	1.3	1.4	1.4	1.2	2.9	1.9	2.2	1.1	0.40	1.3	3.6	0.78	0.10	1.2	0.48	(5)	0.80	(4)	
9.9	12.3	5.8	4.1	1.3	1.6	1.5	1.3	3.3	2.6	2.4	1.1	1.2	1.6	4.0	0.80	0.22	1.3	0.56	0.88	1.2	0.60	
10.9	13.4	6.5	4.4	1.5	1.8	1.6	1.4	3.7	2.8	2.6	1.2	1.6	1.7	4.5	0.70	0.22	—	0.62	0.82	1.3	0.76	
[6]12.0	14.9	7.4	4.9	1.6	2.4	1.8	1.5	4.1	3.0	3.0	1.2	1.9	2.0	5.2	0.80	0.24	1.3	0.78	1.1	1.8	1.1	
[6]12.0	14.4	7.1	4.9	1.5	2.6	1.9	1.5	4.3	3.1	3.4	1.3	2.1	2.4	5.2	0.72	0.24	—	0.88	—	1.9	1.2	
[6]13.4	16.8	8.5	5.4	1.6	2.7	2.0	1.6	4.1	3.4	3.3	1.3	2.4	2.9	6.0	0.66	0.30	—	0.82	—	1.9	1.4	
[6]13.4	16.8	8.5	5.6	1.8	2.6	2.0	1.6	4.7	3.6	3.6	1.5	2.4	2.6	5.7	0.72	0.26	1.3	0.72	—	1.9	1.3	
[6]13.6	16.8	8.5	5.8	2.2	2.4	2.0	1.5	4.4	3.3	3.3	1.3	2.2	2.4	6.2	—	0.28	1.1	0.80	1.4	1.9	1.4	
[6]17.8	22.1	10.7	7.5	2.7	3.2	2.4	1.8	5.7	4.5	4.5	1.6	3.4	3.8	7.2	1.0	0.32	—	1.1	2.3	2.6	2.3	
[6]17.9	22.2	11.2	7.3	2.6	2.9	2.4	1.7	5.7	4.2	4.5	1.7	3.1	3.2	8.0	0.80	0.28	1.3	1.1	—	2.8	2.2	
[6]18.4	22.9	11.0	6.7	2.1	3.0	2.5	1.9	5.9	4.3	4.9	1.8	3.2	3.7	7.0	0.96	0.36	1.4	1.1	2.1	—	1.9	
[6]18.4	23.0	11.0	7.2	1.8	3.4	2.7	1.8	5.7	4.4	5.2	1.8	3.4	3.7	7.0	0.70	0.34	1.3	1.1	2.7	3.0	2.6	
[6]18.6	21.1	12.0	8.0	2.7	3.4	2.6	1.9	5.8	4.3	4.8	1.8	3.4	3.4	8.8	0.72	0.24	1.3	1.1	—	2.6	—	
[7]19.8	24.6	12.0	8.2	2.8	3.3	2.8	2.1	6.4	4.6	5.2	1.8	3.1	3.6	8.2	—	0.36	1.3	1.2	—	2.6	2.2	
[7]20.3	25.3	12.8	8.4	2.8	4.0	2.8	2.0	6.2	4.7	5.3	1.8	—	4.1	9.0	0.80	0.34	1.3	1.2	—	3.0	2.0	
[7]21.6	26.4	13.0	8.4	2.5	4.0	2.8	2.0	7.1	5.2	5.7	2.0	—	4.0	8.6	—	0.14	—	1.2	—	3.2	3.0	
[7]22.1	26.4	14.2	8.9	3.0	4.2	3.0	1.9	7.2	5.3	5.9	2.0	3.4	4.4	9.8	0.72	0.26	—	1.4	2.8	3.2	2.7	
[7]22.2	27.7	14.6	9.3	3.0	4.2	3.0	1.9	6.7	5.1	5.9	2.0	4.2	4.4	10.7	0.46	0.32	—	1.3	2.6	3.1	3.1	
[7]22.4	27.7	13.4	8.4	2.6	3.8	3.1	2.0	7.2	5.6	6.0	2.0	4.1	4.8	8.8	—	0.44	1.1	1.3	3.0	3.2	3.2	
[7]23.8	29.1	15.7	9.4	3.1	4.3	2.9	1.9	7.2	5.2	6.4	2.2	3.9	4.3	10.7	0.40	0.30	—	1.2	2.8	3.4	—	
[7]41.6	49.8	26.2	16.5	4.4	7.0	5.7	2.2	11.8	8.8	7.0	3.4	5.6	7.2	16.6	0.18	—	0.42	2.1	4.9	6.1	6.4	
[8]136.4	169	86.0	51.8	14.0	26.7	18.3	6.7	44.0	32.3	37.6	12.0	19.7	30.0	53.8	1.6	—	1.3	5.7	17.4	20.7	27.0	
[8]183	219	118.1	68.1	18.0	35.8	18.9	11.2	63.3	49.4	48.4	18.0	28.2	42.9	74.5	—	—	0.32	7.0	27.6	31.0	31.0	

[1]Usually third or fourth in larvae, fifth or sixth in juveniles
[2]Usually midfin
[3]The second spine
[4]Not formed
[5]Forming
[6]Transforming
[7]Pelagic juvenile
[8]Benthic juvenile

rather long, averaging 24-26% SL during the pelagic period. Depth of the pectoral fin decreases from 12% in flexion larvae to 9% in benthic juveniles.

Pelvic fin spines and developing rays are visible on the 7.7 mm larva. The adult complement of I, 5 is countable on the smallest postflexion larva, 8.8 mm. The relative length of the pelvic fin increases from 14 to 23% SL with development. The pelvic spine, always shorter than the pelvic fin rays, increases from 8% SL in flexion larvae to 18% in transforming larvae and then decreases to 15% in benthic juveniles.

The adult complement of 8 + 7 principal caudal fin rays can be counted on the 7.7 mm preflexion larva. Flexion is completed by 8.8 mm. Superior and inferior secondary caudal rays on two stained juveniles 22.4 and 23.8 mm long, were 12 + 12 and 11 + 11, respectively.

Bases of dorsal and anal fin spines and rays are visible on the 7.7 mm larva. Rays and spines (including "prespines") are fully formed by 9.9 mm and the adult complements can be counted. "Prespines" become spines in specimens >19 mm. The longest dorsal spine increases from 19% HL in postflexion larvae to 37% in benthic juveniles. The longest dorsal ray, always longer than the longest dorsal spine, increases from 23 to 43% HL during development. The longest anal spine increases from 16 to 49% HL.

Spination (Tables 4, 12).—Spines on the left side of the head of the smallest *S. helvomaculatus* (7.7 mm) include the parietal; first and third anterior preopercular spines; second, third, and fourth posterior preopercular spines; postocular; pterotic; inferior posttemporal; and first spine of the superior infraorbital series.

The parietal spine and ridge are deeply serrated in larvae and pelagic juveniles, but the serrations are no longer visible by 41.6 mm. The parietal spine is very long in flexion larvae, averaging 27% HL. Its length decreases with development to 3% HL in benthic juveniles. The much smaller nuchal spine, which appears by 8 mm, averages 2% HL in flexion larvae and increases to 4 or 5% in postflex-

TABLE 12.—Development of spines in the head region of *Sebastes helvomaculatus* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and – denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Opercular Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
7.7	+	–	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.0	+	–	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.0	+	–	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.8	+	–	+	–	+	+	+	+	+	–	+	–	+	–	–	–	+
9.9	–	+	–	–	+	+	+	+	+	–	+	–	+	–	–	–	+
10.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]12.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]12.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]13.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]13.4	+	+	+	–	+	+	+	–	+	–	+	+	+	–	(2)	(2)	+
[1]13.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(2)	(2)	+
[1]17.8	+	+	+	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[1]17.9	+	+	+	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]19.8	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[2]20.3	+	+	+	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[2]21.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[2]22.1	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[2]22.2	+	+	(2)	–	(2)	+	+	+	+	+	+	+	+	–	+	+	+
[2]22.4	+	+	(2)	–	(2)	+	+	+	+	+	+	+	+	–	+	+	+
[2]23.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[3]41.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[4]136.4	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[4]183	+	+	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 12.—Continued.

Standard length (mm)	Infraorbitals: Inferior 1st	Inferior 2d	Inferior 3d	Superior 1st	Superior 2d	Superior 3d	Superior 4th	Nasal	Coronal	Tympanic	Pterotic	Posttemporal Superior	Posttemporal Inferior	Supracleithral	Cleithral
7.7	–	–		+	–	–	–	–	–	–	+	–	+	–	–
8.0	–	–		+	–	–	–	–	–	–	+	+		–	–
8.0	–	–		+	–	–	–	–	–	–	+		+	–	–
8.8	+	+	–	+	–	–	+	(2)	–	–	+	–	+	+	–
9.9	+	+	–	+	–	–	+	(2)	–	–	+	–	+	+	–
10.9	+	+		+	–	–	+	(2)	–	–	+	–	+	+	–
[1]12.0	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[1]12.0	+	+	+	+	–	–	+	+	–	–	+	+	+	+	–
[1]13.4	+	+	–	+	+	–	+	+	–	–	+	+	+	+	–
[1]13.4	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]13.6	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]17.8	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]17.9	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]18.4	+	+		+	+	+	+	+	–	–	+	+	+	+	(2)
[1]18.4	+	+		+	+	+	+	+	–	–	+	+	+	+	–
[1]18.6	+	+		+	+	+	+	+	–	–	+	+	+	+	–
[1]19.8	+	+		+	+	+	+	+	–	–	+	+	+	+	–
[2]20.3	+	+	–	+	+	+	+	+	–	–	(2)	+	+	+	(2)
[2]21.6	+	+	–	+	+	+	+	+	–	–	(2)	+	+	+	(2)
[2]22.1	+	+		+	+	+	+	+	–	–	(2)	+	+	+	(2)
[2]22.2	+	+		+	(2)	+	–	+	–	–	(2)	+	+	+	–
[2]22.4	+	+		+	(2)	(2)	(2)	+	–	–	(2)	+	+	+	+
[2]23.8	+	+	–	+	–	–	–	+	–	–	(2)	+	+	+	+
[3]41.6	–	–	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]136.4	+	+		–	–	–	–	+	–	+	–	+	+	+	+
[4]183	+	+	–	–	–	–	–	+	–	+	–	+	+	+	–

[1]Transforming
[2]Bump indicating beginning of spine formation
[3]Pelagic juvenile
[4]Benthic juvenile

ion, transforming, and pelagic juvenile stages. The nuchal and parietal spines are fused together by the time juveniles are 42 mm long.

The posterior preopercular spine series is prominent in *S. helvomaculatus* larvae. The third spine of the series is weakly serrated in larvae ~8 mm up to pelagic juveniles. It is relatively long in larvae averaging 27 to 31% HL in flexion and postflexion stages. Its length decreases to 2% in benthic juveniles when it is no longer serrated.

Very weak serrations appear on the second and fourth posterior preopercular spines of most larger larvae and smaller pelagic juveniles. All five posterior preopercular spines are present on specimens >8.0 mm. The first and third anterior preopercular spines seen on the smallest larva are no longer visible on specimens >23 mm. The second anterior preopercular spine never develops.

The superior and inferior opercular spines are present on all specimens >8 mm. The interopercular spine is present at 8.8 mm and persists into benthic juveniles. The subopercular spine is present just above the interopercular spine on the largest benthic juvenile, 183 mm.

The supraocular ridge and the anterior margin of the postocular spine are serrated on specimens up to 23.8 mm. The preocular and supraocular spines are first seen as bumps in a 13.4 mm specimen. Serrations are present on the supraocular spine but disappear along with those on the supraocular ridge on larger pelagic juveniles.

The first superior infraorbital spine is visible up to 23 mm. The second superior infraorbital spine appears on specimens 12 to 23 mm. The fourth superior infraorbital spine is present on larvae >8 mm and the third superior infraorbital spine is present on larvae >13.4 mm. The third and fourth spines both disappear by 23 mm. The first and second spines of the inferior infraorbital series are present on all specimens >8 mm but appear only as blunt projections on benthic juveniles. The third inferior infraorbital spine never develops. The nasal spine appears as a bump by 9 mm and becomes strong and sharp during the larval period.

The tympanic spine develops by 41.6 mm and appears as a strong sharp spine on benthic juveniles. The pterotic spine is present on all specimens >41.6 mm. The inferior posttemporal spine is present on all specimens examined but is minute on the two benthic juveniles, 136 and 183 mm, and probably disappears in larger specimens. The supracleithral spine is present on all specimens >8.0 mm. The superior posttemporal appears at 13.4 mm and is present on all larger specimens. Posterior to the opercle the cleithral spine appears on all specimens >19 mm.

Scale Formation.—Lateral line pores first appear anteriorly and are visible on specimens >17 mm. Scale formation begins on pelagic juveniles >23 mm.

Pigmentation.—The smallest larva of *S. helvomaculatus*, 7.7 mm (similar to the 8.0 mm specimen illustrated), has pigment on the head over the brain. Melanophores line the inner tip of the lower jaw. In the abdominal region, an internal melanistic shield is present over the dorsolateral surface of the gut. No other pigment is visible on the body. The pectoral and pelvic fins are fringed with expanded and fused melanophores and have a light scattering of more contracted, elongate melanophores on the fin blades. Both inner and outer pectoral fin base surfaces are unpigmented.

During larval development, pigment over the brain becomes obscured. At 13.4 mm pigment inside the lower jaw disappears. Specimens >17 mm develop two to six internal melanophores dorsally on the opercle.

During the transformation period, 12.0 to 18.6 mm, two or three melanophores may appear just posterior to the orbit on specimens >18 mm. Internal gut pigment increases ventrolaterally reaching the ventral surface of the gut by 17.9 mm. The anterior margin of the cleithrum is usually unpigmented. A patch of 9 to 10 large stellate melanophores appears laterally on the caudal peduncle at 12.0 mm at the beginning of the transformation period. Melanophores are added to this patch until it extends to the dorsal body surface at ≈18 mm. Melanophores in this patch often appear expanded and fused. The pectoral and pelvic fins remain fringed with pigment although this may not be obvious if the fins are frayed. The number of melanophores on the fin blades generally decreases.

During the pelagic juvenile period, 19.8 to 41.6 mm, pigment appears over the head surface, snout, and upper lip of specimens >22 mm. Melanophores are added along the posteroventral margin of the orbit and a patch of melanophores appears just dorsal to the first superior infraorbital spine. The internal pigment patch on the operculum remains distinguishable. Internal gut pigment becomes increasingly obscured by musculature. A single saddle of melanophores develops on the dorsal surface of the body over the nape and beneath the spinous dorsal fin anterior to dorsal spine XI. The first melanophores generally appear there at the onset of the pelagic juvenile stage, although a few may develop earlier. This saddle extends ventrolaterally from the nape to the vicinity of the supracleithral spine and from the spinous dorsal fin halfway to the lateral line by 22

mm. By 41.6 mm small external melanophores cover all but the ventralmost one-fourth of the abdominal region including most of the pectoral fin base and the dorsal one-fourth of the gut region. The dorsal saddle and internal gut pigmentation still appear as more darkly pigmented areas. The caudal peduncle patch expands to the dorsal and ventral body margins. Specimens >20 mm have a few melanophores extending anteriorly from the peduncle patch along the dorsal body margin under the posteriormost dorsal rays. By 41.6 mm the entire tail region of the body is also covered with small external melanophores, although the caudal peduncle patch and dorsal midline melanophores remain visible. Pectoral and pelvic fins lose all pigment by 41.6 mm, except for a patch of small melanophores on the base of the central pectoral rays. The spinous dorsal fin becomes completely covered with small melanophores by 41.6 mm and small melanophores cover the proximal one-fourth of the soft dorsal fin. Small melanophores extend onto the bases of the caudal fin rays by 41.6 mm.

Melanistic pigment is inconspicuous on the benthic juveniles examined, 136 and 183 mm. The caudal peduncle pigment patch is no longer visible.

Occurrence (Figures 14, 15).—*Sebastes helvomaculatus* ranges from Coronado Bank, off San Diego, Calif., to Albatross Bank, Gulf of Alaska, and occurs in depths from 133 to 456 m (Chen 1971). It is apparently primarily a deepwater species judging by some of the older common names given to it, "deep-water scacciatale" and "deep-water scratch-tail" (Phillips 1957). The largest numbers and smallest larvae were taken 83 and 120 km off Newport beyond the continental shelf break. Most pelagic juveniles were taken at the same locations as the larvae, probably reflecting the increased sampling effort in that area. One benthic juvenile, 136 mm, was taken in an otter trawl at a depth of 370 m (lat. 44°47.9′ N, long. 124°40.9′ W). A second juvenile, 183 mm, was collected after a seismic profiling explosion on Stonewall Bank (≈lat. 44°30′ N, long. 124°25′ W).

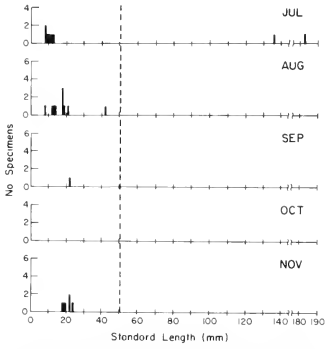


FIGURE 15.—Seasonal occurrence of larvae and juveniles of *Sebastes helvomaculatus* off Oregon. Data from 1961 to 1976 combined. Dashed line separates pelagic and benthic stages.

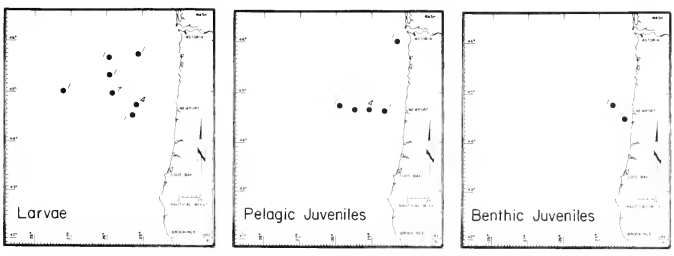


FIGURE 14.—Number of specimens and location of capture of larvae and juveniles of *Sebastes helvomaculatus* off Oregon (1961-76) described in this paper.

Based on examination of gonads, Westrheim (1975) reported that parturition of *S. helvomaculatus* takes place primarily in June from Oregon to British Columbia. We took small larvae >10 mm only in July and August. Pelagic juveniles were captured in August, September, and November. The two benthic juveniles were taken in July.

Adults of *S. helvomaculatus* are uncommon in Oregon trawl landings (Niska 1976). They ranked 9th and 16th in biomass in trawl surveys on the Oregon continental shelf and 8th on the continental slope together with *S. elongatus* and *S. zacentrus* (Demory et al. 1976). Larvae and juveniles were not common in our collections.

COMPARISONS (TABLE 13)

Prior to this paper, developmental series of 7 of the 69 northeast Pacific (including the Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S.* sp. Gulf Type A, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, and *S. paucispinis* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978). While pelagic stages of these species exhibit some similarities to the three described by us, they also differ in a number of characters. The most notable of these are discussed here in a comparative sense.

Flexion and postlarvae of *S. pinniger* are quite deep bodied (38-40% SL) although body depth at the pectoral fin base decreases considerably (33% SL) by the pelagic juvenile stage. Larvae and juveniles of *S. melanostomus* are also deep bodied. Pelagic stages of *S. jordani* are comparatively slender (17-24% SL). Prior to completion of notochord flexion, *S. paucispinis* is also relatively slender bodied. Pelagic stages of *S. crameri*, *S. helvomaculatus*, *S. levis*, and *S. macdonaldi* are somewhat intermediate in body depth. Snout to

TABLE 13.—Morphometric comparison of larvae and juveniles of nine species of *Sebastes* from the northeast Pacific. Values are mean percentages of body proportions related to standard length (SL) or head length (HL). Numbers in italics represent values for two developmental stages combined

Item	*S. cortezi*[1]	*S. crameri*	*S.* Gulf Type A[1]	*S. helvomaculatus*	*S. jordani*[1]	*S. levis*[1]	*S. macdonaldi*[1]	*S. melanostomus*[1]	*S. paucispinis*[1]	*S. pinniger*
Body depth at pectoral fin base SL										
Preflexion	—	—	—	—	17	—	23	—	20	—
Flexion	—	32	—	33	21	28	32	36	23	40
Postflexion	—	32	—	33	*24*	*34*	*34*	39	30	38
Transforming	—	32	—	33						36
Pelagic juvenile	—	33	—	31	22	35	31	37	27	33
Benthic juvenile	—	34	—	33	—	—	—	—	—	35
Snout to anus length SL										
Preflexion	—	—	—	—	36	—	42	—	41	—
Flexion	—	54	—	56	42	49	52	57	45	59
Postflexion	—	60	—	59	*51*	59	60	59	57	60
Transforming	—	61	—	62						61
Pelagic juvenile	—	62	—	63	53	63	64	64	62	61
Benthic juvenile	—	65	—	64	—	—	—	—	—	64
Pectoral fin length SL										
Preflexion	7-9	—	6-9	—	7	9	8	—	—	—
Flexion	9-12	17	—	24	8	35	13	20	27	25
Postflexion	*21*	21	20	24	11	*45*	*19*	22	36	25
Transforming		27	—	26	20					27
Pelagic juvenile	23	32	—	27	22	41	30	26	28	26
Benthic juvenile	—	30	—	27	—	—	—	—	—	24
Pelvic fin length SL										
Preflexion	—	—	—	—	—	—	4	—	—	—
Flexion	—	7	—	14	1	6	6	12	14	14
Postflexion	—	15	—	16	*9*	*21*	*14*	*16*	35	17
Transforming	—	21	—	19						23
Pelagic juvenile	—	21	—	19	14	24	22	20	25	22
Benthic juvenile	—	21	—	23	—	—	—	—	—	21
Parietal spine length HL										
Preflexion	—	—	—	—	—	—	—	—	—	—
Flexion		6		27	—	—		—	—	24
Postflexion	*21-22*	7	*25-34*	18	—	—	*20-23*	—	—	20
Transforming	—	6	—	13	—	—	—	—	—	10
Pelagic juvenile	—	3	—	6	—	—	—	—	—	7
Benthic juvenile	—	—	—	3	—	—	—	—	—	—
Preopercular spine length HL										
Preflexion	—	—	—	—	—	—	—	—	—	—
Flexion	—	18	—	27	—	—		—	—	34
Postflexion	—	17	—	31	—	—	*35*	—	—	32
Transforming	—	18	—	20	—	—	—	—	—	24
Pelagic juvenile	—	12	—	12	—	—	—	—	—	13
Benthic juvenile	—	7	—	2	—	—	—	—	—	5

[1]Values from Moser et al. (1977) and Moser and Ahlstrom (1978)

anus distance is markedly shorter in larvae and juveniles of *S. jordani* (36-53% SL) compared with the other species.

The pectoral fins in *S. jordani* remain comparatively short (7-22% SL) during pelagic development while those of *S. levis* attain an exceptional size (to 45% SL). Late larval stages of *S. paucispinis* also have outstandingly long pectoral fins (36% SL). Fin lengths among the other species are intermediate by comparison and vary to a lesser degree during development. The pelvic fins of *S. paucispinis* also become extraordinarily long (35% SL) during the late larval period whereas those of *S. jordani* remain relatively short.

Parietal spine length varies among species with the largest spines appearing in early larvae of *S. helvomaculatus* (27% HL) and *S.* sp. Gulf Type A (25-34% HL). This spine is noticeably short on *S. crameri* (3-7% HL) during the entire pelagic phase. The third preopercular spine is outstandingly long on early larvae of *S. macdonaldi* (35% HL) and *S. pinniger* (34% HL) but is comparatively short on *S. crameri* (17% HL) as is the parietal.

Pigmentation on the paired fins varies from the unpigmented condition in *S. jordani* to the heavily pigmented fins of *S. macdonaldi* and *S. crameri*. The pectoral fins of *S. cortezi* are pigmented at the fin base but not the outer margin, while pigment is primarily concentrated on the outer margin of the fins in *S. paucispinis*, *S. levis*, and *S. helvomaculatus* at least during the early pelagic period. Pectoral fins of *S. pinniger*, *S. melanostomus*, and *S.* sp. Gulf Type A are lightly pigmented.

General body pigmentation differs among the species considered. Larvae of *S. pinniger* have a characteristic lack of body pigment. A patch of nape pigment develops early in *S. crameri* and *S. macdonaldi*, appearing more pronounced in the former species. Postflexion larvae of both *S. crameri* and *S. macdonaldi* develop pigment on the entire spinous dorsal fin. A characteristic black blotch develops on the posterior portion of the first dorsal fin in pelagic juveniles of *S. pinniger*. Larvae of *S. melanostomus*, *S. paucispinis*, and *S. macdonaldi* have a characteristically low number of ventral midline melanophores, 4 to 11 (mean 8), 6 to 14 (mean 9), and 6 to 14 (mean 8), respectively. A patch of pigment forms on the caudal peduncle of *S. helvomaculatus*, *S. paucispinis*, *S. jordani*, and *S. cortezi*. The form of the patch varies with the species and is most pronounced in *S. helvomaculatus*. One characteristic melanophore appears at the base of the caudal fin in *S. cortezi*, while melanophores form a line of pigment at the base of the caudal fin in *S. jordani*, but not in any of the other species.

Pelagic juveniles of *S. helvomaculatus* develop only one melanistic pigment saddle beneath the spinous dorsal fin. Five distinct saddles form on *S. macdonaldi*, *S. crameri*, *S. levis*, *S. paucispinis*, and *S. pinniger* in comparable locations on the body although a more blotchy pattern develops on *S. pinniger*. On *S. melanostomus*, three pronounced melanistic bars develop on the body. Apparently no obvious saddles or bars develop on pelagic juveniles of *S. jordani* or *S. cortezi*.

These comparisons together with distinguishing features of each species given by us, Moser (1972), Moser et al. (1977), and Moser and Ahlstrom (1978), and range of occurrence should aid in identification of all but the smallest larvae. As additional species are described, such comparisons may also provide insight into relationships within the genus *Sebastes*.

ACKNOWLEDGMENTS

We thank H. Geoffrey Moser for helpful advice and for the use of unpublished data on color pattern in a live juvenile of *S. crameri*. Stuart G. Poss offered useful advice on head spine terminology. During the course of this study the following people provided helpful information on *Sebastes* spp.: Carl Bond, Jerry Butler, William N. Eschmeyer, Colin Harris, Michael Hosie, Andy Lamb, Bruce M. Leaman, Alex E. Peden, Jay C. Quast, David Stein, Arthur D. Welander, Sigurd J. Westrheim, Norman J. Wilimovsky. Range Bayer, Robert A. Behrstock, Carl Bond, Jerry Butler, Colin Harris, Michael Hosie, Robert Lea, Lawrence Moulton, and Alex Peden provided additional specimens of *Sebastes* to examine. Special thanks are extended to William G. Pearcy for allowing us to use his extensive midwater trawl collections from waters off Oregon. Lo-Chai Chen, H. Geoffrey Moser, Stuart G. Poss, and Sigurd J. Westrheim reviewed an earlier draft of the manuscript. This research was supported by a 1-yr (16 June 1976-15 June 1977) contract No. 03-6-208-35343.

LITERATURE CITED

AHLSTROM, E. H.
1961 Distribution and relative abundance of rockfish

(*Sebastodes* spp.) larvae off California and Baja California. Rapp P.-V. Reun. Cons. Int. Explor. Mer 150:169-176.

1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10:31-52.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.

1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. 6, 149 p.

BARSUKOV, V. V.

1973. A systematic analysis of the group *Sebastes wakiya*–*S. paradoxus*–*S. steindachneri*. Communication 2 (containing a redescription of *S. wakiya*). J. Ichthyol. (Engl. Transl. Vopr. Ikhtiol.) 13:824-833.

CHEN, L.-C.

1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr., Univ. Calif. 18, 115 p.

1975. The rockfishes, genus *Sebastes* (Scorpaenidae), of the Gulf of California, including three new species, with a discussion of their origin. Proc. Calif. Acad. Sci. 40:109-141.

DELACY, A. C., C. R. HITZ, AND R. L. DRYFOOS.

1964. Maturation, gestation, and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Wash. Dep. Fish., Fish. Res. Pap. 2(3):51-67.

DEMORY, R. L., M. J. HOSIE, N. TEN EYCK, AND B. O. FORSBERG.

1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl., Completion Rep., July 1, 1971 to June 30, 1975, 49 p.

EFREMENKO, V. N., AND L. A. LISOVENKO.

1970. Morphological features of intraovarian and pelagic larvae of some *Sebastodes* species inhabiting the Gulf of Alaska. *In* P. A. Moiseev (editor), Soviet fisheries investigations in the northeast Pacific. Part V, p. 267-286. (Transl. Isr. Program Sci. Transl.; available Clearinghouse Fed. Sci. Tech. Inf., Springfield, Va., as TT71-50127).

EIGENMANN, C. H.

1892. The fishes of San Diego, California. Proc. U.S. Natl. Mus. 15:123-178.

FOLLETT, W. I., AND D. G. AINLEY.

1976. Fishes collected by pigeon guillemots, *Cepphus columba* (Pallas), nesting on Southeast Farallon Island, California. Calif. Fish Game 62:28-31.

HART, J. L.

1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

LEA, R. N., AND J. E. FITCH.

1972. *Sebastes rufinanus*, a new scorpaenid fish from Californian waters. Copeia 1972:423-427.

MATSUBARA, K.

1943. Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy. I and II. Trans. Sigenkagaku Kenkyusyo, Tokyo, 486 p.

MERKEL, T. J.

1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. Calif. Fish Game 43:249-270.

MILLER, D. J., AND R. N. LEA.

1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MORRIS, R. W.

1956. Early larvae of four species of rockfish, *Sebastodes*. Calif. Fish Game 42:149-153.

MOSER, H. G.

1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.

1972. Development and geographic distribution of the rockfish, *Sebastes macdonaldi* (Eigenmann and Beeson, 1893), family Scorpaenidae, off southern California and Baja California. Fish. Bull., U.S. 70:941-958.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP.

1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.

MOSER, H. G., AND E. H. AHLSTROM.

1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.

NISKA, E. L.

1976. Species composition of rockfish in catches by Oregon trawlers 1963-71. Oreg. Dep. Fish Wildl., Inf. Rep. 76-7, 80 p.

PACIFIC MARINE FISHERIES COMMISSION.

1964-1976. Data series. Bottom or trawl fish section. Pac. Mar. Fish. Comm., Portland, Oreg., p. 1-472, 500-510.

PHILLIPS, J. B.

1957. A review of the rockfishes of California (family Scorpaenidae). Calif. Dep. Fish Game, Fish Bull. 104, 158 p.

1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

POWELL, D. E., D. L. ALVERSON, AND R. LIVINGSTONE, JR.

1952. North Pacific albacore tuna exploration—1950. U.S. Fish Wildl. Serv., Fish. Leafl. 402, 56 p.

PRITCHARD, A. L., AND A. L. TESTER.

1944. Food of spring and coho salmon in British Columbia. Fish. Res. Board Can. Bull. 65, 23 p.

QUAST, J. C., AND E. L. HALL.

1972. List of fishes of Alaska and adjacent waters with a guide to some of their literature. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-658, 47 p.

RICHARDSON, S. L.

1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution and seasonality January 1971 to August 1972. Oreg. State Univ. Sea Grant Coll. Prog. Publ. ORESU-T-77-003, 73 p.

RICHARDSON, S. L., AND W. G. PEARCY.

1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

ROSENBLATT, R. H., AND L.-C. CHEN.

1972. The identity of *Sebastes babcocki* and *Sebastes rubrivinctus*. Calif. Fish Game 58:32-36.

SILLIMAN, R. P.

1941. Fluctuations in the diet of the chinook and silver salmons (*Oncorhynchus tschawytscha* and *O. kisutch*) off Washington, as related to the troll catch of salmon. Copeia 1941:80-87.

SNYTKO, V. A., AND N. S. FADEEV.

1974. Data on distribution of some species of sea perches along the Pacific coast of North America during the sum-

mer - autumn season. Doc. Subm. Canada-USSR Meet. on Fish. in Moscow-Baturni, USSR, November 1974, 14 p. (Transl. 3436, Can. Transl. Ser.)

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.

VERHOEVEN, L. A. (editor).
1976. 28th annual report of the Pacific Marine Fisheries Commission for the year 1975. Pac. Mar. Fish. Comm., Portland, Oreg., 46 p.

WALDRON, K. D.
1968. Early larvae of the canary rockfish, *Sebastodes pinniger*. J. Fish. Res. Board Can. 25:801-803.

WALES, J. H.
1952. Life history of the blue rockfish, *Sebastodes mystinus*. Calif. Fish Game 38:485-498.

WEITZMAN, S. H.
1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyol. Bull. 8(1), 77 p.

WESTRHEIM, S. J.
1966. Northern range extensions for three species of rockfish (*Sebastes flavidus*, *S. paucispinis* and *S. pinniger*) in the North Pacific Ocean. J. Fish. Res. Board Can. 23:1469-1471.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

WESTRHEIM, S. J., AND H. TSUYUKI.
1967. *Sebastodes reedi*, a new scorpaenid fish in the northeast Pacific Ocean. J. Fish. Res. Board Can. 24:1945-1954.
1972. Synonymy of *Sebastes caenaematicus* with *Sebastes borealis*, and range extension record. J. Fish. Res. Board Can. 29:606-607.

WHITNEY, J. P.
1893. Salmon in salt water. Forest Stream 41:120-121.

YOUNG, P. H.
1969. The California partyboat fishery 1947-1967. Calif. Dep. Fish Game, Fish Bull. 145, 91 p.

APPENDIX TABLE 1.—Ranges of eastern North Pacific species of *Sebastes*.[1] This list does not include one new species being described by Lea and Fitch (Chen 1975). Asterisk indicates species in the subgenus *Sebastomus*.

Species	Southern range limit	Gulf of Calif	Baja	South. Calif	North. Calif	Oreg	Wash	B.C.	S.E. Alaska	Gulf of Alaska	Aleutians	Bering Sea	Japan	Northern range limit
S. aleutianus	Monterey, Calif													Aleutians and Japan
S. alutus	La Jolla, Calif													Bering Sea and Japan
S. atrovirens	Pt. San Pablo, Baja													Timber Cove, Sonoma Co., Calif
S. auriculatus	Hipolito Bay, Baja													S.E. Alaska
S. aurora	San Diego, Calif													Amphitrite Pt., Vancouver I., B.C.
S. babcocki	San Diego, Calif													Amchitka I., Alaska
S. borealis	Eureka, Calif													S.E. Kamchatka
S. brevispinis	Santa Barbara I., Calif													Bering Sea
S. carnatus	San Roque, Baja													Eureka, Calif
S. caurinus[2]	San Benito I., Baja													Gulf of Alaska
S. chlorostictus	Cedros I., Baja													Copalis Head, Wash.
S. chrysomelas	Natividad I., Baja													Eureka, Calif.
S. ciliatus	Dixon Entrance, B.C.													Bering Sea
S. constellatus	Thetis Bank, Baja													San Francisco, Calif.
S. cortezi	Gulf of Calif.													Gulf of Calif.
S. crameri	Santa Catalina I., Calif.													Bering Sea
S. dalli	Sebastian Viscaino Bay, Baja													San Francisco, Calif.
S. diploproa	San Martin I., Baja													Alaska Peninsula
S. elongatus	Cedros I., Baja													Green I., Montague I., Gulf of Alaska
S. emphaeus	Punta Gorda, Calif.[3]													Kenai Peninsula, Gulf of Alaska
S. ensifer	Ranger Bank, Baja													San Francisco, Calif.
S. entomelas	Todos Santos Bay, Baja													Kodiak, Alaska
S. eos	Sebastian Viscaino Bay, Baja													San Francisco, Calif. (?Wash.)
S. exsul	Gulf of Calif.													Gulf of Calif.
S. flavidus	San Diego, Calif.													Kodiak, Alaska
S. gilli	Ensenada, Baja													Monterey, Calif.
S. goodei	Magdalena Bay, Baja													Cape Scott, Vancouver I., B.C.
S. helvomaculatus	Coronado Bank, Calif.													Albatross Bank, Gulf of Alaska
S. hopkinsi	Guadalupe I., Baja													Farallon I., Calif.
S. jordani	Cape Colnett, Baja													Le Perouse Bank, Vancouver I., B.C.
S. lentiginosus	Los Coronados I., Baja													Santa Catalina I., Calif.
S. levis	Ranger Bank, Baja													Usal, Mendocino Co., Calif.
S. macdonaldi	Gulf of Calif.													Pt. Sur, Calif.
S. maliger	Pt. Sur, Calif.													Gulf of Alaska
S. melanops	Paradise Cove, Baja													Amchitka I., Alaska
S. melanostomus	Cedros I., Baja													Wash. (?Bering Sea)
S. miniatus	San Benito I., Baja													Vancouver I., B.C.
S. mystinus	Pt. Santo Tomas, Baja													B.C. (?Bering Sea)
S. nebulosus	San Miguel I., Baja													S.E. Alaska
S. nigrocinctus	Pt. Buchon, Baja													S.E. Alaska
S. nohus	Uncle Sam Bank, Baja													Guadalupe I., Baja.
S. ovalis	Cape Colnett, Baja													San Francisco, Calif.
S. paucispinis	Pt. Blanco, Baja													Kodiak, Alaska
S. penduculatus	Gulf of Calif.													Gulf of Calif.
S. phillipsi	Newport, Calif.													Monterey Bay, Calif.
S. pinniger	Cape Colnett, Baja													S.E. Alaska
S. polyspinis	S.E. Alaska													Eastern Kamchatka
S. proriger	San Diego, Calif.													Bering Sea
S. rastrelliger	Playa Mario Bay, Baja													Yaquina Bay, Oreg.
S. reedi	Crecent City, Calif.													Sitka, Alaska
S. rosaceus	Turtle Bay, Baja													San Francisco, Calif. (?Puget Sd., Wash.)
S. rosenblatti	Ranger Bank, Baja													Avila, Calif. (?San Francisco, Calif.)
S. ruberrimus	Ensenada, Baja													Gulf of Alaska
S. rubrivinctus	Cape Colnett, Baja													San Francisco, Calif.
S. rufinanus	San Clemente I., Calif.													San Clemente I., Calif.
S. rufus	Guadalupe I. Baja													Mad River, Calif.
S. saxicola	Sebastian Viscaino Bay, Baja													S.E. Alaska
S. semicinctus	Sebastian Viscaino Bay, Baja													Pt. Pinos, Monterey Co., Calif.
S. serranoides	San Benito I. Baja													Redding Rock, Del Norte Co., Calif.
S. serriceps	Cedros I., Baja.													San Francisco, Calif.
S. simulator	Guadalupe I. Baja													San Pedro, Calif. (?Pt. Conception, Calif.)
S. simensis	Gulf of Calif.													Gulf of Calif.
S. spinorbis	Gulf of Calif.													Gulf of Calif.
S. umbrosus	Pt. San Juanico, Baja													Pt. Conception, Calif.
S. variegatus	Queen Charlotte Sd., B.C.													Unimak Pass, Aleutian I.
S. varispinis	Gulf of Calif.													Gulf of Calif.
S. wilsoni	Cortez Bank, Calif.													S.E. Alaska
S. zacentrus	San Diego, Calif.													Sanak I., Aleutians

[1]Compiled from Bailey et al. (1970), Chen (1971), Lea and Fitch (1972), Miller and Lea (1972), Quast and Hall (1972), Rosenblatt and Chen (1972), Barsukov (1973), Hart (1973), and Chen (1975) and original data for *S. emphaeus*. No records from the Sea of Okhotsk.

[2]Includes *S. vexillaris* (Chen 1975, W. N. Eschmeyer, Senior Curator for Research, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. commun. November 1976).

[3]Based on data obtained during this study.

APPENDIX TABLE 2.—Chart showing interorbital curvature and presence or absence of the supraocular spine for rockfishes (*Sebastes* spp.) occurring off Oregon.[1] x indicates usual condition; o indicates occasional occurrence.

	Interorbital					Interorbital			
	Flat-convex		Concave			Flat-convex		Concave	
	Supraocular spine		Supraocular spine			Supraocular spine		Supraocular spine	
Species	Present	Absent	Present	Absent	Species	Present	Absent	Present	Absent
S. aleutianus	x				*S. jordani*		x		
S. alutus	x	o			*S. maliger*	o	x	o	x
S. auriculatus		x			*S. melanops*		x		
S. aurora	x		x		*S. melanostomus*	x		x	
S. babcocki				x	*S. miniatus*	x			
S. borealis	x		x		*S. mystinus*		x		
S. brevispinis	o	x			*S. nebulosus*				x
S. caurinus		x		x	*S. nigrocinctus*			o	x
S. chlorostictus			x		*S. paucispinis*		x		
S. crameri	x				*S. pinniger*	x			
S. diploproa		x		x	*S. proriger*		x		
S. elongatus				x	*S. rastrelliger*		x		
S. emphaeus		x			*S. reedi*	x	o		
S. entomelas	o	x			*S. rosaceus*[2]			x	
S. eos[2]			x		*S. ruberrimus*			x	
S. flavidus		x			*S. saxicola*		x		x
S. goodei		x			*S. wilsoni*	o	x	o	x
S. helvomaculatus			x		*S. zacentrus*	o	x	o	x

[1]Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 3.—Numbers of dorsal, anal, and pectoral fin soft rays for rockfishes (*Sebastes* spp.) occurring off Oregon.[1] x indicates usual numbers, o indicates occasional occurence.

	Dorsal fin rays							Anal fin rays							Pectoral fin rays								
Species	11	12	13	14	15	16	17	5	6	7	8	9	10	11	15	16	17	18	19	20	21	22
S. aleutianus		o	x	x	o				o	x	o						o	x	x			
S. alutus			o	x	x	x	x		o	o	x	x			o	o	o	x	o			
S. auriculatus		o	x	o	o			o	o	x	o				o	o	o	x	o			
S. aurora		o	x	o				o	x							o	o	o				
S. babcocki			o	x	o				x	x							o	o	x	o		
S. borealis		o	x	o	o				o	x	o						o	o	o	o		
S. brevispinis				o	o	o	o			x	o					o	o	o				
S. caurinus	o	o	x	o				o	x	o						o	x	o				
S. chlorostictus	o	x	o	o	o			o	x	o						o	x	o				
S. crameri		o	x	x				o	o	x								o	x	o		
S. diploproa	o	x	x	o					x	x	o						o	x	o			
S. elongatus		o	x	o					x	o						x	x	o				
S. emphaeus				x	x					x	o						x	o				
S. entomelas				o	x	x					x	o	o				x	o	o			
S. eos[2]	o	x	x						x	o							o	o				
S. flavidus				x	x	o				o	x	o					o	x	o			
S. goodei			o	x							x	o				o	x	o				
S. helvomaculatus		o	x	o					x	o					o	x	o	o				
S. jordani			o	o	o	o					o	x	x	o					x	x	x	o
S. maliger		o	x	x					o	x						o	x					
S. melanops			o	x	x	o				o	x	o						o	x	o		
S. melanostomus		o	x	o	o				o	x	o						o	o	o	o		
S. miniatus			o	x	o				o	x	o					o	o	x				
S. mystinus				x	x	o					x	x	o			o	x	x				
S. nebulosus		o	x	o					o	x	o					o	o	x				
S. nigrocinctus			o	x	o				o	x								o	o	o		
S. paucispinis			o	x	o						o	x	o		x	o						
S. pinniger			o	x	x					x						o	x	o				
S. proriger			o	x	x				o	x						o	x	o				
S. rastrelliger		o	x	o					x									o	o	o		
S. reedi			o	x	x					x	x							o	x	o		
S. rosaceus[2]	o	o	x	o				o	x	o						o	x	o				
S. ruberrimus			o	o	x	o		o	o	x	o							o	x	o		
S. saxicola		o	x	o				o	o	x	o				o	x	o					
S. wilsoni			x	x					x	o						o	x					
S. zacentrus			o	x	x				o	x	o						x	o	o			

[1]Compiled from Phillips (1957), Westrheim (1966), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 4.—Total numbers of gill rakers on first gill arch for rockfishes (*Sebastes* spp.) occurring off Oregon.[1]

Species	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
S. aleutianus									x	x	x	x	x	x												
S. alutus									x	x	x	x	x	x	x	x	x									
S. auriculatus				x	x	x	x	x	x																	
S. aurora			x	x	x	x	x																			
S. babcocki								x	x	x	x	x														
S. borealis						x	x	x	x	x																
S. brevispinis												x	x	x	x											
S. caurinus					x	x	x	x	x	x	x															
S. chlorostictus										x	x	x	x	x	x											
S. crameri								x	x	x	x	x	x													
S. diplopora										x	x	x	x	x	x											
S. elongatus							x	x	x	x	x	x														
S. emphaeus																		x	x	x	x	x	x	x		
S. entomelas													x	x	x	x										
S. eos[2]					x	x	x	x	x	x																
S. flavidus											x	x	x	x	x	x	x									
S. goodei													x	x	x	x	x	x								
S. helvomaculatus							x	x	x	x	x	x														
S. jordani																				x	x	x	x	x	x	x
S. maliger								x	x	x	x	x														
S. melanops												x	x	x	x	x	x									
S. melanostomus						x	x	x	x	x	x	x	x	x												
S. miniatus														x	x	x	x	x	x	x	x	x				
S. mystinus												x	x	x	x	x	x									
S. nebulosus					x	x	x	x	x	x																
S. nigrocinctus						x	x	x	x	x																
S. paucispinis							x	x	x	x																
S. pinniger																			x	x	x	x	x	x		
S. proriger															x	x	x	x	x	x	x	x				
S. rastrelliger	x	x	x	x																						
S. reedi									x	x	x	x	x	x	x											
S. rosaceus[2]								x	x	x	x	x	x													
S. ruberrimus				x	x	x	x	x	x																	
S. saxicola										x	x	x	x	x												
S. wilsoni																		x	x	x	x	x				
S. zacentrus									x	x	x	x	x	x	x											

[1]Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.

[2]Species may be rare off Oregon.

APPENDIX TABLE 5.—Numbers of lateral line pores for rockfishes (*Sebastes* spp.) occurring off Oregon.[1]

Species	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
S. aleutianus			x	x	x	x	x	x																													
S. alutus																		x	x	x	x	x	x	x	x	x	x										
S. auriculatus																x	x	x	x	x	x	x	x														
S. aurora	x	x	x	x	x																																
S. babcocki															x	x	x	x	x	x	x	x															
S. borealis		x	x	x	x	x																															
S. brevispinis																		x	x	x	x	x	x	x	x	x											
S. caurinus										x	x	x	x	x	x	x	x	x	x																		
S. chlorostictus									x	x	x	x	x	x	x	x	x																				
S. crameri														x	x	x	x	x	x	x	x	x	x	x													
S. diploproa							x	x	x	x	x	x	x	x	x	x	x																				
S. elongatus														x	x	x	x	x	x																		
S. emphaeus													x	x	x	x	x	x	x	x	x																
S. entomelas																										x	x	x	x	x	x	x					
S. eos[2]								x	x	x	x	x	x	x	x	x																					
S. flavidus																						x	x	x	x	x	x	x	x	x	x	x	x	x		
S. goodei																					x	x	x	x	x	x	x	x	x	x	x					
S. helvomaculatus								x	x	x	x	x	x	x	x	x	x	x	x																		
S. jordani																										x	x	x	x	x	x	x	x				
S. maliger									x	x	x	x	x	x	x	x	x	x	x	x	x																
S. melanops																				x	x	x	x	x	x	x	x										
S. melanostomus			x	x	x	x	x																														
S. miniatus														x	x	x	x	x	x	x																	
S. mystinus																		x	x	x	x	x	x	x	x	x	x	x	x	x						
S. nebulosus											x	x	x	x	x	x	x	x	x	x	x																
S. nigrocinctus															x	x	x	x	x	x	x	x	x	x													
S. paucispinis																																					
S. pinniger														x	x	x	x	x	x																		
S. proriger																						x	x	x	x	x	x	x									
S. rastrelliger																x	x	x	x	x																	
S. reedi																						x	x	x	x	x	x	x	x								
S. rosaceus[2]										x	x	x	x	x	x	x	x	x	x	x																	
S. ruberrimus													x	x	x	x	x	x	x	x																	
S. saxicola										x	x	x	x	x	x	x																					
S. wilsoni											x	x	x	x	x	x	x	x	x																		
S. zacentrus													x	x	x	x	x	x	x																		

[1]Compiled from Phillips (1957), Westrheim (1966), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 6.—Number of diagonal scale rows below the lateral line for rockfishes (*Sebastes* spp.) occurring off Oregon [1]

Species	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
S. aleutianus											x	x	x	x	x	x	x	x	x									
S. alutus													x	x	x	x	x	x	x									
S. aurriculatus										x	x	x	x	x	x	x												
S. aurora						x	x	x	x	x	x	x	x	x	x													
S. babcocki																												
S. borealis	x	x	x	x	x	x	x	x	x	x	x																	
S. brevispinis																							x	x	x	x	x	x
S. caurinus				x	x	x	x	x	x	x	x	x	x	x	x													
S. chlorostictus								x	x	x	x	x	x															
S. crameri													x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
S. diploproa																		x	x	x	x	x						
S. elongatus							x	x	x	x	x	x	x	x	x	x	x	x	x	x								
S. emphaeus						x	x	x	x	x	x	x	x	x	x													
S. entomelas																							x	x	x	x	x	x
S. eos[2]						x	x	x	x	x	x	x	x															
S. flavidus																				x	x	x	x	x	x			
S. goodei																										x	x	x
S. helvomaculatus							x	x	x	x	x	x	x															
S. jordani																												
S. maliger			x	x	x	x	x	x	x	x																		
S. melanops															x	x	x	x	x	x								
S. melanostomus										x	x	x	x	x	x													
S. miniatus										x	x	x	x															
S. mystinus															x	x	x	x	x	x	x							
S. nebulosus								x	x	x	x	x	x															
S. nigrocinctus									x	x	x	x	x	x	x	x	x	x										
S. paucispinis																												
S. pinniger								x	x	x	x	x	x	x	x													
S. proriger																				x	x	x	x	x	x			
S. rastrelliger										x	x	x	x	x	x													
S. reedi																										x	x	x
S. rosaceus[2]						x	x	x	x	x	x	x	x															
S. rubberrimus										x	x	x	x	x	x													
S. saxicola								x	x	x	x	x	x	x	x	x	x	x										
S. wilsoni										x	x	x	x	x	x													
S. zacentrus								x	x	x	x	x	x	x	x													

[1] Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.

[2] Species may be rare off Oregon.

APPENDIX TABLE 6.—Continued

Species	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
S. aleutianus																											
S. alutus																											
S. aurriculatus																											
S. aurora																											
S. babcocki																											
S. borealis																											
S. brevispinis	x	x	x	x	x	x	x																				
S. caurinus																											
S. chlorostictus																											
S. crameri																											
S. diploproa																											
S. elongatus																											
S. emphaeus																											
S. entomelas	x	x	x																								
S. eos[2]																											
S. flavidus																											
S. goodei	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x												
S. helvomaculatus																											
S. jordani		x	x	x	x	x	x																				
S. maliger																											
S. melanops																											
S. melanostomus																											
S. miniatus																											
S. mystinus																											
S. nebulosus																											
S. nigrocinctus																											
S. paucispinis									x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
S. pinniger																											
S. proriger																											
S. rastrelliger																											
S. reedi	x	x	x	x																							
S. rosaceus[2]																											
S. rubberrimus																											
S. saxicola																											
S. wilsoni																											
S. zacentrus																											

AERIAL SURVEY OF THE BOTTLENOSED DOLPHIN, *TURSIOPS TRUNCATUS*, AND THE WEST INDIAN MANATEE, *TRICHECHUS MANATUS*, IN THE INDIAN AND BANANA RIVERS, FLORIDA

STEPHEN LEATHERWOOD[1]

ABSTRACT

Aerial surveys were conducted of the Indian and Banana Rivers, eastern Florida, to estimate numbers of bottlenosed dolphins and West Indian manatees. Thirty-nine east-west transects, 4.63 km (2.5 n mi) apart, were flown on six successive days in August. Observers at inlets from the ocean inventoried dolphins and manatees entering or leaving the river during the hours of the surveys. There were 64 sightings of dolphins from aircraft, totaling 507 animals. Fifteen dolphins were seen entering or leaving the river. Direction of movement within the inlets appeared unrelated to tidal flow. The population of dolphins in the rivers during the week of the survey (10-15 August 1977) was estimated at 438 ± 127. Calves composed 8.1 to 10.1% of all animals seen. Feeding was observed at widely scattered times and locations. There were 60 sightings of manatees totaling 151 animals. No attempt is made to estimate the size of the manatee population. Calves made up 9.9 to 13.2% of all manatees seen.

The portion of the intracoastal waterway of eastern Florida between about lat. 28°47'N and 27°10'N consists of the connected waters of the Indian and Banana Rivers (Figures 1, 2, 3). Together they form a complex waterway just over 185.0 km (100 n.mi.) long and from < 0.93 km (0.5 n.mi.) to 9.3 km (5.0 n.mi) wide. Below the junction of the two rivers at the southern tip of Merritt Island (approximately lat. 28°09'30"N), the Indian River is connected to the adjacent Atlantic Ocean by boating channels at Sebastian and Fort Pierce Inlets.

Like many other portions of the intracoastal waterway, the Indian-Banana River complex is home to Atlantic bottlenosed dolphin, *Tursiops truncatus*. Although the numbers of dolphins inhabiting the rivers is unknown, they have been rumored to contain as many as 5,000 individuals (Orr[2]). Whatever its actual size, however, this population is at the center of a growing controversy. Commercial fishermen in the river and the adjacent ocean report that the dolphins are a nuisance and menace, annually causing an estimated $441,000 worth of damage to longlines and trammel nets used in the Spanish and king mackerel fisheries and not infrequent injury to fishermen (Cato and Prochaska 1976). The fishermen have reportedly requested assistance from the Federal government in controlling the dolphin populations. (White[3]). Recent attempts to use sounds projected underwater to deter the dolphins from approaching fishing nets and boats have had little effect (Caldwell and Caldwell[4]). Because of restrictions imposed on the "taking" of marine mammals by the Marine Mammal Protection Act of 1972, and concerns about the dolphins' roles in the ecosystem, any attempts to reduce the alleged interference of dolphins with the fishing activity must fall under close scrutiny.

The river complex is also home, at least seasonally, to some endangered West Indian manatees, *Trichechus manatus*. The status of these and other manatees of the mainland United States has been most recently reviewed by Hartman[5] and Irvine and Campbell (1978).

During August 1977, I conducted an aerial survey of Indian and Banana Rivers to estimate the size and productivity (number of calves) of the bottlenosed dolphin population. In addition, I took

[1]Biomedical Group, Naval Ocean Systems Center, San Diego, Calif.; present address: Hubbs-Sea World Research Institute, 1700 South Shores Road, San Diego, CA 92109.

[2]Orr, J. M. 1977. A survey of Tursiops populations in the coastal United States, Hawaii and Territorial Waters. Contract Report No. PL92-522, to the U.S. Marine Mammal Commission, Wash., D.C., 18 p.

[3]J. R. White, Doctor of Veterinary Medicine, 16501 S.W. 184th St., Miami, Fla.; pers. commun. July 1977.

[4]Caldwell, D. K., and M. C. Caldwell. 1975. Dolphins and fisheries. *In* A report on the Sea Grant program, p. 28-29. State University System of Florida.

[5]Hartman, D. S. 1974. Distribution, status and conservation of the manatee in the United States. Unpubl. rep. in files of U.S. Dep. Inter., Natl. Fish. Wildl. Lab., Wash., D.C., 126 p.

Manuscript accepted August 1978.
FISHERY BULLETIN, VOL. 77, NO. 1, 1979.

advantage of the survey to count manatees and to note numbers of manatee calves.

MATERIALS AND METHODS

The survey design follows the recommendations of Leatherwood et al. (1978) for a strip census of bottlenosed dolphins. Thirty-nine east-west transects were placed 4.63 km (2.5 n.mi.) apart. Each day for six successive days (10-15 August) the replicate transects were flown in a Cessna 172 Skyhawk[6] travelling 167.0 km/h (90 kn) at an altitude of 150 m (500 ft).

The visual angle which provided 0.463 km (0.25 n.mi.) coverage on each side was determined prior to the survey and marked by tape on the wing struts and windows. One observer on each side searched for dolphins within 0.463 km of the aircraft. Sightings near the outer boundary of the survey strip were checked using an inclinometer. Sightings outside the survey strip and on connecting legs were ignored. Each time dolphins were sighted within the survey strip, the aircraft diverted to the group and circled until the following information could be obtained: location of the sighting (using landmarks and local navigational aids), number of individuals, number of apparent calves of the year, group activity, and swimming direction.

Each time manatees were sighted, both on the survey transects and on the legs connecting transects, the same procedure was followed. Adults and calves were clearly distinguishable (calves were defined as small animals in the close company of a much larger adult). A total of five individuals of a third class, intermediate-sized animals, were logged separately as possible older calves. Because manatees were secondary targets of the survey, less time was generally spent on manatee than on dolphin sightings.

As an index to through-water visibility, records were maintained on 3 days of the percentage of each transect for which the bottom within the strip was visible from the aircraft. To minimize effects of other potential variables on counts the following controls were exercised: all flights were conducted between 0725 and 1300; observers remained the same and maintained the same positions in the aircraft; altitude and speed were held constant; methods of searching and circling were the same throughout; estimates of totals and numbers of calves were agreed upon by observers before each sighting was logged and transects resumed. Surveys were only conducted when the sea surface and winds were estimated to be a Beaufort number of 1.5 or below. Because weather was generally excellent for all 6 days, this required only one 40-min suspension on 14 August to permit a rain squall and associated winds to pass. Each day, during the hours of the aerial surveys, observers stationed on shore logged numbers of dolphins and manatees entering or leaving Indian River by Sebastian and Fort Pierce Inlets and the direction of travel of these animals relative to tidal flow.

Resultant data on dolphins were analyzed following the procedures outlined by Leatherwood et al. (1978) for a strip census of bottlenosed dolphins. Inherent in the application of this method is the critical assumption that all dolphin herds within the 0.926 km (0.5 n.mi.) are observed. Resultant data on manatees are presented as incidental observations with no attempt to estimate population size.

RESULTS

Dolphins

On each replicate of the transects, I surveyed approximately 174.0 linear km (94 n.mi.) or 161.2 km^2 (47 n.mi.^{2}) of water, an estimated 20% of the surface area of the rivers. In all, 64 sightings of dolphins, totaling 507 animals (Table 1) were made on the transects (Figures 1, 2, 3). Sightings included from 1 to 35 individuals about a mean of 8.2 and a median of 5. The distribution of herd sizes by replicate is shown in Figure 4.

Animals clearly identifiable as calves of the year were seen with 22 groups (34.4%) and comprised 8.1% of all animals seen (Table 1). Slightly larger animals, perhaps older calves of the year,

TABLE 1.—Numbers of herds and individuals of bottlenosed dolphins observed in Indian and Banana Rivers, Fla., during aerial surveys, 10-15 August 1977.

Survey no (replicate)	Date	Total no of herds	Total no of individuals	Total no. of calves of the season
1	10 Aug	11	90	6 (6.7%)
2	11 Aug	10	74	7 (9.5%)
3	12 Aug	16	106	13 (12.3%)
4	13 Aug	7	49	3 (6.1%)
5	14 Aug	7	84	6 (7.1%)
6	15 Aug	13	104	6 (5.8%)
Totals		64	507	41 (8.1%)

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

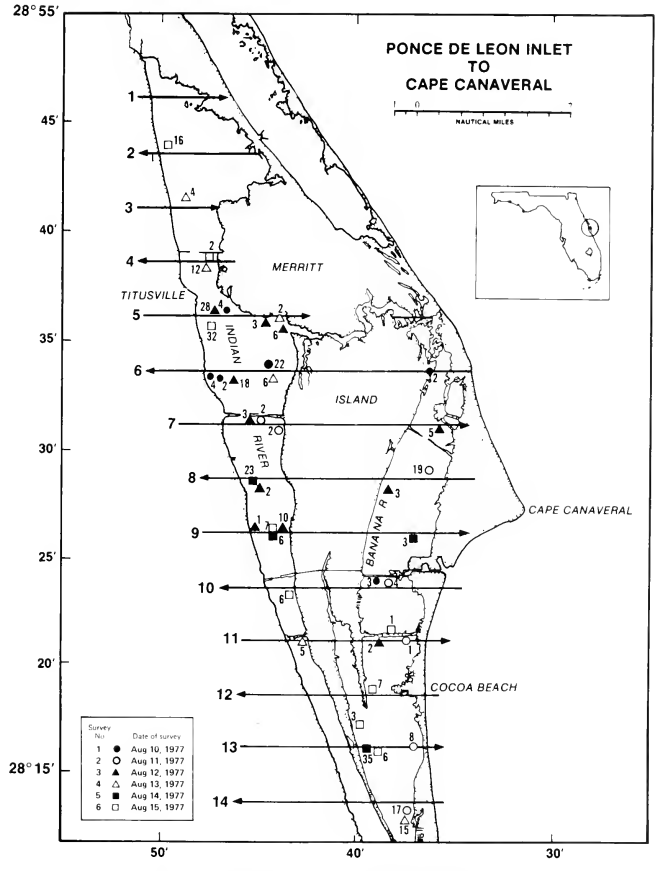


FIGURE 1.—Indian and Banana Rivers, Fla., indicating locations of transects 1-14 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips.

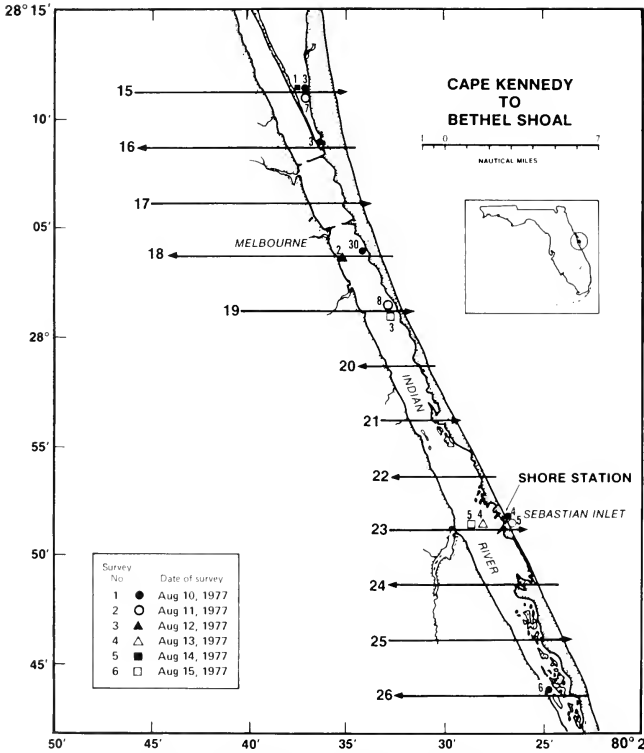


FIGURE 2.—Indian and Banana Rivers, Fla., indicating locations of transects 15-26 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips

were seen with seven groups (10.9%) and composed 2% of all animals seen. Depending on the correct classification of these larger animals, total calves of the year surviving at the time of survey appeared to range from 8.1 to 10.1%. The herd densities (number of herds per square kilometer) and mean herd sizes (mean number of animals per herd) for each replicate and the variances of both values are summarized in Table 2. The estimated densities of dolphins were calculated from:

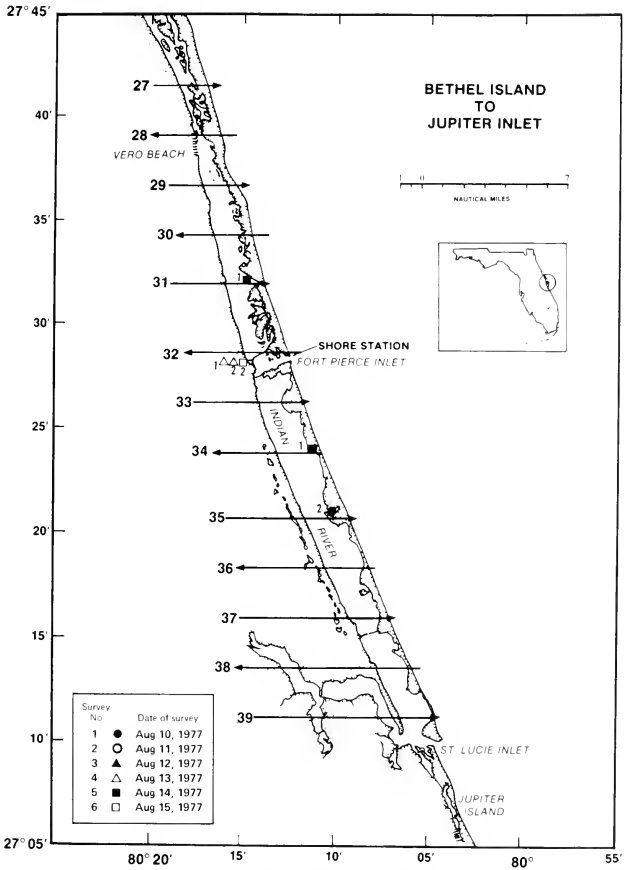


FIGURE 3.—Indian and Banana Rivers, Fla., indicating locations of transects 27-39 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips.

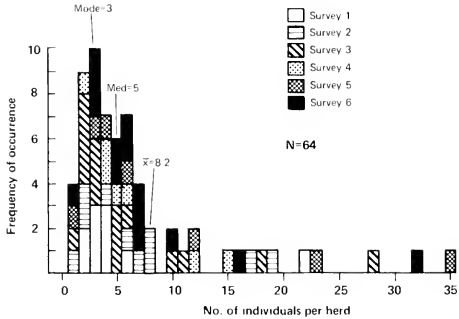


FIGURE 4.—Distribution of herd sizes of bottlenosed dolphins for each of the six replicates.

$$\bar{d} = \bar{h}\bar{a} \qquad (1)$$

where $\bar{h}$ = mean herd size
$\bar{a}$ = mean herd density, described as $(n/w)L$ where L = total length of transects, n = total sightings, and w = the one-sided strip width of 0.463 km (0.25 n.mi.).

The estimated variance of this product ($S^2(\bar{d})$) was calculated from Goodman (1960):

$$S^2(\bar{d}) = \bar{h}^2S^2(\bar{a}) + \bar{a}^2S^2(\bar{h}) - S^2(\bar{a})S^2(\bar{h}), \qquad (2)$$

where $\bar{h}$ = mean herd size
$\bar{a}$ = mean herd density
$S^2(\bar{h})$ = estimated variance of mean herd size
$S^2(\bar{a})$ = estimated variance of mean herd density.

Feeding was observed in portions of 36% (23 of 64) of the groups encountered and was observed in all survey periods and areas. Feeding behaviors were similar to those previously reported for *Tursiops* sp. (Leatherwood 1975).

There was no correlation between the visibility index and the number of sightings on any given transect or set of transects regardless of how data were grouped (rank correlation with Kendall's Tau (Conover 1971) at $\alpha = 0.05$, indicating that significantly larger numbers of animals probably were not missed in the most turbid water).

TABLE 2.—Herd density (number of herds per square kilometer), mean herd size (mean number of dolphins per herd), and dolphin densities (numbers of dolphins per square kilometer) on each replicate. Except where noted means and their variances were calculated over replicates.

Survey no. (replicate)	Date (1977)	Herd density	Mean herd size	Dolphin densities
1	10 Aug	0.068	8.18	0.556
2	11 Aug	0.062	7.40	0.459
3	12 Aug	0.099	6.63	0.656
4	13 Aug	0.043	7.00	0.301
5	14 Aug	0.043	12.00	0.516
6	15 Aug	0.080	8.00	0.640
Means		0.066	8.20	0.521
Variance of means		$9.204 \cdot 10^{-4}$	$6.35 \cdot 10^{-1}$	0.1837

Using alternate method described in text: Density estimate of dolphins $\bar{a}\bar{h}$ = 0.542 (from Equation (1)). Variance of density estimate of dolphins $S^2(\bar{d})$ = 0.094 (from Equation (2)).

Manatees

In all I made 60 sightings of manatees, totaling 151 animals (Figures 5, 6, 7). Sightings ranged from individuals to concentrations of as many as 22 animals with a mean of 2.5. Animals clearly identifiable as calves were part of 14 of the 60 sightings (23.3%) and made up 9.9% (15 of 151) of all manatees seen (Tables 3, 4). Intermediate-sized animals, possibly yearlings or older calves, were part of 5 of the 60 sightings (8.3%) and composed 3.3% (5 of 151) of all manatees seen. If these intermediate-sized animals were also part of this year's crop, total number of calves of the year surviving at the time of the survey may be 13.2%.

No attempt was made to estimate numbers of manatees because all manatees were recorded whether on transects or connecting legs and whether within or outside the transect strip.

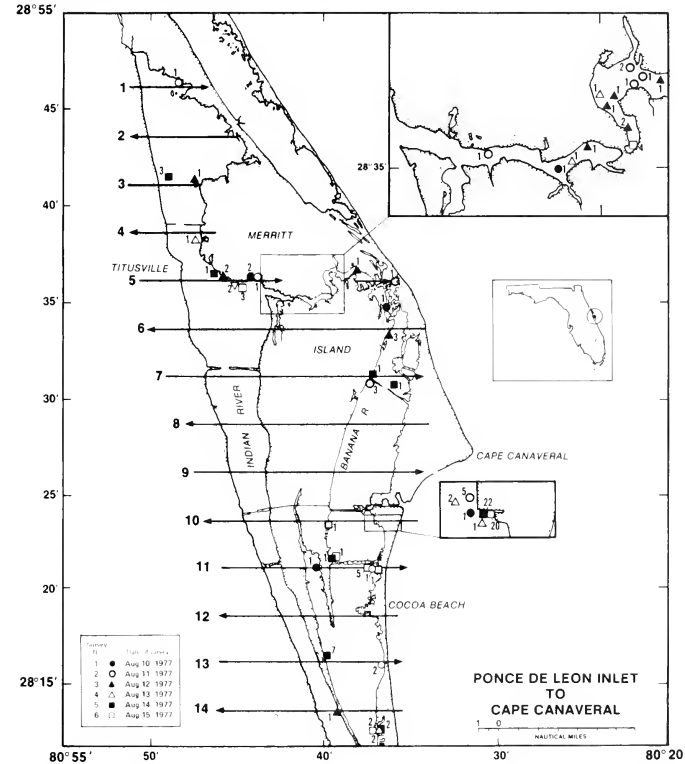


FIGURE 5.—Indian and Banana Rivers, Fla., indication locations of transects 1-14 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

Manatees were often observed in several locations (Figures 5, 6, 7) though the numbers counted in each location varied among days.

A single dark adult manatee with a diagonal yellowish slash (perhaps a scar) across the back, seen 12 August near the east end of transect 3 was again observed 13 August, 200 yd from the east end of transect 4.

Manatees were sighted in the inlets on four occasions during the survey (Table 3), a group of two

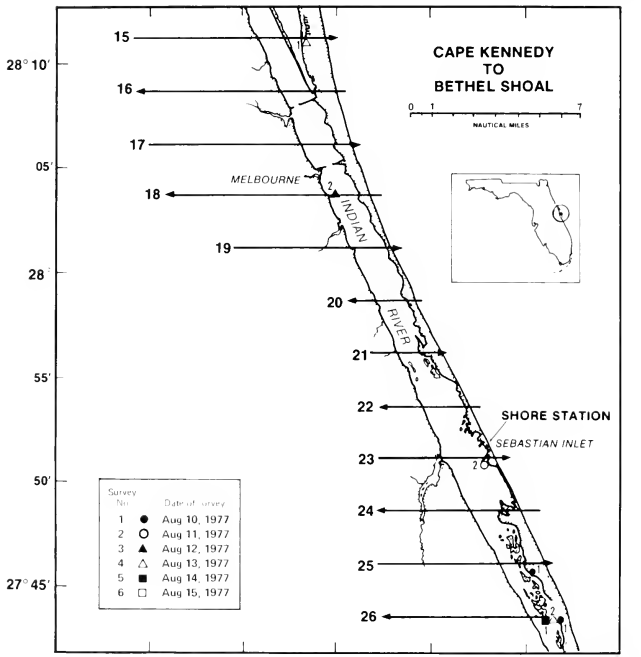


FIGURE 6.—Indian and Banana Rivers, Fla., indicating locations of transects 15-26 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

animals milling within Fort Pierce Inlet, a group of two adults moving against the tide, and two separate individuals moving with the tide.

Like the dolphins', manatees' movements appeared unrelated to tidal flow within the channels.

DISCUSSION

Dolphins

The estimated number of dolphins in the river at the time of the survey (438 ± 127) was considerably smaller than one would have expected for the area based on the accounts of Cato and Prochaska (1976) and Orr (see footnote 2) and on discussions with fishermen and other residents of the area. However, the densities of dolphins observed were generally much higher than those reported from aerial surveys of the waters of Alabama, Mississippi, and Louisiana (Leatherwood et al. 1978) and the west coast of Florida (Odell and

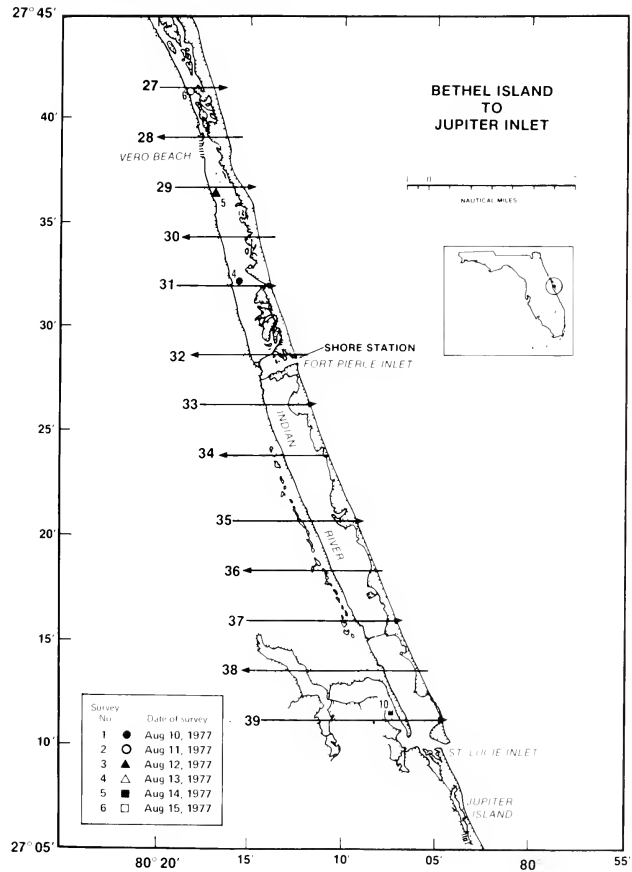


FIGURE 7.—Indian and Banana Rivers, Fla., indicating locations of transects 27-39 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

TABLE 3.—Numbers of bottlenosed dolphins and West Indian manatees entering or leaving the Indian River during the time of the aerial surveys, indicating direction of travel relative to tidal flow.

Date (1977)	Bottlenosed dolphins	West Indian manatees
10 Aug	4 adults moving against tide into river through Sebastian Inlet 2 adults, 2 calves moving with tide from river into Sebastian Inlet then against tide back into river	0
11 Aug	1 adult moving against tide into river through Sebastian Inlet	2 adults milling within Fort Pierce Inlet
12 Aug	0	0
13 Aug	0	2 adults moving against tide into river through Fort Pierce Inlet
14 Aug	0	0
15 Aug	1 juvenile milling within Sebastian Inlet at start of tide	1 adult moving with tide from river to ocean through Sebastian Inlet 1 adult moving with tide from river to ocean through Sebastian Inlet
Total	15 individuals, consisting of 5 moving against tide, 9 moving both with and against tide, and 1 milling within inlet	6 individuals, consisting of 2 milling within inlet, 2 moving against tide, and 2 moving with tide

TABLE 4.—Summary of West Indian manatee sightings by day during the six 1-day aerial surveys, August 1977.

Date	Survey no.	Total no. of sightings	Number of animals: Total	Calves of season	Other possible calves
10 Aug	1	9	13	1(7.6)	1(0.7)
11 Aug	2	12	21	2(4.5)	1(0.7)
12 Aug	3	8	18	2(11.1)	0()
13 Aug	4	11	18	1(5.6)	0()
14 Aug	5	11	41	5(12.2)	0()
15 Aug	6	9	40	4(10.0)	3(2.0)
Total		60	151	15(9.9)	5(3.3)

Reynolds[7]), and were consistent with those reported from aerial surveys conducted in Texas using similar methodology (Barham et al.[8] (Table 5). This consistency and the relatively low variance estimates are evidence that this was a realistic estimate of the numbers of dolphins in the rivers during the time of the survey.

Bottlenosed dolphins have been observed to occur as individuals and in groups of over 200 animals (Leatherwood and Platter[9]). Mean herd sizes of bottlenosed dolphins off eastern Florida and in the Gulf of Mexico vary considerably from one area to another. Groups apparently decrease in size with distance from shore (Odell and Reynolds-see footnote 7); tend in coastal waters to be larger in deeper and in open water areas than in shallow embayments, lagoons, and marshlands (Leatherwood and Platter-see footnote 9, Leatherwood et al. 1978; Shane and Schmidley[10]); and tend to fluctuate in size seasonally with little pattern discernible (Shane and Schmidley-see footnote 10). The mean group size observed during this study (8.2) was well within the limits reported by all authors for eastern Florida and gulf coast waters. This and the lack of correlation between herd size and herd density further support the reasonableness of this population estimate (only if the distribution of herd sizes were normal could the inference technically be made that the two variables were independent (Figure 4)).

Because the estimation of variance in total numbers of animals assumes that herd size and

TABLE 5.—Some estimates of density of bottlenosed dolphins, *Tursiops* sp., in coastal waters of the southeastern United States.

Location	Reference	Dolphins per km²	Dolphins per n.mi²
Mississippi-gulf coast	Leatherwood et al. (1978)	0.23	0.57
Louisiana-gulf coast	Leatherwood et al. (1978)	0.44	1.08
Florida-West Coast	Odell and Reynolds (see footnote 7)	0.23	0.57
Texas-gulf coast	Barham et al. (see footnote 8)	0.65	1.61
Florida-Indian River	This paper	0.68	1.77

[7]Derived from their Table 10 by computing the product of mean herd size (5.43) and mean herd density (0.0497).

[7]Odell, D. K., and J. E. Reynolds III. In press. Distribution and abundance of the bottlenosed dolphin, *Tursiops truncatus*, on the west coast of Florida. Contract Report to the U.S. Marine Mammal Commission, Wash., D.C., 55 p. National Technical Information Service, Wash., D.C.

[8]Barham, E. G., J. C. Sweeny, S. Leatherwood, R. K. Beggs, and C. L. Barham. 1978. Aerial census of bottlenosed dolphins (*Tursiops truncatus*) in a region of the Texas coast. Unpubl. manuscr., 34 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[9]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi, and Louisiana. In D. K. Odell, D. B. Smith, and G. H. Waring (editors), *Tursiops truncatus* assessment workshop, p. 49-86. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021.

[10]Shane, S. H., and D. J. Schmidley. In press. Population biology of Atlantic bottlenosed dolphins, *Tursiops truncatus*, in the Aransas Pass area of Texas. Contract Report to the U.S. Marine Mammal Commission, Wash., D.C., 238 p. National Technical Information Service, Wash., D.C.

herd density are mutually independent, the data by day were examined for correlation. Using Kendall's rank correlation coefficient (Conover 1971) at $\alpha = 0.05$, mean herd size and mean herd density were demonstrated to be uncorrelated within the area surveyed.

The dolphin densities per square kilometer were then multiplied by the area surveyed and a factor of 5 (since the survey covered 20% of the total area) and the 95% confidence limits calculated for the estimate. The figures support an estimate of 438 ± 127 dolphins for the Indian and Banana Rivers during the time of the survey.

As an alternate method for estimating dolphin densities, I took the average density over replicates from column 3, Table 2. This procedure results in a density estimate of 0.40 dolphin km^2 (1.36 dolphins n.mi.^{2}), a value very close to the estimate obtained using the method described above (0.41 dolphin km^2, 1.41 dolphins n.mi.^{2}), but having a variance twice as large (0.1837 vs. 0.094). Because of the higher variance, it can be argued that the first method used, because it takes into account both average herd size and average herd density, is preferable in this case.

The numbers of dolphins entering or leaving the river at Sebastian (4 groups totaling 15 animals) and Fort Pierce Inlets (none sighted) were negligible and were judged as insignificant to the total population size. Two of those groups were entering the river against an outgoing tide, one moved from the river into the inlet on an ebbing tide, then turned around and reentered the river, and one was milling within the inlet (Table 3).

The surprisingly low estimate does, of course, raise an important question. Is the population of bottlenosed dolphins in the river complex always this small (and only appears larger because of periodic concentrations of animals in limited areas) or is it augmented seasonally by influxes of animals from other areas migrating into the rivers in response to the movement of fishes?

Caldwell (1955) and others have suggested limited home ranges for bottlenosed dolphins. Wells et al.,[11] Irvine et al.,[12] and Shane and Schmidley (see footnote 10) have all clearly demonstrated limited home ranges for portions of the populations in their study areas; Wells et al. (see footnote 11) have shown differences in size and locations of home ranges based on age and sex classes, and all these authors have reported some movements of animals into and out of their study areas.

Caldwell and Caldwell (1972) summarize the views of the fishermen from eastern Florida that there are "river" and "ocean" *T. truncatus* populations. Caldwell et al. (1975) presented evidence from the distribution of cases of "Lobos" disease (lobomycosis) in bottlenosed dolphins that indicate greatest susceptibility to the disease in riverine-estuarine stocks and suggest isolation of river from ocean stocks.

Shane[13] reported that the offshore population of bottlenosed dolphins off Texas rarely interacted with the bay population but that the winter population in the Port Aransas area was at least twice as large as that in summer, because the bay population was augmented by "large numbers" of dolphins entering that area for the winter either from the adjacent gulf or from adjacent bay systems. Whether or not a similar influx occurs in the Indian River is unclear. Additional surveys during the peak seasons of the most important midwinter fisheries (king and Spanish mackerel, bluefish, spots, and pompano) might provide answers.

In considering the questions of the dolphins' population size and alleged damage to nets, it should be remembered that bottlenosed dolphins, at least in some areas, are not uniformly distributed but tend to concentrate in areas of high fish productivity (Leatherwood and Platter see footnote 9) which are often areas of highest human use (Leatherwood 1975). Irvine et al. (see footnote 12), for example, reported that short-term movements of bottlenosed dolphins near Tampa Bay appear to correlate with movements of mullet. Frequent joint use of resources by dolphins and humans make the dolphins highly visible and could result in inflated estimates of their numbers.

Even if not augmented seasonally by immigration from other areas, the relatively small dolphin population in Indian and Banana Rivers could be responsible for net damage of the types reported by Cato and Prochaska (1976). Feeding by dolphins near seine and gill net fisheries is well known

[11]Wells, R. S., A. B. Irvine, and M. D. Scott. 1977. Home range characteristics and group composition of the Atlantic bottlenosed dolphin *Tursiops truncatus* on the west coast of Florida. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 15.

[12]Irvine, A. B., M. D. Scott, and R. S. Wells. 1977. Movements and activities of Atlantic bottlenosed dolphins. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 16.

[13]Shane, S. H. 1977. Population biology of *Tursiops truncatus* in Texas. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 57.

(Leatherwood 1975), and dolphins sometimes become entangled as a consequence (Mitchell 1975). An entangled adult dolphin, struggling for escape, is certainly capable of ripping a small-mesh net apart. Further, bottlenosed dolphins have been documented stealing fish from longlines (Iverson[14]). Even so, dolphins may not actually be responsible for all or even the majority of the damage in Indian River. Cato and Prochaska (1976) refer to damage to nets by sharks and cite the need for deterrents. D. K. Caldwell[15] reviewed the evidence and concluded that the majority of damage to nets in the Indian River was probably caused by sharks and not by dolphins, citing as support numerous reports by fishermen and others working the area of sharks around nets. He also concluded, however, that dolphins were stealing fish and damaging gear in the king mackerel fishery in the nearby Atlantic Ocean. During the aerial surveys, I observed huge concentrations of sharks on the sand bars at the entrance of St. Lucie Channel. Therefore, the question of what causes the damage to nets is still open and regulation of the dolphin population based on its supposed size and levels of damage to the fisheries would be premature.

Irvine et al. (see footnote 12) reported that in spring calves composed as much as 14% of the bottlenosed dolphin population near Tampa Bay. Shane (see footnote 13) reported that calves constituted from 3.65% (February) to 12.92% (May) of the dolphins in the Port Aransas area ($\bar{x}$ = 7.61); Leatherwood et al. (1978) reported summer figures from 7.7 to 7.9% calves for coastal Alabama, Mississippi, and Louisiana. The 8.1-10.1% calves observed during this survey therefore are well within the reported ranges of percentages of calves in local bottlenosed dolphin populations.

It has been noted that in areas where tidal flow is negligible, as is the case within these rivers, dolphin movements appear to be related to some factor other than tide (Shane and Schmidley see footnote 10). Shane and Schmidley found that the dolphins in areas of swiftest current moved against tidal flow. The inability to ascertain a relationship between swimming direction of groups and tidal flow in the river inlets in this study is perhaps related to our small sample size.

Manatees

Hartman (see footnote 5) and Irvine and Campbell (1978) reported that Florida manatees concentrated near warmwater refugia during winter months but dispersed during the remainder of the year. The 151 manatees (some no doubt repeats on successive days) sighted during this survey were distributed throughout the nearshore waters of the Indian-Banana River complex, including several less saline canals, and animals were not concentrated near the St. Lucie power station or other potential warmwater areas where winter concentrations have been reported (Irvine and Campbell 1978). No manatees were observed in the deeper open water of the rivers. All were in shallower coastal waters, marinas, creek mouths, bayous, and canals. The number of calves observed, composing from 9.9 to 13.2%, depending on the correct classification of the intermediate-sized animals observed, falls within the ranges of 9.6% calves (winter) and 13.4% calves (summer) reported by Irvine and Campbell (1978).

ACKNOWLEDGMENTS

I thank the following for help with this project: aircraft from Orlando Flying Service, Orlando, Fla., were flown by Steve Negrich. Glen Young, Sea World of Florida, flew as second observer. Both men were very competent and patient with the arduous flight schedule. Ed Asper, Sea World, Inc., provided observers at the ocean inlets and offered valuable advice on the animals of the river. Leola Hietala and Louise Anello Irwin typed the manuscript. D. K. Caldwell, A. B. Irvine, Mari Schaeffer, J. Powers, T. J. Quinn, S. Shane, and R. Wells reviewed the manuscript and made useful suggestions for its improvement. *Fishery Bulletin* reviewers L. L. Eberhardt and J. R. Gilbert were especially thorough in their treatment.

LITERATURE CITED

CALDWELL, D. K.
1955. Evidence of home range of an Atlantic bottlenose dolphin. J. Mammal. 36:304-305.

CALDWELL, D. K., AND M. C. CALDWELL
1972. The world of the bottlenosed dolphin. J. B. Lippincott Co., Phila., 157 p.

[14]Iverson, R. T. B. 1975. Bottlenosed dolphins stealing fish from Hawaiian fishermen's lines. Unpubl. manuscr., 12 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[15]D. K. Caldwell, University of Florida, Biocommunication and Marine Mammal Research Facility, Rt. 1, Box 121, St. Augustine, FL 32084, pers. commun. September 1977.

CALDWELL, D. K., M. C. CALDWELL, J. C. WOODARD, L. AJELLO, W. KAPLAN, AND H. M. MCCLURE
1975. Lobomycosis as a disease of the Atlantic bottlenosed dolphin (*Tursiops truncatus* Montagu, 1821). Am. J. Trop. Med. Hygiene 24:105-114.

CATO, J. C., AND F. J. PROCHASKA
1976. Porpoise attacking hooked fish ark and injure Florida fishermen. Natl. Fisherman 56(9):3B, 16B.

CONOVER, W. J.
1971. Practical nonparametric statistics. John Wiley and Sons, Inc., N.Y., 462 p.

GOODMAN, L. A.
1960. On the exact variance of products. J. Am. Stat. Assoc. 55:708-713.

IRVINE, A. B., AND H. W. CAMPBELL
1978. Aerial census of the West Indian manatee, *Trichechus manatus*, in the southeastern United States. J. Mammal. 59:613-617.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops cf. T. gillii*) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.

LEATHERWOOD, S., J. R. GILBERT, AND D. G. CHAPMAN
1978. An evaluation of some techniques for aerial censuses of bottlenosed dolphins. J. Wildl. Manage. 42:239-250.

MEDELLÍ, E.
1975. Porpoise, dolphin and small whale fisheries of the world: status and problems. Int. Union Conserv. Nat., Monogr. 3. 129 p.

DEVELOPMENT OF PELAGIC LARVAE AND POSTLARVA OF *SQUILLA EMPUSA* (CRUSTACEA, STOMATOPODA), WITH AN ASSESSMENT OF LARVAL CHARACTERS WITHIN THE SQUILLIDAE

STEVEN G. MORGAN[1] AND ANTHONY J. PROVENZANO, JR.[2]

ABSTRACT

Larvae of the predatory crustacean *Squilla empusa* were collected from the plankton in Chesapeake Bay and reared in the laboratory to permit description of the pelagic stages before the postlarval stage.

Characters such as rostral length and spinulation, carapace spinulation, relative size of telson, overall body size, and appearance probably are of more value for specific than for generic identification. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may be useful characters in determining generic alliances of larvae belonging to the Squillidae, but present data are not adequate for construction of generic keys to stomatopod larvae.

Mantis shrimps are formidable predators, able to slice a swimming shrimp in half or smash open a bivalve with enlarged second maxillipeds (MacGinitie and MacGinitie 1968). Even though the strike occurs under water, it is one of the fastest movements known in the animal kingdom taking 4 to 8 ms to complete and traveling at a velocity of 1,000 cm/s (Burrows 1969). Basically, any animal of appropriate size may fall prey to a stomatopod including fish, shrimp, crabs, annelids, clams, mussels, snails, squids, and echinoderms (Piccinetti and Manfrin 1970).

Stomatopod larvae are often met with in great swarms, particularly in tropical waters. The planktonic larval stages constitute a considerable portion of the diet of reef fishes and commercially important pelagic fishes such as the tunas, skipjack tuna, mackerel, herring, and snapper (Sunier 1917; Fish 1925; Reintjes and King 1953; Randall 1967; Dragovich 1970).

Squilla empusa Say 1818 is found in the western Atlantic Ocean and ranges from Massachusetts, U.S.A. to northern South America, including Trinidad, Venezuela, Surinam, and French Guiana (Manning 1969). It is abundant throughout its range, but is especially prevalent in commercial shrimp beds, and is believed to be a serious predator of the shrimp. Hildebrand (1954) observed that it is the most abundant crustacean in the offshore trawl fishery of the Gulf of Mexico except for *Penaeus* sp. and *Callinectes* sp. Stomatopods are fished and eaten in most Mediterranean countries, Japan, and the tropical Pacific (Kaestner 1970).

Like the adult, the larvae of *S. empusa* are rapacious predators. Able to attain a length of 17 mm, they can capture zooplankters as large as themselves by using their second maxillipeds (Lebour 1924). *Squilla empusa* larvae not only fill a role as predators, but also as prey. To date very little has been published on the ecology of the larvae nor has the sequence of pelagic stages been established for this species.

Of the 350 known species of stomatopods, only 1 in 10 can be identified with their larvae and only 1 has been reared from hatching to metamorphosis. Difficulty in rearing the larvae has forced investigators to base their accounts on reconstructions made from preserved specimens or from holding planktonic larvae through one ecdysis to connect successive stages. The species of stomatopods for which larvae are definitely known by the rearing of late stage larvae through metamorphosis were listed by Provenzano and Manning (1978). Stomatopod species for which larvae are definitely known by the hatching of eggs also are listed by Provenzano and Manning.

The only description of the developmental sequence of *S. empusa* was made almost 100 yr ago by Brooks (1878) who captured larvae at Fort Wool near the mouth of the Chesapeake Bay. Because

[1]Institute of Oceanography, Old Dominion University, Norfolk, Va.; present address: Institute of Marine Science, University of North Carolina, Morehead City, NC 28557.

[2]Institute of Oceanography, Old Dominion University, Norfolk, VA 23508.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

none of Brooks' larvae metamorphosed into postlarvae, he could not be sure of their identity. However, of the thousands he collected, all appeared to Brooks to be "specifically identical" and the series of forms were so complete with the differences between the successive stages so slight that he concluded there was "no reason to doubt that they are all of the same species, and that species the only one which is known to occur in the Chesapeake Bay." However, we now know that early larval stages of at least one other species of stomatopod occur at the mouth of Chesapeake Bay (Provenzano and Goy, pers. obs.) Brooks' description is inadequate to permit stages to be adequately assigned to larvae.

Brooks apparently was unable to obtain successful molting in his larvae, but instead had to rely on reconstruction to describe the larval history. He provided no conjecture as to the number of pelagic stages, and only partially described four stages. Furthermore, the illustrations which Brooks included were of whole specimens only; detailed figures of appendages, necessary for accurate species identification, were not made.

Faxon (1882), working in Rhode Island, held what he considered to be the last pelagic stage of *S. empusa* until it metamorphosed and could be identified. However, the last stage larva and postlarva appear to belong to another species, not *S. empusa* (see Discussion).

In this paper we describe the pelagic larval development and postlarval stage of *S. empusa*. Because egg masses were not collected, hatched, and reared, the propelagic stages remain undescribed. Furthermore, because larvae were obtained from the plankton, we are not positive that the larvae described as stage I are the true first pelagic stage. However, of the hundreds of larvae collected these stage I larvae are the least developed and closely resemble stage I larvae of other species reared from eggs.

A brief review of previous efforts to associate stomatopod larvae with adults and a discussion of possible specific and generic larval characters within the Squillidae is presented.

METHODS

Larval specimens of *S. empusa* were collected weekly 1 to 2 km north of Cape Henry at the mouth of the Chesapeake Bay where we have determined that a population of adults exists. A ½-m plankton net (153-μm mesh) was used to make 10-min stepped oblique tows, as the ship circled the collection site at idle speed.

Each plankton sample was placed into one or two 1.9-l (½-gal) jars filled with seawater until stomatopod larvae could be separated from the sample. Separation of larvae from the samples was started aboard ship and completed in the laboratory. Larvae were sorted according to size to minimize cannibalism, and held temporarily in aerated 1.9-l jars filled with seawater.

The larvae were then placed in compartmentalized plastic trays, one per compartment. Each tray contained 18 compartments measuring 4.5 × 5 × 4 cm. Medium for rearing the larvae was made from Instant Ocean Synthetic Sea Salts[2] (Aquarium Systems, Inc., Eastlake, Ohio) and tapwater.

Larvae were reared over a range of temperatures (10° to 25°C) and salinities (10 to 35‰) in an attempt to insure survival of at least some larvae since optimum conditions were unknown. Because the larvae were not hatched in the laboratory under the temperature-salinity combination at which they were reared, some larvae had to be acclimated to the test conditions. Lavae were never acclimated to temperature changes of more than 5°C and 10‰/day. The larvae were maintained in total darkness except for brief periods (15 to 20 min/day) when they were examined and transferred to newly prepared trays.

Each larva was reared in 25 ml of water and given approximately 30 *Artemia salina* nauplii/ml daily. Decapod larvae and *A. salina*, grown on yeast or an algal culture of *Dunaliella*, were fed to larvae that became too large to capture or obtain substantial nutrition from the *A. salina* nauplii. Larvae were transferred daily, early stages by means of a pipette, later stages with a spoon, into compartments containing freshly prepared seawater and food. During this transfer, frequency of molting, duration of larval development, survival, and the stage of development were recorded. Dead larvae were preserved in 70% ethyl alcohol and 10% glycerin. Preserved larvae were heated in a 5% potassium hydroxide solution to dissolve the tissue so that only the exoskeleton remained. The larvae were then stained in acid fuchsin red to facilitate description and illustration. Larvae and exuviae were dissected in lactic acid. All larval appendages were illustrated using a Tasco camera lucida on a Unitron binocular compound scope,

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

while the postlarval appendages were illustrated with the aid of a Bausch and Lomb microprojector.

The descriptions of all larval stages were based on five specimens; four specimens were used to describe the postlarva. Carapace length (CL) indicates the distance from the tip of the rostrum to the median posterior margin of the carapace, exclusive of the median spine; telson length (tL), distance from the articulation with the sixth abdominal somite to the median posterior margin of the telson. The term pleotelson (Kaestner 1970) is used to refer to the telson before the sixth abdominal somite has become completely articulated. Pleotelson length (PL) indicates the distance from the articulation with the fifth abdominal somite to the median posterior margin of the pleotelson; telson width (TW) and pleotelson width (PW), distance across the widest portion; rostral length (RL) of the larva, distance from the tip of the rostrum to the base of the anterolateral spines of the carapace; rostral length of the postlarva, distance from the tip of the rostrum to the posterior margin of the rostrum; rostral width (RW) of the postlarva, distance from the tip of the rostrum to the median posterior margin of the telson; and total length (TL) of the postlarva, distance from the anterior margin of the rostrum to the median posterior margin of the telson.

Maxillules, maxillae, pleopods, distal spinules of the rostrum, and most epipods were omitted from illustrations of the whole animal for the sake of clarity.

RESULTS

The pelagic larval development of *S. empusa* was found to include nine stages before the postlarval stage. Juvenile stages reared for several months after metamorphosis attained sizes of approximately 30 to 40 mm TL and could be positively identified with the adult. Although none of the 576 larvae reared at the 16 different temperature and salinity combinations was reared through the entire pelagic development to metamorphosis, larvae survived well and molted frequently at two of the test combinations. Of larvae kept at 20°C, 25‰ salinity, or at 25°C, 25‰ salinity, 47% molted three or more times, 24% underwent at least five ecdyses, and 3% molted seven times over a 6-wk period. Thirty-four animals molted to postlarva. Great increases in size from the first to the last stage necessitated adjustments in food size and quantity. Detailed results of effects of various experimental conditions are being prepared by Morgan for publication elsewhere.

The difficulty in rearing the larvae through the lengthy pelagic development made it necessary to reconstruct the developmental sequence by observing the larvae molt through successive stages.

Stage I (Figure 1A)

Measurements (mm): RL, 0.70 to 1.10; PL, 0.4 to 0.8; TL, 2.9 to 3.3; CL, 0.80 to 1.30; PW, 0.3 to 0.6.

Rostrum deflexed, extending slightly beyond antennular flagella, ventral spinules absent.

Carapace with one pair of supraorbital spines. Lateral margins of carapace convex, armed ventrally with four spinules. Posterior margin of carapace deeply notched, armed with a median dorsal spine. Posterolateral spines, armed with one ventral spinule, extending to fourth abdominal somite.

Ocular somite articulated, armed with one spine on median ventral margin. Antennular somite not articulated.

Antennule (Figure 2A) with long two-segmented inner flagellum, apical segment armed with one strong and one weak seta distally and a pair of weak setae medially, proximal segment armed with one strong and two weak setae distally. Outer flagellum armed with one large and one small seta distally, followed by one weak seta and six aesthetascs arranged 1-2-3 along inner margin. Median flagellum absent.

Antenna (Figure 3A) armed with nine plumose setae, endopod absent.

Mandible (Figure 4A) serrate, mandibular palp absent.

Maxillule (Figure 5A) with coxal endite bearing three spinules and one seta, basal endite with one strong tooth flanked by two strong setae, palp with one long seta, endopod absent.

Maxilla (Figure 6A) unsegmented, armed with six setae.

First maxilliped (Figure 7A) with dactylus small, pointed. Propodus with two extremely minute spinules, inner margin bearing seven strong setae arranged 2-3-2. Carpus with one strong seta distally, merus without setae, epipod absent.

Second maxilliped (Figure 8A) large, basis with stout proximal spine. Propodus with 1 strong terminal tooth followed by 17 to 20 denticles on inner margin. Dactylus armed with spinules, distal

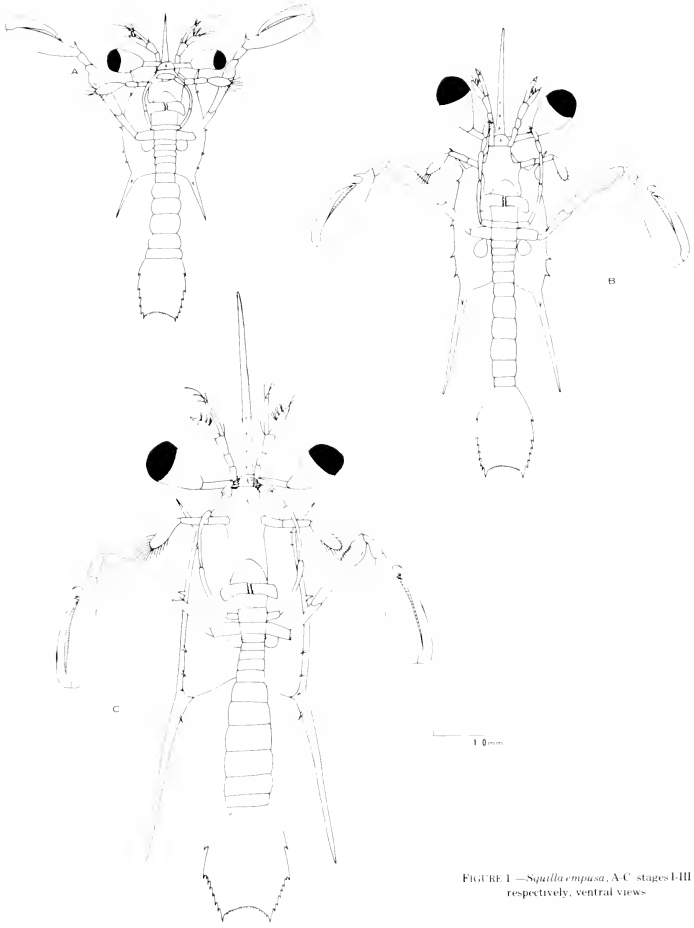


FIGURE 1.—*Squilla empusa*, A-C stages I-III respectively, ventral views.

FIGURE 2.—*Squilla empusa*. A-I stages I-IX respectively, antennules

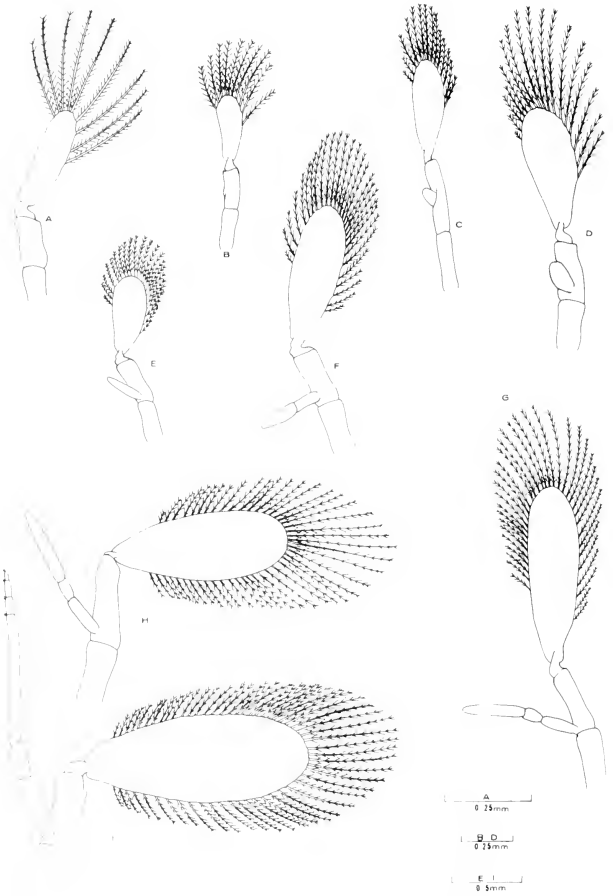


FIGURE 3.—*Squilla empusa*, A-I stages I-IX respectively, antennae.

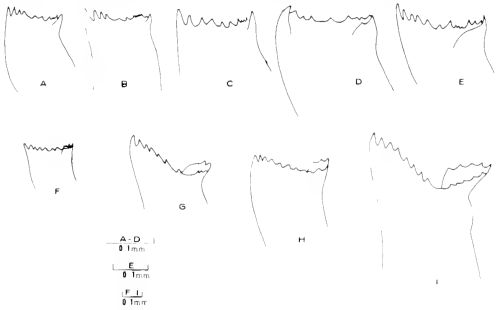


FIGURE 4.—*Squilla empusa*, A-I: stages I-IX respectively, mandibles.

FIGURE 5.—*Squilla empusa*, A-I: stages I-IX respectively, maxillules.

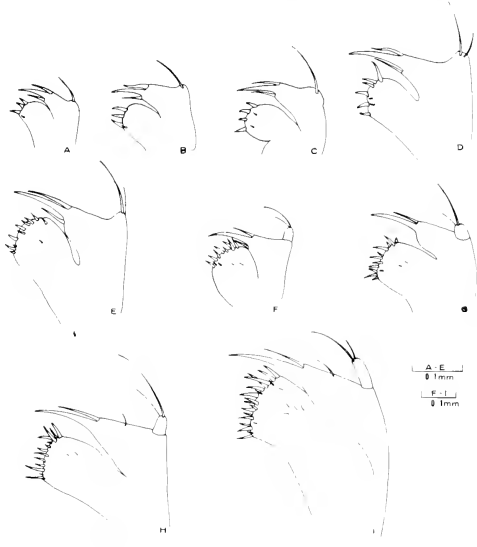


FIGURE 6.—*Squilla empusa*, A-I, stages I-IX respectively; maxillae.

portion of cutting edge minutely serrate. Epipod present.

Third, fourth, and fifth maxillipeds absent.

Pereiopods absent.

Posterolateral angles of pleomeres rounded. Pleopods (Figure 9A to 9D) one through four present with appendix interna. Pleopod setation of this and other larval stages presented in Table 1.

Sixth pleomere not articulated, submedian spines absent, uropods absent.

Pleotelson (Figure 10A) with paired lateral, intermediate, and posterolateral spines, 4 pairs of intermediate denticles, 15 submedian denticles bearing spinules.

Stage II (Figure 1B)

Measurements (mm): RL, 1.35 to 1.55; PL, 0.70 to 0.90; TL, 4.20 to 4.60; CL, 1.05 to 1.30; PW, 0.55 to 0.75.

Rostrum extending well beyond end of antennular flagellum, armed with one to four ventral spinules.

Carapace slightly convex, posterolateral spines extend to anterior section of telson.

Antennule (Figure 2B) as in previous stage.

Antenna (Figure 3B) with 10 to 13 plumose setae, endopod present as incipient bud.

FIGURE 7.—*Squilla empusa*, A-I stages I-IX respectively, first maxillipeds

FIGURE 8.—*Squilla empusa*, A-I stages I-IX respectively, second maxillipeds.

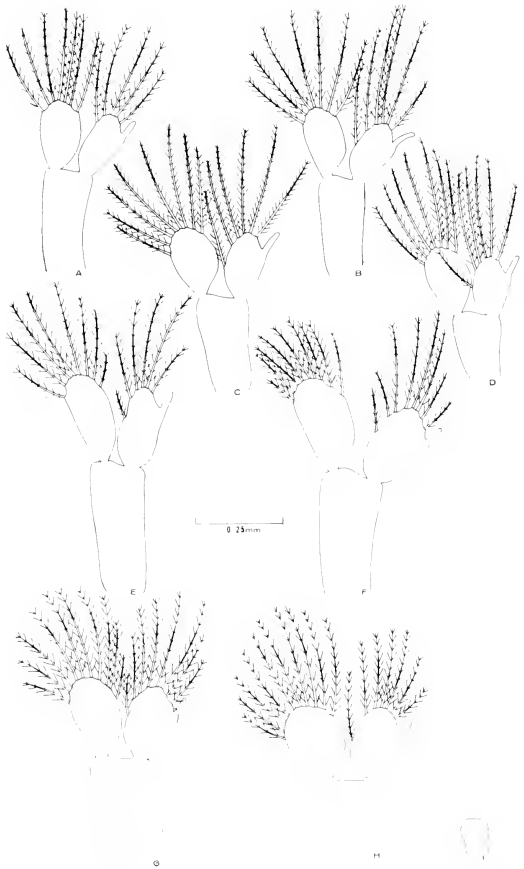


FIGURE 9.—*Squilla empusa*. A-D stage I, first to fourth pleopods respectively. E-I stage II, first to fifth pleopods respectively.

TABLE 1.—Number of setae on margins of pleopods for pelagic larval stages I to IX of *Squilla empusa*. Fifth pleopod does not appear until stage V.

	Abdominal somite									
	Endopod					Exopod				
Stage	1	2	3	4	5	1	2	3	4	5
I	6	6	6-7	6-7	—	7	7	7-9	7-9	—
II	6	7-8	7-8	7	—	7-8	9-10	9-11	9-10	—
III	8-10	9-13	10-14	9-14	—	9-10	12-13	13-14	11-14	—
IV	12-13	14-15	15-16	15-17	—	12	16-17	17-18	16-17	—
V	14-15	15-18	16-18	16-20	—	14-15	17-19	19-20	18-19	7-8
VI	16-20	18-25	20-27	20-27	3-8	15-20	21-26	23-29	21-27	12-16
VII	22-28	26-28	26-31	26-32	23-28	22-30	26-31	29-33	28-31	20-23
VIII	25-29	27-32	28-36	31-38	30-39	24-30	32-36	32-38	31-38	24-31
IX	27-31	32-39	35-42	36-45	40-47	36-41	36-41	38-46	37-45	33-39

Mandible (Figure 4B), maxillule (Figure 5B), maxilla (Figure 6B), and first maxilliped (Figure 7B) as in previous stage.

Second maxilliped (Figure 8A) with propodus bearing proximal tooth followed by another large tooth and 19 to 21 denticles along inner margin.

Pleopods one through four (Figure 9E to 9H) increase setation slightly (Table 1). Fifth pleopod (Figure 9I) present as bifurcated bud.

Pleotelson (Figure 10B) as in previous stage.

Stage III (Figure 2C)

Measurements (mm): RL, 1.90 to 2.10; PL, 1.00 to 1.10; TL, 5.80 to 6.50; CL, 1.50 to 1.78; PW, 0.75 to 0.95.

Rostrum with four to eight spinules ventrally for stages III to VIII.

Carapace with lateral margins straight, armed with two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. Posterolateral spines extend to posterior region of pleotelson.

Antennule (Figure 2C) with two-segmented inner flagellum, proximal segment armed with one strong distal seta. Outer flagellum two-segmented with 9 or 10 mesial aesthetascs arranged in three groups of 2 or 3, each group with a weak seta.

Antenna (Figure 3C) with 13 to 16 plumose setae, length of unsegmented endopod increased.

One median ventral spine situated between base of antennules and antennae.

Mandible (Figure 4C) essentially unchanged.

Maxillule (Figure 5C) with coxal endite bearing four to eight teeth.

Macilla (Figure 6C) with six to eight setae.

First maxilliped (Figure 7C) with 9 or 10 strong setae arranged in four groups of 2 or 3 on propodus, carpus with 1 or 2 strong setae distally.

Second maxillped (Figure 8C) with propodus bearing 23 to 27 denticles, basis with proximal spine well developed.

Third maxilliped present as bud.

Pleopods one through four (Figure 11A to 11D) increase setation (Table 1). Fifth pleopod (Figure 11E) biramous, nonsetose.

Sixth pleomere partially articulated, one pair of small submedian spines present. Uropods (Figure 10C) present as buds.

Pleotelson (Figure 10C) with 8 to 10 pairs of intermediate denticles, including 1 pair in axis of intermediate spines 15 to 27 submedian denticles.

Stage IV (Figure 12)

Measurements (mm): RL, 2.50 to 2.90; PL, 1.20 to 1.40; TL, 6.50 to 6.90; CL, 1.80 to 2.25; PW, 1.00 to 1.20.

Rostrum with a row of minute spinules distally for stages IV to VIII.

Antennule (Figure 2D) with three-segmented inner flagellum armed with two strong setae on distal half of proximal segment. Outer flagellum divided into a two-segmented median flagellum, and a broader outer flagellum with 10 or 11 aesthetases arranged in four groups of 2 or 3, a small seta with each group. Antennular somite articulated.

Antenna (Figure 3D) with 17 to 19 plumose setae, length of unsegmented endopod increased slightly.

Mandible (Figure 4D) essentially unchanged.

Maxillule (Figure 5D) with coxal endite bearing seven to nine teeth, palp with two setae.

Maxilla (Figure 6D) with eight to nine setae.

First maxilliped (Figure 7D) with 12 or 13 strong setae arranged in five groups of 2 or 3 on propodus, carpus with 4 distal setae, merus with 1 strong distal seta.

Second maxilliped (Figure 8D) with propodus bearing proximal tooth followed by 2 strong teeth in opposition and 25 to 33 denticles along inner margin.

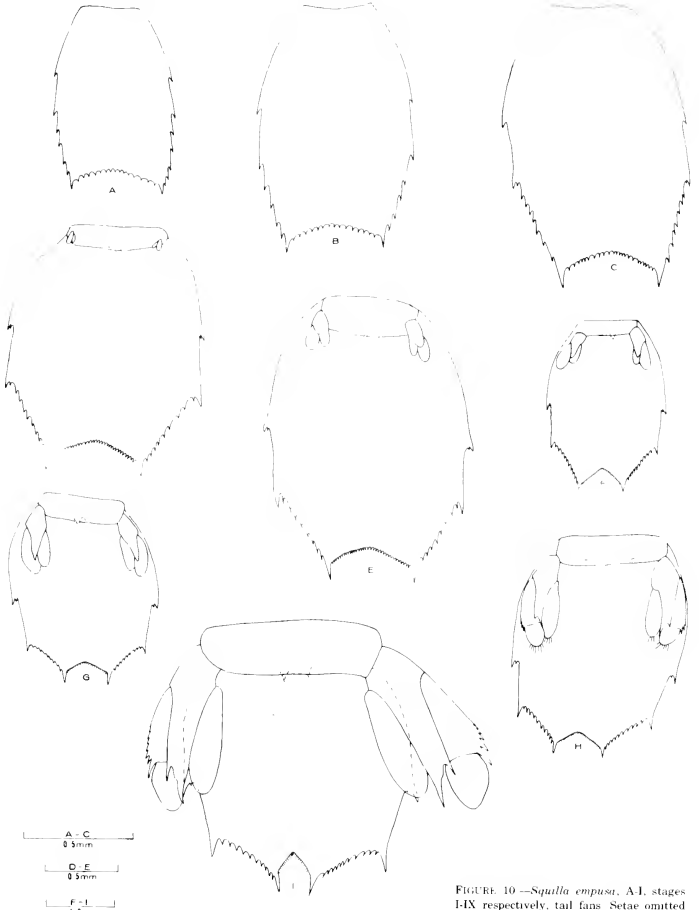


FIGURE 10.—*Squilla empusa*, A-I, stages I-IX respectively, tail fans. Setae omitted from uropods of stage IX.

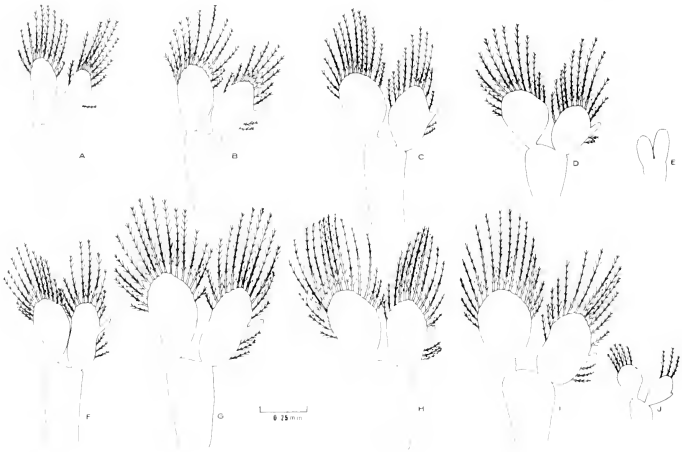


FIGURE 11.—*Squilla empusa*, A-E stage III, first to fifth pleopods respectively, F-J stage IV, first to fifth pleopods respectively.

Third, fourth, and fifth maxillipeds (Figure 13A to 13C) unsegmented buds.

Pereiopods (Figure 14A to 14C) present as buds.

Posterolateral angles of pleomeres acute. Pleopods one through four (Figure 11F to 11I) increase setation. Fifth pleopod (Figure 11J) setose and possessing appendix interna.

Sixth abdominal somite articulated. Uropods (Figure 10D) biramous.

Pleotelson (Figure 10D) with 1 denticle in axis of lateral spine, 8 or 9 pairs of intermediate denticles, 23 to 30 submedian denticles.

Stage V (Figure 15)

Measurements (mm): RL, 2.50 to 3.25; PL, 1.50 to 1.65; TL, 8.50 to 9.00; CL, 2.30 to 2.50; PW, 1.40 to 1.60.

Antennule (Figure 2E) with three-segmented inner flagellum armed with two to four setae on distal half of proximal segment; median flagellum also three-segmented.

Antenna (Figure 3E) with 19 to 23 plumose setae, length of unsegmented endopod now nearly equal to segments bearing it.

Epistome with small apical spine.

Mandible (Figure 4E) essentially unchanged.

Maxillule (Figure 5E) with coxal endite bearing 8 to 12 teeth.

Maxilla (Figure 6E) with 10 or 11 setae.

First maxilliped (Figure 7E) with 13 to 17 strong setae arranged in five or six groups of 2 to 4, carpus with 5 to 8 distal setae.

Second maxilliped (Figure 8E) with propodus armed with 30 to 43 denticles.

Third, fourth, and fifth maxillipeds (Figure 13D to 13F) still unsegmented, but increased in length.

Pereiopods (Figure 14D to 14F) present as bifurcated buds.

Uropods (Figure 10E) with basal prolongation present.

Pleotelson (Figure 10E) with 8 to 10 pairs of intermediate denticles, 28 to 33 submedian denticles.

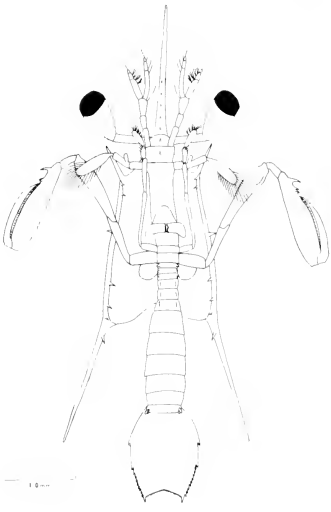


FIGURE 12.—*Squilla empusa*, stage IV, ventral view

Stage VI (Figure 17A)

Measurements (mm): RL, 3.00 to 3.50; PL, 1.65 to 2.00; TL, 9.80 to 10.60; CL, 2.65 to 2.95; PW, 1.45 to 1.75.

Antennule (Figure 2F) with four-segmented inner flagellum. Median flagellum with three segments. Outer flagellum with 12 to 14 aesthetascs arranged in four groups of 2 or 3, each group with a seta.

Antenna (Figure 3F) with 22 to 25 plumose setae, endopod now two-segmented.

Mandible (Figure 4F) essentially unchanged.

Maxillule (Figure 5F) with coxal endite bearing 10 to 12 marginal teeth and 1 or 2 very short medial setae, palp well developed, armed with 2 setae.

Maxilla (Figure 6F) five-segmented, subproximal segment with endite bearing 14 to 19 setae. Palp articulated.

First maxilliped (Figure 7F) with 18 to 22 strong setae arranged in six or seven groups of 2 to 4 on propodus, carpus with 8 to 12 distal setae, conspicuous epipod present.

Second maxilliped (Figure 8F) with 33 to 47 denticles along inner margin of propodus.

Third maxilliped (Figure 13G) with endopod four-segmented, dactylus not reflected against propodus.

Fifth maxilliped (Figure 13I) with endopod unsegmented.

Pereiopods (Figure 14G to 15I) unsegmented, distally bifurcate, increased in length.

Pleopods one through five (Figure 16F to 16J) with gills present as buds on inner proximal margin of exopod.

Uropods (Figure 10F) with basal prolongation half length of endopod, exopod with or without one spine on outer margin.

Pleotelson (Figure 10F) with 8 to 10 pairs of intermediate denticles, 29 to 33 submedian denticles.

Stage VII (Figure 17B)

Measurements (mm): RL, 3.20 to 3.70; PL, 2.00 to 2.20; TL, 11.60 to 13.60; CL, 2.85 to 3.55; PW, 1.85 to 2.30.

Antennule (Figure 2G) with seven-segmented inner flagellum, median flagellum five-segmented, outer flagellum with 18 or 19 aesthetascs arranged in five or six groups of 2 or 3, each with a seta.

Antenna (Figure 3G) with 32 to 39 plumose setae, endopod with three segments.

Mandible (Figure 4G) essentially unchanged.

Maxillule (Figure 5G) with coxal endite bearing 13 marginal teeth and 2 medial setae, endite with spine flanked by 1 strong seta. Palp unchanged.

Maxilla (Figure 6G) four-segmented, the two more proximal segments each with one endite. Maxilla armed with 32 to 34 setae.

First maxilliped (Figure 7G) with 23 to 26 strong setae on propodus, in seven or eight groups of 2 to 4, carpus with 21 to 27 setae.

Second maxilliped (Figure 8G) with 52 to 60 denticles along inner margin of propodus.

Third, fourth, and fifth maxillipeds (Figure 13J to 13L) fully articulated.

Third maxilliped (Figure 13J) with dactylus armed with spinules and reflected against propodus, latter armed with 10 or 11 spinules, carpus with 4 to 6 spinules.

FIGURE 13.—*Squilla empusa*. A-C, stage IV, third to fifth maxillipeds respectively. D-F, stage V, third to fifth maxillipeds respectively. G-I, stage VI, third to fifth maxillipeds respectively. J-L, stage VII, third to fifth maxillipeds respectively. M-O, stage VIII, third to fifth maxillipeds respectively. P-R, stage IX, third to fifth maxillipeds respectively.

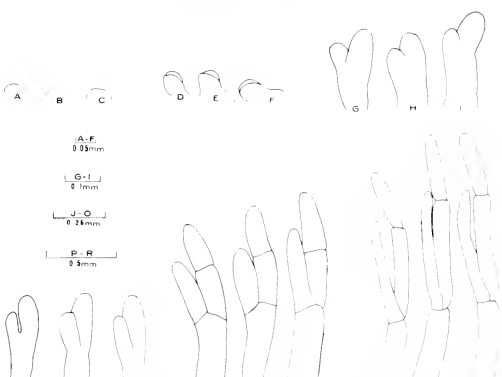


FIGURE 14.—*Squilla empusa*, A-C: stage IV, first to third pereiopods respectively; D-F: stage V, first to third pereiopods respectively; G-I: stage VI, first to third pereiopods respectively; J-L: stage VII, first to third pereiopods respectively; M-O: stage VIII, first to third pereiopods respectively; P-R: stage IX, first to third pereiopods respectively

Fourth maxilliped (Figure 13K) with dactylus armed with spinules and partially reflected against propodus, latter armed with four to eight spinules, carpus with four to six spinules, epipod present.

Fifth maxilliped (Figure 13L) segmented, dactylus unarmed and not reflected against unarmed propodus, carpus with zero to three spinules.

Pereiopods (Figure 14J to 14L) with clearly differentiated endopods and exopods, though segmentation not yet distinct.

Pleopods (Figure 18A to 18E) with bilobed rudimentary gills.

Sixth pleomere partially separated from telson. Uropods (Figure 10G) with basal prolongation acute. Exopod with one or two spines on outer margin, armed with zero to five plumose setae. Endopod with zero to two plumose setae.

Pleotelson (Figure 10G) with 9 or 10 pairs of intermediate denticles, 32 to 35 submedian denticles.

Stage VIII (Figure 19)

Measurements (mm): RL, 3.25 to 3.45; tL, 2.30 to 2.50; TL, 13.90 to 15.30; CL, 3.90 to 4.35; TW, 2.25 to 2.65.

Antennule (Figure 2H) with inner flagellum bearing 9 to 11 distinctly articulated segments. Median flagellum with five to seven distinct segments. Outer flagellum with 21 to 23 aesthetascs arranged in six or seven groups of 2 or 3, each group with a seta in addition.

Antenna (Figure 3H) with 40 to 55 plumose seta.

Mandible (Figure 4H) essentially unchanged.

Maxillule (Figure 5H) with coxal endite bearing 15 to 19 marginal teeth and 2 to 4 medial setae, distal margin of basis with 1 median seta.

Maxilla (Figure 6H) armed with 40 to 58 setae.

First maxilliped (Figure 7H) with 29 to 31 strong setae on propodus arranged in eight groups of 2 to 5, carpus with 37 to 44 setae.

FIGURE 15.—*Squilla empusa*, stage V, ventral view.

Second maxilliped (Figure 8H) with 61 to 75 denticles on propodus.

Third, fourth, and fifth maxillipeds (Figure 13M to 13O) with dactylus armed with spinules and reflected against propodus, epipods present.

Third maxilliped (Figure 13M) with propodus armed with 12 to 21 spinules, carpus with 6 to 9 spinules.

Fourth maxilliped (Figure 13N) with propodus armed with 12 to 16 spinules, carpus with 5 to 8 spinules.

Fifth maxilliped (Figure 13O) with propodus armed with 6 to 11 spinules, carpus with 4 to 7 spinules.

Pereiopods (Figure 14M to 14O) with two-segmented exopods, endopods shorter, unsegmented.

Pleopods (Figure 20A to 20E) with trilobed gills.

Sixth abdominal somite completely separated from telson. Uropods (Figure 10H) with two-segmented exopod. Basal segment with 2 to 4 spines on outer distal margin, apical segment with 4 to 14 plumose setae on distal margin. Endopod of uropod with four to eight plumose setae on distal margin.

Telson (Figure 10H) with 10 pairs of intermediate denticles and 31 to 35 submedian denticles.

Stage IX (Figure 21)

Measurements (mm): RL, 2.40 to 4.50; tL, 2.30 to 2.60; TL, 13.00 to 17.50; CL, 3.00 to 3.90; TW, 2.10 to 2.80.

Rostrum with decrease in number of spinules, now with two to six spinules; with or without minute distal spinules.

Antennule (Figure 2I) with inner flagellum bearing 14 to 20 distinctly articulated segments. Median flagellum with 8 to 11 distinctly articulated segments. Outer flagellum with 23 to 33 aesthetascs arranged in seven to nine groups of 2 to 7, each group with a seta.

Antenna (Figure 3I) with 48 to 60 plumose setae, endopod with 6 to 9 segments.

Mandible (Figure 4I) essentially unchanged.

Maxillule (Figure 5I) with coxal endite bearing 20 to 25 marginal teeth and 1 or 2 medial setae, margin of basal endite with 1 or 2 setae.

Maxilla (Figure 6U) with 78 to 131 setae.

First maxilliped (Figure 7I) with 35 to 44 setae arranged in 9 or 10 groups of 2 to 5, carpus with 59 to 107 setae, dactylus with or without cluster of setae on median outer margin, propodus with or without cluster of setae on distal outer margin.

Second maxilliped (Figure 8I) with 71 to 92 denticles on propodus.

Dactylus of third, fourth, and fifth maxillipeds (Figure 13P to 13R) with or without regularly spaced setae along outer margin, propodus with or without a cluster of setae on distal outer margin.

Third maxilliped (Figure 13P) with propodus bearing 19 to 56 spinules, carpus with 11 to 22 spinules.

Fourth maxilliped (Figure 13Q) with propodus bearing 17 to 51 spinules, carpus with 10 to 28 spinules.

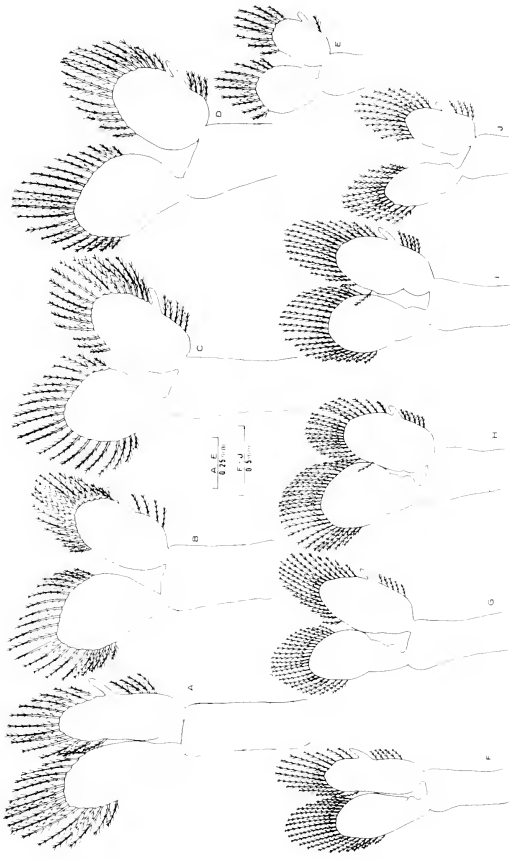


FIGURE 16.—*Squilla empusa*, A-E, stage V, first to fifth pleopods respectively; F-J, stage VI, first to fifth pleopods respectively.

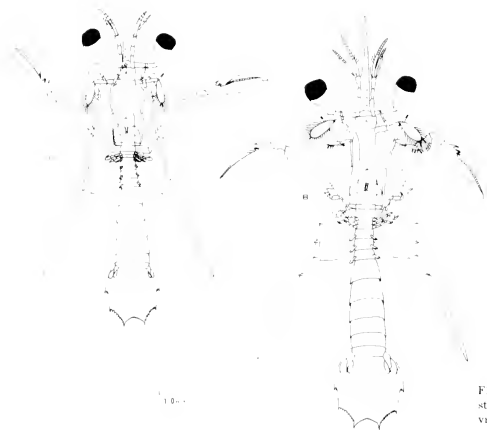


FIGURE 17.—*Squilla empusa*, A-B stages VI and VII respectively, ventral views.

Fifth maxilliped (Figure 13R) with propodus bearing 18 to 40 spinules, carpus with 9 to 20 spinules.

Pereiopods (Figure 14P to 14R) slender with or without distal segment of exopods setose.

Pleopods (Figures 22A to 22C; 23A, 23B) with distal lobe of gill pinnate.

Uropod (Figure 26C) with basal segment of exopod armed with 6 to 8 spines, apical segment of exopod with 17 to 60 plumose setae. Endopod of uropod with 10 to 38 plumose setae. Inner spine of basal prolongation with blunt spine on outer proximal margin. Basal uropod segment with a dorsal spine on distal margin.

Telson (Figure 14I) with 8 to 10 pairs of intermediate denticles, 26 to 34 submedian denticles.

Postlarva (Figure 21)

Measurements (mm): RL, 0.50 to 0.60; CL, 2.90 to 3.30; TW, 2.55 to 3.10; RW, 0.65 to 0.75; tL, 1.95 to 2.55; TL, 12.3 to 14.20.

Eyes large, extending to middle of second segment of antennular peduncle. Cornea bilobed, set obliquely on stalk. Ocular scales rounded, anterior margin of opthalmic somite evenly rounded.

Antennular process produced into blunt spine directed anterolaterally, antennular peduncle slightly shorter than carapace, antennule (Figure 25A) with inner flagellum bearing 34 segments, median flagellum with 30 segments, outer flagellum with 15 segments and 22 aesthetascs arranged in eight groups of 2 or 3.

Antenna (Figure 25B) with 63 to 75 plumose setae, endopod with 16 segments.

Rostral plate wider than long, lateral margins tapering to rounded apex. Median carina present.

Anterolateral angle of carapace without spine, almost forming right angle, posterolateral margins broadly rounded, carinae poorly developed, median carina not bifurcate anteriorly or posteriorly, intermediate and lateral carinae present, reflected carinae absent.

Mandible (Figure 25C) serrate, mandibular palp absent.

Maxillule (Figure 25D) with coxal endite bearing 26 to 27 strong marginal teeth and 6 to 9 small medial teeth. Basal endite with one spine flanked

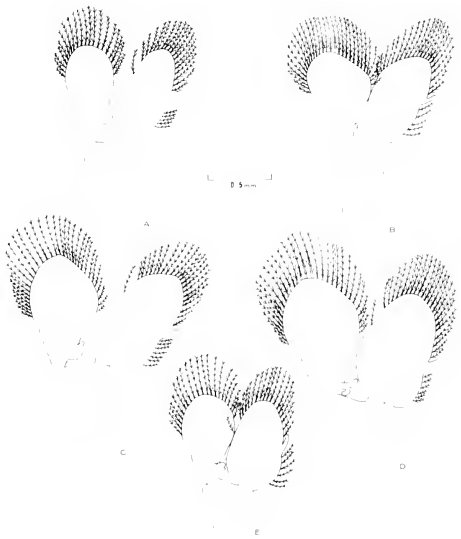


FIGURE 18.—*Squilla empusa*, A-E stage VII, first to fifth pleopods respectively

by one strong seta. Distal margin of basis with three setae. Endopod present as palp on distal margin of basis, armed with two setae.

Maxilla (Figure 25E) four-segmented, two proximal segments with endites, second bilobed.

Five pairs of maxillipeds (Figure 25F to 25J) each maxilliped with one epipod. First maxilliped (Figure 25F) with distal margin of propodus bearing 14 teeth, inner margin with 48 to 50 strong setae arranged in 10 transverse rows, 2 or 3 most distal setae spatulate with strong setules.

Second maxilliped (Figure 25G) with dactylus bearing six teeth, pectinate propodus with three moveable proximal spines, dorsal ridge of carpus undivided.

Pereiopods (Figure 26A) with setose endopod and exopod.

Last three thoracic somites with unarmed submedian and intermediate carinae. Lateral process of fifth thoracic somite subacute, sloping posteriorly. Lateral processes of next two somites bilobed each with a small anterior lobe and a large broadly rounded posterior lobe. Median ventral keel of eighth somite with rounded apex.

Abdomen broad, depressed. Submedian, intermediate, lateral, and marginal carinae present. Abdominal spines in submedian carinae of sixth somite, intermediate and lateral carinae of fifth and sixth somites, and marginal carinae of fifth somite, formula: submedian 6; intermediate 5 to 6; lateral, 5 to 6; marginal, 5. Sixth abdominal somite with sharp ventral spine anterior to uropod articulation.

Pleopods (Figure 26B to 26F) with gills. Pleopod setation presented in Table 2.

Uropod (Figure 26G) with eight graded moveable spines on outer margin of proximal segment of exopod, last extending to middle of apical segment. Apical segment of exopod extending posteriorly to apex of intermediate spine. Basal seg-

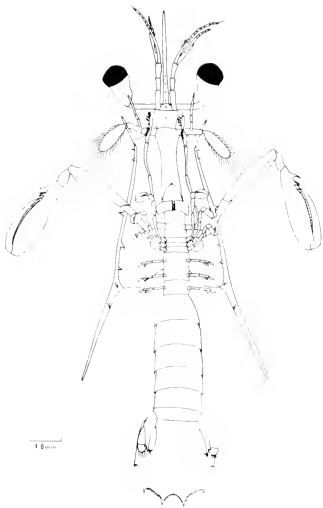


FIGURE 19.—*Squilla empusa*, stage VIII, ventral view

ment of uropod with dorsal spine on distal margin. Basal prolongation of uropod with two spines, mesial longer. Single rounded lobe between spines of prolongation. Mesial margin of basal prolongation sinuate.

Telson (Figure 24) as wide as long, median carina with sharp posterior spine, prelateral lobes absent, postanal ventral carina absent, submedian teeth with moveable apices, denticle formula: submedian, 8 to 10; intermediate, 7 to 10; lateral, 1.

Postlarva white with brown chromatophores on eyes and all appendages except mouthparts. Carapace with few chromatophores. Exposed thoracomeres with chromatophores along posterior margin. Pleomeres with chromatophores along intermediate and lateral carinae and posterior margin. Telson with chromatophores along curved dorsal striations and posterior spine.

TABLE 2.—Number of setae on margins of pleopods of the postlarva of *Squilla empusa*.

Structure	Abdominal somite				
	1	2	3	4	5
Protopod	12-15	12-15	12-15	12-14	8-11
Endopod	55-60	60-71	65-72	63-72	59-67
Exopod	55-59	61-64	62-64	61-63	53-56

DISCUSSION

Brooks (1878) and Faxon (1882) have produced the only prior publications on the larvae of *Squilla empusa*. Brooks partially described the development by reconstruction, and Faxon held an unidentified last stage through metamorphosis to attempt to identify it with the adult. Although Brooks' illustrations and descriptions indicate that he probably was working with *S. empusa*, Faxon's do not. The carapace of Faxon's last stage larvae appears to be too broad, the posterolateral spines are too short, and a spinule is present on the posterior margin of the carapace midway between the dorsal and posterolateral spines. Furthermore, in Faxon's illustrations both the last larval stage and postlarva have broad abdomens with the first pleomere being as wide as the sixth, but in *S. empusa*, the abdomen is tapered with smaller anterior pleomeres grading into larger posterior ones.

Faxon collected his larva from Newport, R.I., where only four species of stomatopods are known to reside: *S. empusa*, *Nannosquilla gravi*, *Heterosquilla armata*, and *Platysquilla enodis* (Manning 1974). Because the telson of Faxon's postlarva bears four intermediate denticles, it can be attributed to the Squillidae, and *S. empusa* is the only squillid known to inhabit the area; the other three species belong to the Lysiosquillidae. Few larval descriptions have been made on southern species of squillid larvae, and of these none possesses the pair of spines on the posterior margin of the carapace, seen in Faxon's larva, nor does *S. empusa*. If Alikunhi (1952, 1967) was correct in his identification of the late larva and postlarva, these spines occur on *Cloridopsis scorpio* from the Indian Ocean. The spines may be only a specific character or they may be diagnostic for the genus *Cloridopsis*. The only member of that genus inhabiting the waters of the Western Atlantic is *C. dubia* which ranges from South Carolina to Brazil. Perhaps Faxon collected a larva of *C. dubia* which drifted north with the Gulf Stream. Until more larval descriptions are worked out for western At-

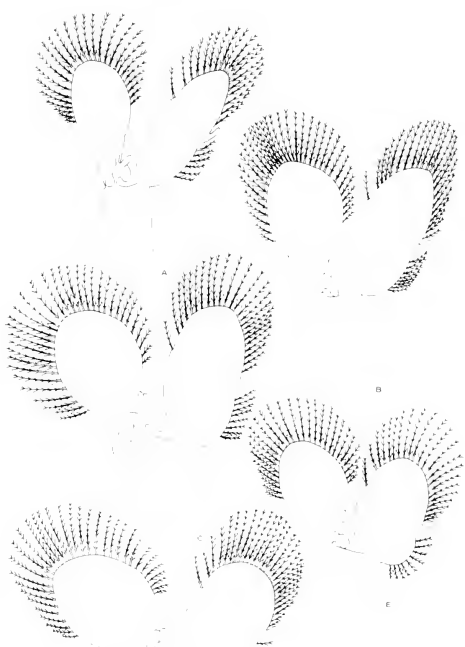


FIGURE 20.—*Squilla empusa*, A-E stage VIII, first to fifth pleopods respectively

lantic species of stomatopods, the identity of Faxon's larva will remain uncertain.

To identify larvae of *S. empusa* the spinules of the carapace and denticles of the telson should be examined. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.

Except for Provenzano and Manning (1978), who reared *Gonodactylus oerstedii* from hatching to metamorphosis, experimenters who have at-

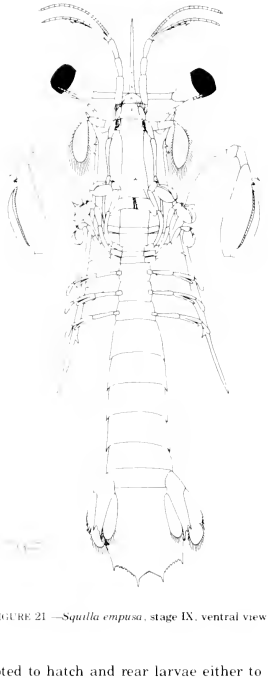


FIGURE 21.—*Squilla empusa*, stage IX, ventral view

tempted to hatch and rear larvae either to link them with an adult or to describe the entire larval development have been unsuccessful at rearing larvae past the first pelagic stage because the larvae could not be induced to feed (Manning and Provenzano 1963). Pyne (1972) was unable to rear *Pterygosquilla armata schizodontia* eggs past the first pelagic stage, but did hold stages I to VII larvae taken from the plankton for periods as long as 10 to 16 days wherein the larvae passed through at least one ecdysis. Pyne also found it possible to keep later stage larvae for very much longer periods of up to 165 days during which time they molted as many as six times. Pyne reared his larvae in mass culture using 4-in (10.2-cm) finger bowls. Alikunhi (1975) reared planktonic larvae of *Oratosquilla nepa* in aquaria through metamorphosis until they reached adulthood, bred, and produced eggs.

The manner in which all species of Squillidae develop is similar. All Squillidae hatch as pseudozoeae with four pairs of pleopods and develop into the alima form. Some, if not all, pass through two propelagic stages before the first truly planktonic stage. The alima is characterized by a telson with four or more intermediate denticles, the distance between the submedian spines in later stages being not larger than that between the intermediate and submedian spines, the propodus of the second maxilliped bearing three basal spines, the antennular somite generally having a median spine, the posterolateral spine of the carapace having a basal accessory spine, the eyestalks long, and the exopod of the uropod being longer than the endopod (Gurney 1942, 1946). Alikunhi (1952) added that alima larvae possess carapaces armed with a varying number of spinules on the lateral margins, the sixth abdominal somite usually being equipped with a pair of submedian dorsal spines, and in advanced larvae, the posterolateral angles of the abdominal somites ending in acute or subacute spines.

Alikunhi (1952) noted that between allied species, the specific differences are often "trivial" but remarkably constant. He determined that some features, such as the size of the final pelagic stage, the shape and spinulation of the carapace, telson, and uropods, and the presence or absence of teeth other than the terminal on the dactylus of the second maxilliped, hardly show any variation within a species. These characters may be used for specific determinations but are presently of little aid in defining generic alliances for three reasons.

First, relatively few stomatopods have been associated definitely with the adult of the species.

Second, most of these have had described only one larval stage of the entire development. Only 19 of the Squillidae have been definitely connected with their larval forms. Provenzano and Manning (1978) listed 17 species of identified stomatopod larvae, but *O. massavensis* was omitted and *S. empusa* has now been added to the list. Of the 19 species, only 2, *P. armata schizodentia* and *S. empusa*, have been reared in the laboratory through essentially their entire pelagic development. Two additional species have been hatched from eggs obtained from a known adult and the first pelagic stage described, i.e., *Clorida chopra* by Gurney

FIGURE 22.—*Squilla empusa*. A-C, stage IX, first to third pleopods respectively.

FIGURE 23.—*Squilla empusa*. A-B, stage IX, fourth to fifth pleopods respectively. C, stage IX, uropod.

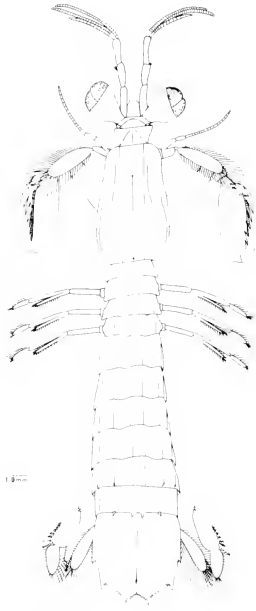


FIGURE 24.—*Squilla empusa*, postlarva, dorsal view

(1946) and *S. mantis* by Giesbrecht (1910), and the remainder have had the last stage described by holding the final pelagic stage until metamorphosis occurred and the stomatopod could be correlated with an adult of the species. Reconstructions of the larval development of three species, *S. mantis* by Giesbrecht (1910), *O. oratoria* by Komai and Tung (1929), and *O. massavensis* by Gohar and Al-Kholy (1957), were attempted by collecting larval stages from the plankton and piecing them together. Metamorphosis from the last larval stage was obtained for *O. massavensis*, but since the larvae were not reared, the larval histories may not be entirely factual. Thus, because so few larval forms have been identified and because most of these have had only one stage described, it is difficult to discover which characters are shared by all members of a genus and which characters are only specific. Of the nine genera of Squillidae which have had larvae described, four genera have had one or more larval stages of a single species described, four more genera have had two species identified, and one genus has had larvae of eight species described. A determination of generic characters is difficult at best for those genera for which only one or two species have been described, especially since there are no adequately represented genera with which to compare characters.

The third reason why specific characters are of little help in generic definition lies in the incomplete descriptions of the larval stages. Characters noted by one author are frequently omitted by another, so that even for the genus *Oratosquilla*, represented by larval descriptions of eight species, consistent characters are difficult to recognize.

An assessment of larval characters was attempted to determine which ones were constant within each genus. Most characters mentioned in the descriptions appeared to vary a great deal for the species within a genus, or the characters that varied relatively little within a genus were frequently found in other species of different genera. Of possible value in defining generic associations is the presence or absence of teeth (other than the terminal) on the dactylus of the second maxilliped. These teeth occur during the last stage in the genera *Anchisquilla*, *Clorida*, *Pterygosquilla*, and *Squilloides*, although for each of these genera larvae of only one species have been described. The dactylus of *P. armata schizodontia* is armed with 5 to 8 teeth and the first stage is easily diagnosed by the posterior spines of the carapace which bear 6 to 16 spirally arranged, proximal spinules. The spinules are replaced by three ventral spinules in the remaining stages (Pyne 1972). The dactyl of the second maxilliped is equipped with two free teeth in *A. fasciata*, three teeth in *S. lata*, and in *C. latreillei* is usually armed with one tooth, rarely with two (Alikunhi 1952). Newly hatched larvae of *C. choprai* were too inadequately described to be compared with *C. latreillei* (Tweedie 1935; Gurney 1946), but the dactylus of the second maxilliped was observed to be unarmed. This is not surprising since *C. latreillei* and *S. lata* develop teeth on the dactylus of the second maxilliped in the later stages and *P. armata schizodontia* develops its first tooth in the third stage.

FIGURE 25.—*Squilla empusa*, postlarva. A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F-J, first to fifth maxillipeds respectively.

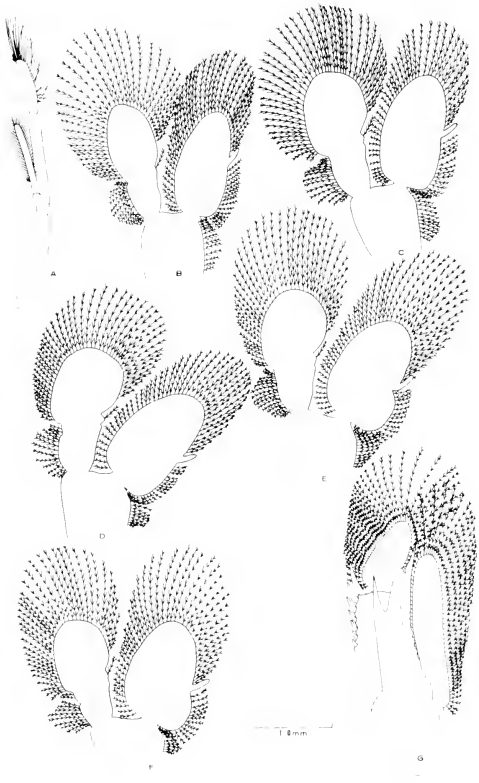


FIGURE 26.—*Squilla empusa*, postlarva, A, first pereiopod, B-F, first to fifth pleopods respectively, G, uropod

The second maxilliped of the remaining described larvae is unarmed throughout the larval development. To distinguish these genera, other characters, such as the presence or absence of a spine on the basis of the second maxilliped, must be relied on. The spine is definitely born by seven of the eight species of *Oratosquilla*, but was not mentioned for *O. massavensis*. Other species, *Squilla empusa*, *P. armata schizodontia*, *Alima hyalina*, and *Meiosquilla lebouri* have the spine, while *Harpiosquilla harpax* and *A. fasciata* definitely do not.

The development of epipods on five pairs of maxillipeds in older larvae appears to be a generic character of *Squilla* as most other genera bear four pairs of epipods.

Characters such as rostral length and spinulation, carapace and telson shape, size, and spinulation, and overall body size and appearance have been too variable within the limited number of species presently described to use them in defining generic associations of the larvae. Deriving characters which apply to the youngest larvae as well as the old will be difficult since far fewer characters are present in the early stage larvae, and the gross appearance of the young larvae is very similar due to the small degree of differentiation. Other characters such as antennular segmentation, mouthpart morphology, setation, spination of the maxillipeds, or the presence of ocular, antennular, epistomal, or basal uropodal spines may also need to be examined. The setation and spination of the first maxilliped may be of great value in defining alliances of the species as well as in making specific determinations. However, many more complete descriptions of the larval developments undergone by the various species must be accomplished before larval characters can be used in establishing generic relationships.

The postlarva of *Squilla empusa* exhibited the basic features of first stage postlarva as determined for other species by Alikunhi (1967). These include the absence of anterolateral spines on the carapace, the extremely poorly developed carination of the carapace, acutely pointed marginal denticles of the telson, and moveable apices of the submedian spines of the telson. As with the adult, the postlarva possesses the full complement of teeth on the raptorial dactylus, just as Alikunhi (1967) found. Furthermore, the five pairs of epipods found in the adult are also possessed by the postlarva. Other adult characters were developed upon the next molt. The dorsal carinations of the carapace were developed, the lateral processes of the exposed thoracic somites five through eight resembled those of the adult, the marginal denticles of the telson were not as acute, and the submedian spines were fixed. The abdominal spinal formula was still not equal to that of the adult. Nevertheless, after the postlarva had undergone its first molt more than enough characters were shared with the adult to make a definite determination of the species.

CONCLUSIONS

1. *Squilla empusa* undergoes nine pelagic stages before attaining the postlarval stage.
2. The last stage stomatopod larva and postlarva described by Faxon (1882) are not *S. empusa*.
3. Larvae of *S. empusa* may be identified by the spinules of the carapace and the intermediate denticles of the telson. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.
4. Rostral length and spinulation, carapace and telson size and spinulation, and overall body size and appearance probably are specific rather than generic characters.
5. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may all be useful characters in determining generic status of larvae belonging to the Squillidae. However, many more complete descriptions of the larval developments undergone by the various species are needed before larval characters can be used in establishing generic relationships.

ACKNOWLEDGMENTS

We are indebted to the National Science Foundation for its support of this work under grant DEB76-11716 to the Old Dominion University Research Foundation.

LITERATURE CITED

ALIKUNHI, K. H.
1952. An account of the stomatopod larvae of the Madras plankton. Rec. Indian Mus. (Calcutta) 49:239-319.
1967. An account of the post-larval development, moulting, and growth of the common stomatopods of the Madras coast. *In* Symposium on Crustacea, Ernakulam, India, 1965, p. 824-939. Mar. Biol. Assoc. India, Symp. Ser. 2.
1975. Studies on Indonesian stomatopods. 1. Growth, maturity and spawning of *Squilla nepa*. Bull. Shrimp Cult. Res. Cent. 1(1):27-32.

BROOKS, W. K.
1878. The larval stages of *Squilla empusa* Say. Johns Hopkins Univ., Chesapeake Zool. Lab. Sci. Res. 1878:143-170.

BURROWS, M.
1969. The mechanics and neural control of the prey capture strike in the mantid shrimps *Squilla* and *Hemisquilla*. Z. vgl. Physiol. 62:361-381.

DRAGOVICH, A.
1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 68:445-460.

FAXON, W.
1882. I.—Crustacea. *In* A. Agassiz, W. Faxon, and E. L. Mark (compilers), Selections from embryological monographs. Mem. Mus. Comp. Zool. (Harv. Univ.) 9(1), 14 plates.

FISH, C. J.
1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. [U.S.] Bur. Fish. 41:91-179.

GIESBRECHT, W.
1910. Stomatopoden. Erster Theil. Fauna Flora Golfes von Neapel, Monogr. 33, 239 p.

GOHAR, H. A. F., AND A. A. AL-KHOLY
1957. The larval stages of three stomatopod Crustacea (from the Red Sea). Publ. Mar. Biol. Stn., Al-Ghardaqa (Red Sea) 9:85-130.

GURNEY, R.
1942. Larvae of decapod Crustacea. Ray Soc. (Lond.) Publ. 129, 306 p.
1946. Notes on stomatopod larvae. Proc. Zool. Soc. Lond. 116(1):133-175.

HILDEBRAND, H. H.
1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 3:233-366.

KAESTNER, A.
1970. Invertebrate zoology. Vol. 3, Crustacea. Wiley Interscience, N.Y., 523 p.

KOMAI, T., AND Y. M. TUNG
1929. Notes on the larval stages of *Squilla oratoria*, with remarks on some other stomatopod larvae found in the Japanese Seas. Annot. Zool. Jpn. 12:187-214.

LEBOUR, M. V.
1924. Young anglers in captivity and some of their enemies. A study in a plunger jar. J. Mar. Biol. Assoc. U.K. 13:721-734.

MAC GINITIE, G. E., AND N. MAC GINITIE.
1968. Natural history of marine animals. 2d ed. McGraw-Hill, N.Y., 523 p.

MANNING, R. B.
1969. Stomatopod Crustacea of the western Atlantic. Stud. Trop. Oceanogr. (Miami) 8, 380 p.
1974. Marine flora and fauna of the northeastern United States. Crustacea: Stomatopoda. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-387, 6 p.

MANNING, R. B., AND A. J. PROVENZANO, JR.
1963. Studies on development of stomatopod Crustacea I. Early larval stages of *Gonodactylus oerstedii* Hansen. Bull. Mar. Sci. Gulf Caribb. 13:467-487.

PICCINETTI, C., AND G. P. MANFRIN
1970. Prime osservazioni sull'alimentazione di *Squilla mantis* L. Bologna Univ. Inst. Zool. Note 3(10):251-263.

PROVENZANO, A. J., JR., AND R. B. MANNING
1978. Studies on development of stomatopod Crustacea II. The later larval stages of *Gonodactylus oerstedii* Hansen reared in the laboratory. Bull. Mar. Sci. 28:297-315.

PYNE, R. R.
1972. Larval development and behaviour of the mantis shrimp *Squilla armata* Milne Edwards (Crustacea: Stomatopoda). J. R. Soc. N.Z. 2:121-146.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

REINTJES, J. W., AND J. E. KING.
1953. Food of yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 54:91-110.

SUNIER, A.
1917. The Stomatopoda of the collection "Visscherystation" at Batavia. Contrib. Faune Indes. Neerl. 1(4):62-75.

TWEEDIE, M. W. F.
1935. Two new species of *Squilla* from Malayan waters. Bull. Raffles Mus. 10:45-52.

VARIATION IN THE FOURBEARD ROCKLING, *ENCHELYOPUS CIMBRIUS*, A NORTH ATLANTIC GADID FISH, WITH COMMENTS ON THE GENERA OF ROCKLINGS

DANIEL M. COHEN[1] AND JOSEPH L. RUSSO[2]

ABSTRACT

Enchelyopus cimbrius, the fourbeard rockling, is a gadid fish living around the rim of the North Atlantic Ocean. It varies geographically in color pattern; anal, dorsal, and pectoral fin ray counts; and vertebral and gill racker counts. There is a lack of overall concordance in patterns of variation in color and meristics. Morphometric characters do not distinguish populations from different geographical areas, and the fourbeard rockling is considered to be a single species.

New distributional records include the Gulf of Mexico, West Greenland, and West Africa.

We classify the rocklings as a tribe, Gadropsarini, of the subfamily Lotinae. Characters previously used to separate rocklings into five genera—skull shape, vomerine tooth patch shape, number and distribution of supratemporal pores, length of first dorsal fin ray, and size of jaw teeth—do not distinguish nominal genera. Number of snout barbels divides rocklings into three groups that we tentatively recognize as genera: *Gaidropsarus*, the threebeard rocklings, with two snout barbels, *Enchelyopus*, the fourbeard rockling, with three snout barbels; and *Ciliata*, the fivebeard rocklings, with four or more snout barbels. *Onogadus* and *Antonogadus* are referred to the synonymy of *Gaidropsarus*.

The correct generic name for the fourbeard rockling is *Enchelyopus* Bloch and Schneider 1801, with *Rhinonemus* Gill 1863 as a junior synonym. It is not preempted by *Enchelyopus* Gronovius 1760 in Zoarcidae, which was used in a work that was not consistently binominal.

The fourbeard rockling, *Enchelyopus cimbrius*, is a locally abundant gadid fish found around the margins of the North Atlantic Ocean. Although this fish has been recorded in the literature for more than 200 yr, many aspects of its biology are obscure. Adults are sedentary bottom dwellers taken at depths ranging from about 1 to 650 m [we have been unable to verify depth records to 1,325 m given by Goode and Bean (1896)]. There is some indication that seasonal offshore-onshore movements occur (Bigelow and Schroeder 1953; Tyler 1971). The pelagic larval stages are similar in appearance to young hakes (*Urophycis*) and sometimes occur in silvery swarms near the surface (Bigelow and Schroeder 1953).

Recent collections discussed in this paper show that fourbeard rocklings are more widely distributed than previously was known and that geographical variation is present. One of our objectives in this paper is to describe, compare, and evaluate geographical variation of selected characters and to show that a single species is represented throughout the range of the fish.

The rockling group of the family Gadidae, which is characterized by several distinctive features, recently was divided into five genera (Wheeler 1969), although most ichthyologists have recognized only three (albeit under a variety of names). The second of our objectives is to show that at present there are valid reasons for only three.

The fourbeard rockling is currently named *Enchelyopus cimbrius* by North American ichthyologists and *Rhinonemus cimbrius* by Europeans. Our final objective is to show that *Enchelyopus* is the correct generic name.

METHODS

All observations were made on museum specimens listed in the Appendix. Counts of dorsal and anal fin rays and vertebrae were taken from X-ray photographs. Vertebral counts do not include the terminal ural element. Gill raker counts include all rakers on upper and lower arms of the first arch. Head pores were examined with the aid of a compressed air jet. Measurements and their

[1]Systematics Laboratory, National Marine Fisheries Service, National Museum of Natural History, Washington, DC 20560.
[2]Systematics Laboratory, National Marine Fisheries Service, National Museum of Natural History, Washington, D.C.; present address: Department of Biological Sciences, The George Washington University, Washington, DC 20006.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

statistical analysis are described under Body Proportions. Statistical tests were performed on the IBM 370-148[3] computer at The George Washington University, using computer programs written and maintained at the Systematics Laboratory, NMFS, NOAA, and following statistical methods presented by Zar (1974).

GEOGRAPHICAL VARIATION

The distribution of the fourbeard rockling may be summarized as the coastal waters of the North Atlantic. In the western Atlantic the species occurs in: West Greenland (new record); the northwestern Gulf of Saint Lawrence and around Newfoundland as well (Leim and Scott 1966 and this paper) to Cape Fear (about lat. 34°N) (Bigelow and Schroeder 1953); the northeast coast of Florida (Bullis and Thompson 1965); off the Florida Keys (new record); and in the northern Gulf of Mexico (new record). In the eastern Atlantic the species occurs: around Iceland (Saemundsson 1949) and the Faroes (Joensen and Taaning 1970); from northern Norway at about lat. 71°N in the Barents Sea and south along the coasts of Scandinavia (Andriyashev 1954); in the western Baltic (rarely to the Gulf of Finland, Svetovidov 1973); throughout the North Sea and around the British Isles to the northern Bay of Biscay (Wheeler 1969; Du Buit 1968); and off Cape Blanc, Mauritania (new record). It is not known from the Mediterranean. Figure 1 shows the approximate localities from which we have studied specimens. More detailed locality data are presented in the Appendix.

Sampling Areas

We have compared fish from the following geographical areas.

Gulf of Mexico. Only 3 localities are represented in our collections. These specimens are among the most darkly pigmented of any we have studied.

Southern Atlantic. Specimens taken from the South Carolina coast at about lat. 33°N to about lat. 29°N on the east coast of Florida, which is as far south as specimens have been caught in the western Atlantic outside of the Gulf of Mexico. There is no reason to doubt that this population is continuous with those farther north, and the northern boundary as here given is arbitrarily limited by available study material.

Intermediate. Fish caught in the vicinity of Cape Hatteras from about lat. 35°N to the vicinity of Norfolk Canyon at about lat. 37°N are included in

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

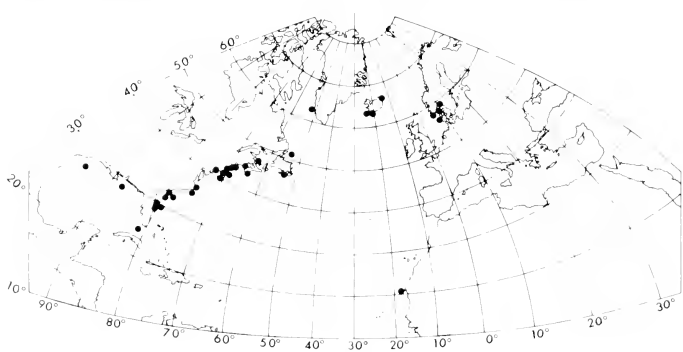


FIGURE 1.—Localities for our specimens of *Enchelyopus cimbrius*. Some dots represent more than one collection. For detailed data on localities see Appendix

this area, which we separate because it is geographically between the region to the south, where fishes are mostly dark colored.

Northern Atlantic. This region extends along the western Atlantic coast from north of the vicinity of Norfolk Canyon to the northern North American limit of *E. cimbrius* occurrence.

Greenland. A single specimen from West Greenland is apparently the only known occurrence of *E. cimbrius* from Greenland.

Iceland. The region around Iceland.

Europe. Although *E. cimbrius* occupies a considerable area we have examined only a small sample, mainly from Denmark and Norway.

Africa. Two specimens from off the coast of Mauritania ca. lat. 21°N are the most southerly known.

Color

Enchelyopus cimbrius from the Gulf of Mexico and Southern Atlantic areas have on the average more of the dorsal fin colored with dark pigment than do fourbeard rocklings from other areas (Table 1). We have attempted to quantify this character by coding it on a 0-10 scale with 0 representing a fin with no dark pigment and 10 representing a fin that is completely dark. Values were subjectively assigned by a single observer (Cohen). Figure 2A shows a New England fish that would be coded as 1; Figure 2B shows the color pattern of a fish from the Gulf of Mexico, which would be coded as 6. Note that fish are morphologically intermediate and most variable in the Intermediate region[4] where the mean is 3.8 and the standard deviation is highest at 2.8.

Two other pigment characters were noted; however, neither was quantified. Fish with light fins lacked dark pigment in the groove along the base of the row of filaments between the strong first dorsal ray and the beginning of the normally developed dorsal fin (Figure 3A); fish with dark dorsal fins had varying amounts of dark pigment in this region (Figure 3B). Also, in many Gulf, Southern Atlantic, and Intermediate fish the body was dusky; in most others the body was a rather light straw color.

TABLE 1.—Frequency distributions of degree of dorsal fin pigmentation in *Enchelyopus cimbrius* from eight geographical areas. 0 = no dark pigment in dorsal fin; 10 = entire fin darkly pigmented.

	Degree of pigmentation													
Area	0	1	2	3	4	5	6	7	8	9	10	*N*	$\bar{x}$	*SD*
Gulf of Mexico			2	1	5	2	4	1	1	2		18	6.2	2.1
Southern Atlantic		1	—	2	6	1	6	17	6	6	2	47	6.7	1.9
Intermediate		7	6	4	6	—	—	2	1	3	1	30	3.8	2.8
Northern Atlantic		29	5	7	3	—	2					46	1.8	1.3
Greenland						1						1	5	—
Iceland		5	2	2	1							10	1.9	1.1
Europe		1	26	1	1	1	2					32	1.4	0.9
Africa			1	1								2	1.5	—

Meristics

Frequencies of both anal fin rays and dorsal fin rays show a pattern similar to, though less pronounced than, that shown by dorsal fin pigmentation in the western Atlantic (Tables 2, 3), with fish from the Intermediate area being intermediate between fish from the north and the south. Also, for anal fin rays the standard deviation is larger in fish from the Intermediate area than in adjacent samples. These two characters differ from dorsal pigmentation in having the highest mean in the Iceland sample.

Frequencies of pectoral fin rays and vertebrae for North American samples from the Intermediate area have nearly identical means in both

[4]Detailed descriptions of color variation in samples from Norfolk Canyon and comparisons with specimens from the northeast coast of Florida have been presented by P. Szarek 1974. A preliminary study of Norfolk Canyon *Enchelyopus cimbrius* Ichthyology Term Paper, Virginia Institute of Marine Science.

TABLE 2.—Frequency distributions of numbers of anal fin rays in *Enchelyopus cimbrius* from eight geographical areas.

	Number of anal fin rays																	
Area	36	37	38	39	40	41	42	43	44	45	46	47	48	49	*N*	$\bar{x}$	*SD*
Gulf of Mexico				6	4	2	4								16	40.2	1.2
Southern Atlantic				6	11	18	8	3							46	40.8	1.1
Intermediate				1	2	5	4	7	2	2	2	—	—	1	26	42.8	2.2
Northern Atlantic						8	8	9	13	9	2	2	1		52	43.5	1.7
Greenland								1							1	43	—
Iceland									2	4	3	1			10	45.3	0.9
Europe		1	—	1	1	—	2	1	3	6	1	—	—	1	17	42.6	3.0
Africa									1	1					2	44.5	—

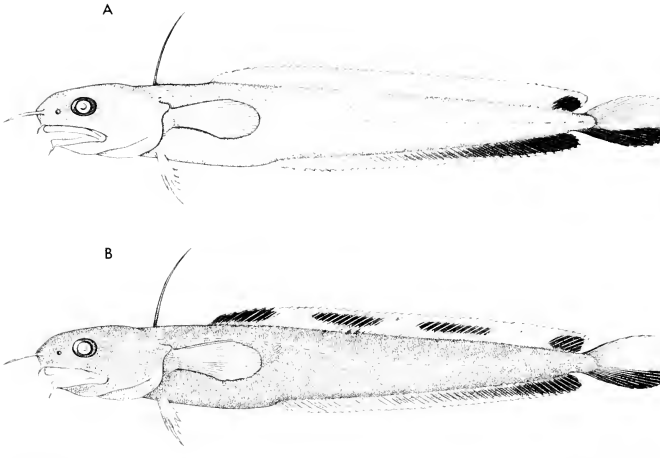


FIGURE 2.—*Enchelyopus cimbrius*. A, USNM 213501, standard length 282 mm, off Cape Cod, dorsal fin pattern coded as 1 (see text). B, color pattern of a fish from the Gulf of Mexico (USNM 217843) drawn on the outline of the fish shown in Figure 2A, dorsal fin pattern coded as 6 (see text).

TABLE 3.—Frequency distributions of numbers of dorsal fin rays in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of dorsal fin rays											N	$\bar{x}$	SD
	45	46	47	48	49	50	51	52	53	54	55			
Gulf of Mexico	1	1	11	3								16	47.0	0.7
Southern Atlantic	1	8	10	12	7	8	1					47	47.9	1.5
Intermediate			1	3	8	9	5	—	2	1		29	49.9	1.6
Northern Atlantic	1	—	—	6	13	8	12	4	4	3	1	52	50.4	1.9
Greenland							1					1	51	—
Iceland						5	2	3				10	50.8	0.9
Europe		1	2	3	3	4	3	1				17	49.2	1.7
Africa						2	—	—	—	—	—	2	50.0	—

of these characters with Northern Atlantic fish, rather than being intermediate (Tables 4, 5); however, for pectoral fin rays, fish from these two areas have lower counts that are in between Gulf and Atlantic, and Greenland, Iceland, and Europe samples. Iceland fish average highest of all in dorsal and anal fin ray counts and in vertebral counts (not including the few specimens from Greenland and Africa). In pectoral counts, however, Iceland and Europe specimens have identical means.

In total gill raker counts (Table 6) eastern Atlantic samples have higher means than do western Atlantic samples, with the highest standard deviation being in the Northern Atlantic samples.

Body Proportions

Measurements were taken of the following eight body parts and compared for six of them in fish from the six geographical areas listed below and described previously under sampling areas (Greenland and Africa are not included in the present analysis). Linear regressions were calculated for the following dependent variables, with standard length as the independent variable:

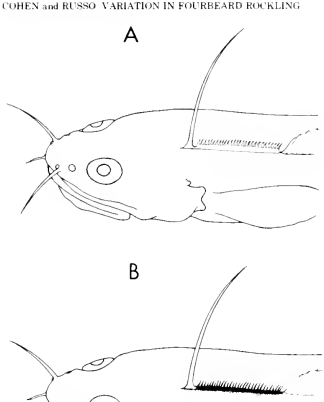


FIGURE 3.—*Enchelyopus cimbrius*. A, USNM 213501, head length 62.8 mm, off Cape Cod, note absence of dark pigment along base of fin with short rays. B, USNM 217843, head length 33.2 mm, Gulf of Mexico, note dark pigment along base of fin with short rays.

TABLE 4.—Frequency distributions of numbers of vertebrae in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of vertebrae							N	$\bar{x}$	SD
	49	50	51	52	53	54	55			
Gulf of Mexico			9	7				16	51.4	0.5
Southern Atlantic	1	1	18	22	10			52	51.8	0.9
Intermediate			4	7	12	6	1	30	52.8	1.0
Northern Atlantic			3	14	26	15	1	59	52.9	0.9
Greenland						1		1	54	—
Iceland					4	3	3	10	53.9	0.9
Europe			2	3	7	3		15	52.7	1.0
Africa						1	1	2	54.5	—

snout to first dorsal fin (pre D_1 distance); first dorsal fin to the dorsal fin beginning posterior to the row of small filamentous rays (D_1-D_2 distance); head length; pectoral fin length; upper jaw length; horizontal diameter of eye (orbit length); length of barbel on lower jaw; and ventral fin length. Numbers of specimens measured and their size ranges (standard length in millimeters) were: Gulf of Mexico 17 (125-228); Southern Atlantic 46 (125-263); Intermediate 29 (104-202); Northern Atlantic 53 (50.5-297); Iceland 10 (151-327); Europe 27 (93.8-300).

TABLE 5.—Frequency distributions of numbers of pectoral fin rays in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of pectoral fin rays					N	$\bar{x}$	SD
	15	16	17	18	19			
Gulf of Mexico	1	2	9	6	1	19	17.2	0.9
Southern Atlantic		9	21	14	1	45	17.2	0.8
Intermediate	2	9	14	4		29	16.7	0.8
Northern Atlantic	5	21	21	5	1	53	16.5	0.9
Greenland			1			1	17	—
Iceland	1	2	2	5		10	17.1	1.1
Europe	1	2	8	4	1	16	17.1	1.0
Africa		2				2	16	—

TABLE 6.—Frequency distributions of total numbers of gill rakers on first arch in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of gill rakers									N	$\bar{x}$	SD
	5	6	7	8	9	10	11	12	13			
Gulf of Mexico				5	3	2	—	1		11	9.0	1.3
Southern Atlantic			2	9	12	17	4			44	9.3	1.0
Intermediate			1	1	11	6	5			24	9.5	1.0
Northern Atlantic	3	1	1	8	8	12	6	2		41	9.1	1.8
Greenland					1					1	9	—
Iceland					2	5	2	1		10	10.2	0.9
Europe					6	4	3	1	1	15	10.1	1.3
Africa					1	—	1			2	10.0	—

Analysis of covariance was used to compare regression lines (Tables 7, 8) for six measurements that we have treated as linear based on a coefficient of determination (r^2) of 0.73 or higher (Table 8). Two measurements, ventral fin length and barbel length, had coefficients of determination ranging from 0.42 to 0.61 and were not further analyzed.

Fishes from all six geographical areas demonstrated overall coincidence at the 0.05 level of significance in two characters, head length and upper jaw length. Hypotheses concerning overall coincidence of regressions for the other characters were rejected and hypotheses concerning the equality of slopes and intercepts were simultaneously tested.

The hypothesis concerning the equality of slopes was rejected for the D_1-D_2 distance versus standard length regression lines. Regression data were

TABLE 7.—Significance of differences in six morphometric characters in *Enchelyopus cimbrius* from six geographical regions. Independent variable is standard length.

Dependent variable	N	Overall coincidence	Equality of slopes	Equality of intercepts
Pre D_1 distance	165	[1]0.0048	0.5342	[2]$4.9 \cdot 10^{-7}$
D_1-D_2 distance	165	[1]0.0024	[1]0.0111	[1]0.0012
Head length	182	0.3004	—	—
Pectoral fin length	150	[1]0.0061	0.0617	[1]0.0011
Orbit length	166	[2]$2.0 \cdot 10^{-5}$	0.1839	[2]$2.4 \cdot 10^{-7}$
Jaw length	166	0.2892	—	—

[1]Rejection of hypothesis of equality at the 0.05 level of significance
[2]Rejection of hypothesis of equality at the 0.001 level of significance

TABLE 8.—Y intercepts in millimeters, slopes, coefficients of determination (r^2), and N for regression lines calculated on *Enchelyopus cimbrius* from six geographical areas. Independent variable is standard length

Geographical area	Measurement					
	Pre D_1 distance	D_1 D_2 distance	Head length	Pectoral fin length	Upper jaw length	Orbit length
Gulf of Mexico						
Y intercept	2.91	2.21	2.29	0.17	-3.08	0.10
Slope	0.16	0.12	0.18	0.14	0.11	0.04
r^2	0.89	0.86	0.93	0.87	0.87	0.79
N	16	16	17	14	17	17
Southern Atlantic						
Y intercept	0.11	-4.74	0.22	0.89	-1.83	0.76
Slope	0.17	0.15	0.20	0.15	0.11	0.04
r^2	0.96	0.89	0.94	0.91	0.89	0.90
N	43	44	46	43	44	44
Intermediate						
Y intercept	-0.60	-0.74	-0.71	0.48	-2.69	-0.06
Slope	0.18	0.12	0.21	0.14	0.11	0.05
r^2	0.95	0.86	0.92	0.87	0.92	0.79
N	29	29	29	29	29	28
Northern Atlantic						
Y intercept	-0.32	0.47	-0.43	-2.22	-3.38	1.64
Slope	0.16	0.12	0.21	0.16	0.12	0.04
r^2	0.97	0.89	0.97	0.92	0.87	0.92
N	51	51	53	38	51	50
Iceland						
Y intercept	0.47	3.59	2.09	6.02	-5.71	2.65
Slope	0.17	0.10	0.20	0.12	0.13	0.03
r^2	0.79	0.92	0.99	0.87	0.98	0.98
N	10	10	10	10	9	10
Europe						
Y intercept	-0.61	-4.37	-0.74	-2.06	-4.70	1.29
Slope	0.18	0.16	0.21	0.15	0.12	0.04
r^2	0.97	0.73	0.91	0.90	0.91	0.94
N	16	16	27	16	16	17

submitted to a Newman-Keuls multiple range test in order to determine which population sample or groups of population samples were different from others. This procedure failed to detect differences between any slopes, a not uncommon occurrence due to the fact that the analysis of covariance is a more powerful test than is the multiple range test. The sample from Iceland had the lowest slope at 0.10, the Northern Atlantic, Gulf of Mexico, and Intermediate samples each had a slope of 0.12, the Southern Atlantic sample had a slope of 0.15, and the sample from Europe had a slope of 0.16.

The hypotheses concerning the equality of Y intercepts was rejected at the 0.05 level of significance for all four characters tested. These regression data also were submitted to a Newman-Keuls multiple range test in order to determine which population sample or groups of population samples were different from others. Again, this procedure failed to detect significant differences between any Y intercepts.

If a more stringent 0.001 level of significance is used, only orbit length tests as being significantly different with respect to overall coincidence. Data for this regression from each of the six samples were submitted to a continuation of analysis of covariance to determine whether differences in the regression lines were attributable to the slopes and/or the Y intercepts. We accept equality of the slopes with a probability of 0.85. However we reject the equality of the Y intercepts after calculating a probability of equality of 2.06×10^{-5}. Regression data were submitted to a Newman-Keuls test, which failed to detect differences between any pairs of intercepts. Inspection of our data shows that rocklings from Iceland appear to have a proportionally larger eye than do other rocklings; however, our sample is small and may be biased by larger fishes; hence we do not draw inferences from this apparent difference.

Although differences between samples apparently exist, we do not interpret them as representing the kind of discontinuity that indicates distinct species. Their significance is beyond the scope of this paper.

Discussion

We believe that the fourbeard rockling is best considered as a single species throughout its entire range. Differences in pigment pattern, meristics, and the relative size of several body parts do exist; however, there are neither trenchant discontinuities in variation nor is there any overall

concordance in patterns of variation. Differences between and similarities among samples are summarized in Figure 4 and discussed below for meristics and color pattern. Differences in morphometric characters are so slight that we do not further consider them.

Gulf of Mexico and Southern Atlantic samples are quite similar, although at this time the two might be semi-isolated from each other. The clockwise loop current system in the Gulf of Mexico provides a possible pathway for the dispersal of young, pelagic stage rocklings out of the gulf; there is no present avenue for recruitment into the Gulf of Mexico. If the single rockling taken off the Florida Keys represents more than a stray, then perhaps Gulf of Mexico and Southern Atlantic populations are continuous; otherwise, the north Gulf-northeast Florida distribution pattern is similar to that noted first in fishes by Ginsburg (1952). Although *E. cimbrius* seems rare in the Gulf of Mexico its occurrence at two widely separated localities, with a collection of 16 individuals from one of them, indicates that the species is established there. Although pelagic stages have not yet been taken from the Gulf of Mexico or Southern Atlantic areas, it seems reasonable to assume that they occur there and are available for dispersal in the Gulf Stream system.

Rocklings from the Intermediate area are indeed intermediate between adjacent populations to the north and south in degree of pigmentation and in dorsal and anal ray counts. Furthermore, for two of these characters, color and number of anal fin rays, the standard deviation is larger than in other populations, implying that recruits from different spawning populations are entering the area or that the characters are genetic and variability is being maintained during spawning in the Intermediate area. For two characters, numbers of vertebrae and pectoral fin rays, Intermediate and Northern Atlantic fish are nearly identical and differ from Southern Atlantic and Iceland samples. These characters must be determined or mediated differently than are color pattern and dorsal and anal fin ray counts. Gill raker count appears to reflect still a third method of character determination as the means are different on the two sides of the Atlantic. Although pelagic early stages have not been taken in the Intermediate area, they may be available for dispersal to the northeast by means of the Gulf Stream and to the southwest in coastal currents that parallel the Gulf Stream. Such dispersal patterns would help to account for the occurrence of dark-colored rocklings in the north and light-colored ones in the south.

Rocklings from the Northern Atlantic area more closely resemble fish from Europe and Iceland in degree of pigmentation and number of vertebrae than they do their immediate neighbors to the south. Conversely they are closer to other North American samples in numbers of pectoral

CHARACTER	GEOGRAPHICAL AREA					
	Gulf	S. Atl.	Intermed.	N. Atl.	Iceland	Europe
Color	6.2	6.7	3.8	1.8	1.9	1.4
Anal Rays	40.2	40.8	42.8	43.5	43.3	42.6
Dorsal Rays	47.0	47.9	49.9	50.4	50.8	49.2
Vertebrae	51.4	51.8	52.8	52.9	53.9	52.7
Pectoral Rays	17.2	17.2	16.7	16.5	17.1	17.1
Gill Rakers	9.0	9.3	9.5	9.1	10.2	10.1

FIGURE 4.—Summary of means of character states for *Enchelyopus cimbrius* from six geographical areas. Heavy lines are drawn around entries that are discussed in the text as separate entries and that illustrate overall lack of convergence in character states.

rays and gill rakers. Spawning is known to occur in the Northern Atlantic area. Eggs have been taken from surface tows in Passamaquoddy Bay, where spawning peaked at bottom temperatures of 9° to 10°C (Battle 1930). In Long Island Sound eggs were found to be most abundant in the upper 12 m (Williams 1968). In reviewing the natural history of *E. cimbrius* in the Gulf of Maine, Bigelow and Schroeder (1953) mentioned the possibility of planktonic existence as long as 3 mo. Given such a time span, the complex hydrographic regime of the area might occasionally distribute early stages to the south inshore of the Gulf Stream or even more rarely might transport them via the Gulf Stream to the eastern Atlantic.

Iceland rocklings are usually light colored, as are fish from the Northern Atlantic and Europe areas. For counts of dorsal and anal fin rays, and vertebrae, Iceland fish have the highest means of all (ignoring the two fish from Africa); perhaps these characters are influenced by temperature, as Iceland has the lowest temperatures of any of the six areas. In numbers of pectoral rays, Iceland and European fish are identical and in gill rakers nearly so, and different from counts of North American ones. Adults at least of the Iceland population may be isolated as Kotthaus and Krefft (1967) did not catch *E. cimbrius* along the Iceland-Faroe ridge. *Enchelyopus cimbrius* spawns at least around the southwest coast of Iceland (Einarsson and Williams 1968).

The linear range of the fourbeard rockling along the coasts of Europe is about as great as along the coasts of North America. We have examined only a small sample, from southern Scandinavia; hence, it is possible that more variation exists than we have recorded. However, we point out that in our sample the color pattern resembles that of Iceland and Northern Atlantic fish, that counts of anal and dorsal fin rays and vertebrae are lower than those in Iceland, and that in numbers of pectoral fin rays and gill rakers Europe and Iceland fish are more like each other than they are like North American populations. Rocklings are known to spawn in European waters [Svetovidov (1973) gives several references]. *Enchelyopus cimbrius* could have reached Europe from the west via the Gulf Stream system; it seems unlikely that east to west dispersal is possible.

We do not know whether the West Greenland specimen of *E. cimbrius* represents a breeding population or a stray.

The two West African examples are so far removed from their nearest known neighbors (Bay of Biscay) that we forego conjecture as to their origin.

THE GENERA OF ROCKLINGS

The rocklings are classified in the subfamily Lotinae of the family Gadidae (Svetovidov 1948) and can be distinguished by the nature of the three dorsal fins, which, although scarcely separated from each other, bear quite different kinds of rays (Figure 5). The first dorsal fin consists of a single, unsegmented ray which is not bilaterally divided (we have examined microscopic sections) and is supported by a strong pterygiophore. The ray is thicker than any others in the dorsal fin and in many species is longer as well. In *Enchelyopus cimbrius* it is soft, being ossified only proximally. Sharply distinguished from the first and third dorsal fins is a row of small, unsegmented, bilaterally divided filaments which appear fleshy, although they stain with alizarin. These small rays originate on a compressed ridge that rises from a middorsal groove. Although Bogoljubsky (1908) followed by Svetovidov (1948) did not consider these filaments to be true fin rays they should be considered as such, as examination of an alizarin preparation and of sections shows that a simple, ossified, rod-shaped skeletal support is present for each. The third dorsal fin is composed of ordinary, bilaterally divided, segmented rays, each with a well-developed pterygiophore.

A second characteristic of the rocklings is the presence on the snout of prominent barbels (the closest approach to this character among other gadids being a nasal cirrus in *Lota*) in addition to the barbel at the tip of the lower jaw.

Thus, the rocklings are distinguished by two specialized characters and can be considered as a distinct tribe of Lotinae, the Gaidropsarini [classified as a distinct family by some, for example, de Buen (1934)].

Although rocklings have been treated under as many as 14 different generic names [see Svetovidov (1973) for synonyms], many ichthyologists (for example, Andriyashev 1954; Norman 1966) follow Svetovidov (1948) in recognizing three. More recently, however, five genera have been recognized (Wheeler 1969). How many genera should be recognized and why?

In his 1948 treatment of the rocklings, Svetovidov provided diagnoses for the three genera that he recognized based on barbel number, skull shape, vomerine tooth patch shape, and

FIGURE 5.—*Enchelyopus cimbrius*, USNM 217900, standard length 135 mm; photograph of an alizarin preparation in glycerin showing the three different kinds of dorsal fin rays and their skeletal supports.

number and distribution of supratemporal pores (our Table 9). Unfortunately, he was unable to study all of the species. We have examined six of the nominal *Gaidropsarus* species that he recognized, both species of *Ciliata*, and, of course, *Enchelyopus* (study material of all genera is listed in the Appendix).

Number of barbels is the only character that unequivocally divides our material according to Svetovidov's classification.

Proper evaluation of the skull-width character will require the examination of osteological preparations, which we have not done. We note, however, that although *Ciliata mustela* has a notably broad skull, that of *C. septentrionalis* appears to be narrower. Also, although most species of *Gaidropsarus* appear to have narrow skulls, that of *G. guttatus* appears broad.

Regarding the size and shape of the vomerine tooth patch, it is highly variable, and although it may serve to distinguish some species it is of doubtful value at the genus level.

TABLE 9.—Summary of diagnostic characters for three rockling genera given by Svetovidov (1948)

Genus and no. of species	Characters			
	No. of barbels	Skull shape	Vomer	Supratemporal pores
Gaidropsarus (13)	3	Narrow	Head large, apex angular	3 = 1 pair + 1 median
Enchelyopus (1)	4	Narrow	Small	3 = 1 pair + 1 median
Ciliata (2)	5 or more	Broad	Head small, anterior a semicircle	2 = 1 pair

Number of supratemporal pores also is a variable character. Five of the *Gaidropsarus* species that we have studied show the pattern given for the genus by Svetovidov (1948), one median and one pair of pores (= 3). However, *G. argentatus* has two pairs and no median pores (= 4). In *Ciliata*, *C. mustela* has one pair (= 2), while *C. septentrionalis* has three pairs (= 6).

As noted above, Wheeler (1969) recognized five genera, the three recognized by Svetovidov (1948): *Enchelyopus*, *Ciliata*, and *Gaidropsarus*; and also *Onogadus* de Buen 1934; and a genus introduced for the first time, *Antonogadus*.

Onogadus was originally proposed for *Gaidropsarus ensis*, one of the threebeard rocklings, because of its elongate first dorsal ray. Wheeler (in Svetovidov 1973) has subsequently assigned to *Onogadus*, *G. argentatus*, a species with a far shorter first dorsal fin ray. We have found the length of the first dorsal fin to be highly variable in *Enchelyopus*. As presently used, this character does not separate genera. (Wheeler[5] has informed us that *Onogadus* may be differentiated on the basis of vertebral counts. Due to insufficient data we have no comment on this character.) As we have mentioned above, *G. argentatus* differs from *G. ensis* and resembles *Ciliata* in lacking a median supratemporal pore.

[5]A. Wheeler, Department of Zoology, British Museum (Natural History), Cromwell Road, London S.W. 7, England. Pers. Commun. March 1978.

Antonogadus Wheeler 1969 was first introduced in the combination *Antonogadus macrophthalmus* (Günther), unfortunately, in a key to species rather than a treatment of genera. Subsequently, another threebeard rockling, *Gaidropsarus megalokynodon* (Kolombatovic 1894), was referred to *Antonogadus* (Wheeler in Svetovidov 1973) in a checklist. There is no way to tell if the original key characters describing dentition, mouth size, and color are diagnostic of the genus *Antonogadus* or the species *A. macropththalmus*; however, we assume that they apply to the genus. Color may be discounted as a generic character as it is highly variable among the species of *Gaidropsarus* and varies geographically in the single species of *Enchelyopus*. Regarding mouth size, Wheeler (1969) noted "mouth large, extending well past eye"; however, figures of *macrophthalmus* given by Günther [1867, pl. 5, fig. B and 1887, pl. 42, fig. D, the latter as *Onus carpenteri*, a junior synonym of *macrophthalmus* according to Wheeler in Svetovidov (1973)] show fish with small mouths. The second species referred to *Antonogadus*, *megalokynodon*, is figured by Söljan (1963) as having a large and capacious mouth, but he shows the same condition for several other species of threebeard rocklings. So far as we can tell mouth size is not a useful generic character. Carrying on to dentition, Wheeler (1969) noted, "A pair of large, fang-like, teeth (sometimes three or four) in front of the upper jaw." If *Antonogadus* is recognized on the basis of such a character then it would be necessary to place the two species of *Ciliata* in separate genera, as *C. mustela*, the type-species of the genus has bands of equal-sized teeth in the upper and lower jaws, while *C. septentrionalis* has in addition to these bands a much enlarged outer row of teeth in the upper jaw and an enlarged inner row in the lower jaw.

It is by no means clear that number of barbels alone divides the rocklings into natural species assemblages; convergence may have occurred and other groupings based on different characters may produce a phyletically more correct classification. Obviously, thorough study and a careful analysis of characters is required. For the present there seems insufficient information available to do other than recognize on the basis of number of barbels a single genus with three subgenera, or three genera. We follow the latter course as it is the most conservative in terms of the present usage of names. We recommend therefore, that for the present *Onogadus* be relegated once again to the synonymy of *Gaidropsarus* where it should be joined by *Antonogadus*.

THE CORRECT GENERIC NAME FOR THE FOURBEARD ROCKLING

Although differences at the species level have not evolved in populations of the fourbeard rockling on both sides of the North Atlantic, curiously enough geographical isolation seems to have affected the evolution of different generic names. *Rhinonemus* is used by European ichthyologists (see, for example, Svetovidov 1973); North American ichthyologists use *Enchelyopus* (see, for example, Leim and Scott 1966). Which is the correct name?

Enchelyopus Gronovius 1760 was the first of the two names proposed. Although only a brief color description was given, reference was made to the same author's pre-Linnean Museum Ichthyologicum published in 1754, in which work under the names *Mustela vivipera* and viviparous eelpout is presented a recognizable description of the species presently named *Zoarces viviparus* (Linnaeus). This identification is further verified by a Gronovius specimen still extant in the British Museum, which Wheeler (1958) has suggested is a type-specimen of *Blennus viviparus* Linnaeus. Use of *Enchelyopus* in Zoarcidae, where it is a senior synonym of *Zoarces* Cuvier 1829 has been accepted by Norman (1966) and noted as being correct by Andriyashev (1973). Some ichthyologists (Gill 1863b; Jordan 1917), however, seem to have overlooked Gronovius (1760) and attributed the name to Gronovius (1763) in his Zoophylaceum, a work subsequently ruled on by the International Commission on Zoological Nomenclature (Opinion 89) as being unavailable for purposes of zoological nomenclature. The Commission noted in its ruling that combinations used in the Zoophylaceum were "binary" though not "binomial," which interpretation complied with the then current edition of the Rules, and the work was declared unavailable by suspension of the Rules.

Although Gronovius (1760) never has been ruled on by the Commission it follows the same system of nomenclature as does Gronovius (1763) and clearly is not binominal. The same is true of Gronovius (1762), which has been rejected (Opinion 332). Under the provisions of the present Code (Article 11(c)), names published in Gronovius (1760) are not available as the author did not con-

sistently apply the principles of binominal nomenclature. Although Article 11.(c)(i) ("Uninominal genus-group names published before 1931 without associated nominal species are accepted as consistent with the principles of binominal nomenclature, in the absence of evidence to the contrary.") might serve as a basis for arguing that the names in Gronovius (1760) are available, the interests of stability would be served best by considering the work unavailable, as its acceptance would require not only that *Enchelyopus* Gronovius 1760 replace *Zoarces* Cuvier 1829, but also that *Cyclogaster* Gronovius 1760 replace *Liparis* Scopoli 1777.

If Gronovius (1760) is considered as unavailable for purposes of zoological nomenclature then the first valid use of *Enchelyopus* is by Bloch and Schneider (1801). The type-species was stated by Jordan (1917) as *Gadus cimbrius* Linnaeus 1766 as first restricted, and Svetovidov (1973) gave the type as *Gadus cimbrius* Linnaeus 1766 by monotypy. However, neither of these methods of type fixation is correct as Bloch and Schneider referred 12 species to the genus, and although *cimbrius* is the first one in order, there is no action that could be construed as a type designation. The earliest type designation for *Enchelyopus* Bloch and Schneider 1801 that we have been able to find is that of Jordan (1917) as *Gadus cimbrius* Linnaeus 1766.

Rhinonemus Gill (1863a) was proposed for *Motella caudacuta* Storer 1848, a junior synonym of *Gadus cimbrius* Linnaeus (Goode and Bean 1879) and is therefore a junior synonym of *Enchelyopus* Bloch and Schneider.

ACKNOWLEDGMENTS

We are grateful to A. Wheeler for information and discussions about rockling taxonomy, P. Szarek for allowing us to read her unpublished manuscript, and S. Johnson for information on zoarcid nomenclature. For reading and commenting on all or part of the manuscript we thank A. Cohen, B. Collette, L. Dempster, M. Fahay, and W. J. Follett. G. S. Myers assisted by allowing access to rare literature. For access to study material we thank D. McAllister, National Museums of Canada; R. Jenkins, Cornell University; J. Kaylor, NMFS, NOAA, Gloucester, Mass.; M. Dick, Harvard University; R. Wigley, NMFS, NOAA, Woods Hole, Mass.; C. Wenner and J. Musick, Virginia Institute of Marine Science; G. Jónsson, Marine Research Institute, Reykjavik; J. G. Nielsen, University of Copenhagen; A. Wheeler, British Museum (Natural History); and M. L. Bauchot, Natural History Museum, Paris.

For assistance with computer processing we thank K. K. Beach, E. M. Hamilton, and the Office of Technical Assistance at The George Washington University Center for Academic and Administrative Computing. Figures 1-4 were prepared by Keiko Hiratsuka Moore. George Clipper took X-ray photographs. Histological sections of the dorsal fin were prepared by Margaret Melville. The manuscript was typed by A. McClain and V. Tucker.

LITERATURE CITED

ANDRIYASHEV, A. P.
1954 Ryby severnykh morey SSSR Opred Faune SSSR 53, 566 p Akad. Nauk SSSR. (Transl 1964, Fishes of the northern seas of the U.S.S.R. Keys to the fauna of the U.S.S.R. 53, 617 p., U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. OTS 63-11160.)
1973 Zoarcidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Vol. I, p. 540-547. UNESCO, Paris.

BATTLE, H. I.
1930. Spawning periodicity and embryonic death rate of *Enchelyopus cimbrius* (L.) in Passamaquoddy bay. Contrib. Can. Biol. Fish., New Ser. 5:363-380.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BLOCH, M. E., AND J. G. SCHNEIDER.
1801. Systema Ichthyologiae. Berlin, 584 p.

BOGOLJUBSKY, S.
1908. Zur kenntnis der dorsalflosse bei "Motella tricirrata". Z. Wiss. Zool. 90:327-333.

BUEN, F. DE
1934 Notas sobre los Gaidropsaridae (Peces). Un nuevo genero (*Onogadus* nov. gen.) y una nueva especie (*Gaidropsarus barbatus* nov. sp.). Bol. Soc. Esp. Hist. Nat. 34:499-504.

BULLIS, H. R., JR., AND J. R. THOMPSON.
1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

CUVIER, G.
1829. Le regne animal. Nouvelle ed. tom. II. Paris, 406 p.

DU BUIT, M. H.
1968 Notes biometriques et biogeographiques ser deux poissons teleosteens consideres comme rares dans l'Atlantique Nord. Trav. Fac. Sci. ser. Oceanogr. Biol. Univ. Rennes 1 1:5-17.

EINARSSON, H., AND G. C. WILLIAMS.
1968 Planktonic fish eggs of Faxafloi, southwest Iceland, 1948-1957. Rit Fiskideildar 4(5), 15 p.

GILL, T. N.
1863a. Synopsis of the North American gadoid fishes. Proc. Acad. Nat. Sci. Phila. 1863:229-242.
1863b. Synopsis of the family Lycodoidae. Proc. Acad. Nat. Sci. Phila. 1863:254-262.

GINSBURG, I.
1952. Eight new fishes from the Gulf coast of the United States, with two new genera and notes on geographic distribution. J. Wash. Acad. Sci. 42:84-101

GOODE, G. B., AND T. H. BEAN
1879. The identity of *Rhinonemus caudacuta* (Storer) Gill with *Gadus cimbrius*, Linn. Proc. U.S. Natl. Mus. 1:348-349.
1896 (1895). Oceanic ichthyology. U.S. Natl. Mus. Spec. Bull. 2, 551 p.

GRONOVIUS, L. T.
1754. Museum Ichthyologicum, sistens piscium indigenorum et quorundam exoticorum, qui in Museo Laur. Theod. Gronovii, adservantur, descriptiones, ordine systematico; accedunt nonnullorum exoticorum piscium icones, aeri incisae, vol. 1. Lugduni, 70 p.
1760. Animalium in Belgio habitantium centuria prima. Acta Helv. 4:243-270.
1762. Animalium Belgicorum observatorum centuria quinta. Acta Helv. 5:353-382.
1763. Zoophylacii Gronoviani, fasc. 1. Leiden, 136 p.

GUNTHER, A.
1867. Additions to the British fauna. Ann. Mag. Nat. Hist., Ser. 3, 20:288-291.
1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873-76. Zoology of the Challenger Expedition. Part 57, 335 p.

JOENSEN, J. S., AND A. V. TAANING.
1970. Marine and freshwater fishes. *In* S. L. Tuxen (editor), Zoology of the Faroes, 241 p. Vald. Pedersen, Copenh.

JORDAN, D. S.
1917. The genera of fishes, pt. 1. Stanford Univ. Publ. Univ. Ser. 27:1-161.

KOTTHAUS, A., AND G. KREFFT.
1967. Observations on the distribution of demersal fish on the Iceland-Faroe Ridge in relation to bottom temperatures and depths. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 157:238-267.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155, 485 p.

LINNAEUS, C.
1766. Systema Naturae Tom. 1, 12th ed. Holmiae. 532 p.

NORMAN, J. R.
1966. A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates. Br. Mus. (Nat. Hist.), Lond., 649 p.

SAEMUNDSSON, B.
1949. Marine Pisces. *In* A. Frioriksson and S. L. Tuxen (editors), The zoology of Iceland, 4(72), 150 p. Munksgaard, Copenh. and Reyk

SCOPOLI, J. A.
1777. Introductio ad historiam naturalem. Pragae, 506 p.

SÖLJAN, T.
1963. Fishes of the Adriatic. Revised Engl. ed. NOLIT, Belgr., 428 p.

SVETOVIDOV, A. N.
1948. Treskoobraznye. Faune SSSR, Ryby 9(4), 221 p. Akad. Nauk SSSR. (Transl. 1962, Gadiformes, Fauna USSR, Fishes 9(4), 304 p. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va. OTS 63-11071.)
1973. Gadidae. *In* J. C. Hureau and Th. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Vol. I, p. 303-320. UNESCO, Paris.

TYLER, A. V.
1971. Periodic and resident components in communities of Atlantic fishes. J. Fish. Res. Board Can. 28:935-946.

WHEELER, A. C.
1958. The Gronovius fish collection: a catalogue and historical account. Bull. Br. Mus. (Nat. Hist.) Hist. Ser. 1:187-249.
1969. The fishes of the British Isles and North-West Europe. Macmillan, Lond., Melb., Toronto, 613 p.

WILLIAMS, G. C.
1968. Bathymetric distribution of planktonic fish eggs in Long Island Sound. Limnol. Oceanogr. 13:382-385.

ZAR, J. H.
1974. Biostatistical analysis. Prentice Hall Inc., Englewood Cliffs, N.J., 620 p.

APPENDIX

The following abbreviations indicate institutions or collections: CU, Cornell University; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National d'Histoire Naturelle, Paris; NEFC, Northeast Fisheries Center, Woods Hole, Mass.; NMC, National Museum of Natural Sciences, Ottawa; USNM, National Museum of Natural History, Washington, D.C.; ZMUC, Zoologisk Museum, Copenhagen. The "Intermediate" region, below, extends from about lat. 35°N to about lat. 37°N in the western Atlantic.

Enchelyopus cimbrius

GULF OF MEXICO—USNM 190346 (3 specimens), *Silver Bay* stn 294, 27°54'N, 95°23'W, 79 m. USNM 217843 (16), *Oregon* 3724, 29°04'N, 88°31'W, 403 m. USNM 217939 (1), *Oregon* 5795, 24°16'N, 82°30'W, 439 m.

SOUTHERN ATLANTIC—USNM 217923 (2), *Silver Bay* 1611, 29°06'N, 80°00'W, 339-384 m. USNM 217924 (2), *Silver Bay* 223, 29°14'N, 80°05'W, 247 m. USNM 217935 (1), *Oregon* 5798, 29°14'N, 80°05'W, 357 m. USNM 217933 (5), *Oregon* 5098, 29°17'N, 80°05'W, 379 m. USNM 217931 (1), *Silver Bay* 4227, 29°20'N, 80°05'W, 348 m. USNM 217949 (2), *Silver Bay* 224, 29°29'N, 80°09'W, 329 m. USNM 217937 (1), *Combat* 475, 29°30'N, 80°10'W, 293 m. USNM 217934 (3) *Oregon* 5093, 29°31'N, 80°09'W, 384 m. USNM 217932 (1), *Silver Bay* 219, 29°34'N, 80°09'W, 348 m. USNM 217917 (1), *Silver Bay* 1607, 29°34'N, 80°09'W, 371 m. USNM 217943 (1), *Combat* 325, 29°35'N, 80°10'W, 366 m. USNM 217936 (1), *Combat* 314, 29°38'N, 80°11'W, 329 m. USNM 217918 (1), *Oregon* 5238, 29°39'N, 80°12'W, 348 m. USNM 217916 (2), *Silver Bay* 1606, 29°40'N, 80°12'W, 348 m. USNM 217940 (1), *Silver Bay* 217, 29°41'N, 80°08'W, 348 m. USNM 217919 (2), *Silver Bay* 458, 29°49'N, 80°10'W, 220 m. USNM 217921 (2), *Silver Bay* 1552, 29°43'N, 80°12'W, 302 m. USNM 217948 (1), *Combat* 435, 29°46'N, 80°12'W, 366 m. USNM 217920 (1), *Silver Bay* 3742, 29°50'N, 80°13'W, 275 m. USNM 217950 (5), *Silver Bay* 1604, 29°50'N, 80°10'W, 302 m. USNM 217947 (2), *Silver Bay* 3678, 29°53'N, 80°11'W, 329 m. USNM 217944 (3), *Silver Bay* 3675, 29°55'N, 80°11'W, 329 m. USNM 217922 (1) *Silver Bay* 4367, 29°55'N, 80°11'W, 320 m. USNM 217945 (1), *Oregon* (1), 5233, 29°54'N, 80°10'W, 348 m. USNM 217925 (1), *Combat* 471, 29°57'N, 80°12'W, 329 m. USNM 217946 (3), *Pelican* 182-8, 32°09'N, 79°02'W, 275 m. USNM 217938 (1), *Combat* 300, 32°15'N, 78°51'W, 348 m. USNM 217927 (1), *Combat* 289, 33°03'N, 77°09'W, 366 m.

INTERMEDIATE—USNM 45898 (1), *Albatross*, 35°40'N, 74°52'W. USNM 45895-6 (7), *Albatross*, 36°02'N, 74°48'W. USNM 217941 (1), *Oregon II* 10763, 36°01'N, 74°48'W, 311-567 m. USNM 217951 (1), *Oregon II* 10664, 36°12'N, 74°47'W, 249-329 m. USNM 217942 (2), *Oregon II* 10724, 36°14'N, 74°45'W, 366-421 m. USNM 217929 (2), *Columbus Iselin* 73-10-40, 36°33'N, 74°42'W, 296 m. USNM 217928 (3), *Columbus Iselin* 73-10-47, 36°37'N, 74°42'W, 316 m. USNM 217926 (3), *Columbus Iselin* 73-10-89, 37°02'N, 74°38'W, 367 m. USNM 217930 (7), *Columbus Iselin* 73-10-73, 37°05'N, 74°43'W, 194-479 m.

NORTHERN ATLANTIC—USNM 28994 (1), *Albatross*, 38°39'N, 73°11'W, 238 m. USNM 45969 (1), *Albatross*, 38°54'N, 72°51'W. USNM 28917 (1), 39°43'N, 71°32'W. USNM 45891 (1), *Albatross*, 39°48'N, 71°49'W. MCZ 37492 (1), *Capt. Bill II* 20, 39°57'N, 71°07'W, 412 m. USNM 28843 (1), *Fish Hawk*, 39°57'N, 70°32'W. USNM 28816 (1), 39°N, 71°W. MCZ 38039 (1), *Caryn* 3-1, 39°59'N, 70°48'W, 381 m. USNM 33352 (1), *Fish Hawk*, 40°20'N, 70°35'W. USNM 28709 (1), 40°24'N, 70°42'W. USNM 35680 (1), 40°21'N, 70°29'W. USNM 28890 (2), 40°28'N, 70°44'W. USNM 126948 (1), *Fish Hawk*, Long Island Sound, 22 m. USNM uncat. (1), *Albatross IV*, 41°14'N, 71°41'W. USNM 213501 (7), *Blesk* 68-18, 22-01, 41°52'N, 68°12'W, 198 m. USNM uncat. (1), *Blesk* 68-18, 24-02, 41°36'N, 68°52'W, 138 m. USNM uncat. (1), *Blesk* 68-18, 28-01, 42°N, 69°39'W, 210 m. USNM 16656 (1), Woods Hole, Mass. CU 18353 (3), *Albatross III* 27-45, 41°53'N, 69°10'W, 212 m. USNM uncat. (1), *Delaware* 60-1-11, 41°52'N, 68°14'W, 227 m. CU 18274 (1), *Albatross III* 61-1, 41°49'N, 68°14'W, 154 m. USNM 23761 (1), Provincetown, Mass. CU 45869 (1), *Albatross IV* 63-5-69, 42°07'N, 67°31'W. NEFC uncat. (3), *Albatross III* 70-23, 42°10'N, 68°38'W, 183 m. NEFC uncat. (1), *Albatross III* 101-103, 42°15'N, 67°10'W, 168 m. CU 23620 (3), *Albatross III* 27-55, 42°41'N, 69°49'W, 256 m. NEFC uncat. (1), *Albatross III* 47B-3-2, 42°41'N, 70°09'W, 84-139 m. USNM 83925 (1), Mass. Bay. USNM 21918 (1), Mass. Bay.

134 m. USNM 131920 (6), Mass. Bay. USNM 21918-9 (2), Mass. Bay. MCZ 34614 (3), 42°56'N, 70°18'W, 165 m. MCZ 34611 (3), *Albatross II*, 43°07'N, 70°10'W, 154 m. USNM 37847 (1), Ipswich Bay, Mass. MCZ 34612 (9), *Albatross II*, 43°03'N, 70°09'W. USNM 45897 (1), *Albatross*, 43°34'N, 63°56'W. MCZ 34613 (4), 43°39'N, 68°12'W, 192 m. MCZ 12340 (1), Eastport, Maine. USNM 39060 (1), Prince Edward Island. USNM 43229 (1), 47°15'N, 53°58'W. NMC 63-151 (1), 51°28'N, 53°52'W.

GREENLAND—ZMUC uncat. (1), *Adolf Jensen* 4420, 64°22'N, 52°54'W, 460-540 m.

ICELAND—ZMUC 95-96, (2), North coast of Iceland, ca. 66°N, 18°30'W. ZMUC 830-32 (3), Vestman Islands. ZMUC 26-27 (2), 63°46'N, 22°56'W. ZMUC P379 (1), south of Iceland. USNM 217909 (1), 65°37'N, 21°00'W, 110 m. USNM 217911 (1), 65°41'N, 21°20'W, 137-152 m.

EUROPE—USNM 39724 (1), Denmark. ZMUC 84-85 (2), 90-93 (4), 501, 503-4 (3), P37284-292 (9), P37294-96 (3), P37298 (1), Denmark. ZMUC P37283 (1), Limfjord, Denmark. P37297 (1), Kallundborg Fjord, Denmark. ZMUC 88 (1), 502 (1), Snekkersten, Denmark. ZMUC 86 (1), 98 (1), Oresund, Denmark. ZMUC 22-23 (2), Skagerak, 200 m. ZMUC 25 (1), off Lindesnøs, Norway, 220 m. USNM 44514 (1), Drobak, Norway.

AFRICA—MNHN 38-110 111 (2), off Cape Blanc, Mauritania.

Ciliata mustela

USNM 130840 (4), Europe. USNM 44510 (1), Norway. USNM 216711 (2), Oresund, Denmark.

Ciliata septentrionalis

ZMUC 371656-7 (2), Faroe Islands.

Gaidropsarus argentatus

MCZ 38353,38387 (2), western North Atlantic. USNM 217907 (1), Iceland. USNM 217912 (1), Iceland. USNM 217910 (1), Spitsbergen. USNM 217908 (2), Iceland.

Gaidropsarus ensis

MCZ 37554 (1), western North Atlantic. MCZ 27882 (1), western North Atlantic. MCZ 38425 (1), western North Atlantic. MCZ uncat. (1), western North Atlantic. USNM 217913 (1), western North Atlantic.

Gaidropsarus guttatus

USNM uncat. (2), (1), (5), San Miguel Island, Azores.

Gaidropsarus mediterraneus

USNM uncat. (1), Tunisia.

Gaidropsarus vulgaris

USNM uncat. (1), (1), (3), Tunsia.

Gaidropsarus sp.

USNM uncat. (5), Amsterdam Island.

EARLY DEVELOPMENT OF SEVEN FLATFISHES OF THE EASTERN NORTH PACIFIC WITH HEAVILY PIGMENTED LARVAE (PISCES, PLEURONECTIFORMES)

B. Y. SUMIDA, E. H. AHLSTROM, AND H. G. MOSER[1]

ABSTRACT

Eggs and larval series are described for six species of flatfishes occurring off California with heavily pigmented larvae. These are the pleuronectids *Pleuronichthys coenosus*, *P. decurrens*, *P. ritteri*, *P. verticalis*, and *Hypsopsetta guttulata* and the bothid, *Hippoglossina stomata*. A brief description of postflexion larvae of the Gulf of California species, *P. ocellatus*, is also presented.

Eggs of *Pleuronichthys* are unusual among flatfishes in possessing a sculptured chorion composed of a network of polygonal walls, whereas the chorions of *Hypsopsetta guttulata* and *Hippoglossina stomata* eggs are smooth and unornamented. Eggs of *Hypsopsetta guttulata* and *P. ritteri* are unusual among those of pleuronectid flatfishes in possessing an oil globule.

A combination of pigmentation, morphology, and meristics can distinguish the seven species of flatfishes with heavily pigmented larvae. Larvae of two species, *H. guttulata* and *P. decurrens*, have a distinctive pterotic spine on either side of the head. Sizes at hatching, at fin formation, and at transformation are important considerations to distinguish these species. Meristic counts, particularly of precaudal and caudal groups of vertebrae, are important to relate a larval series to its juvenile and adult stages and thus substantiate identification of the series.

This report deals primarily with the eggs, larvae, and early juveniles of flatfishes of the genus *Pleuronichthys*. Descriptions are included for complete series of larvae of four species, *P. decurrens* (curlfin turbot),[2] *P. coenosus* (C-O turbot), *P. verticalis* (hornyhead turbot), and *P. rittert* (spotted turbot). A brief account of postflexion larvae of the Gulf of California species, *P. ocellatus* (Gulf turbot), is also given. Larvae of *Pleuronichthys* are heavily pigmented, even at hatching, as are those of the pleuronectid, *Hypsopsetta guttulata* (diamond turbot), and the bothid, *Hippoglossina stomata* (bigmouth sole). To identify heavily pigmented flatfish larvae obtained in plankton collections from the eastern North Pacific, it is necessary to know the larval developmental series of all of the above species. These species comprise minor incidental catches within California commercial and sport fisheries and are reported as a general grouping of "turbots." Species most commonly caught in the fisheries are *P. decurrens*, *P. coenosus*, *P. verticalis*, and *Hypsopsetta guttulata* (Frey 1971; Bell 1971; Oliphant 1973; Pinkas 1974; McAllister 1975). No specific catch data are available for *Hippoglossina stomata*, but the species is probably caught incidentally and included in the "miscellaneous sole" category of catch data.

In a review of the genus *Pleuronichthys*, Fitch (1963) recognized six species including the five listed above and *P. cornutus* from off Japan and China. In an earlier review of the genus, Starks and Thompson (1910) recognized these six species and *P. nephelus* Starks and Thompson. Norman (1934) concurred with Starks and Thompson in recognizing seven species. Fitch (1963), however, agreed with Hubbs (1928) in finding no grounds for the separation of *P. nephelus* from *P. coenosus* after his examination of the type material of *P. nephelus*. Fitch's review is thorough; he examined more than 5,700 individuals of the genus. We follow his classification.

The first descriptions of the eggs and early-stage larvae of *Pleuronichthys* were given by Budd (1940) who dealt with *P. coenosus*, *P. decurrens*, and *P. verticalis*. Orton and Limbaugh (1953) described the eggs of *Hypsopsetta guttulata* and *P.*

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]The common name turbot is used for all species of *Pleuronichthys*, a usage consistent with Fitch (1963), Miller and Lea (1972), and Gates and Frey (1974:79). The American Fisheries Society's list of common names (Bailey et al. 1970) designates *P. coenosus* and *P. decurrens* as soles, but we disagree with giving species within a genus different common general names.

Manuscript accepted September 1978
FISHERY BULLETIN VOL. 77, NO. 1, 1979

ritteri. Larvae of *P. verticalis* were illustrated in Ahlstrom and Moser (1975), and Eldridge (1975) described and illustrated larvae of *H. guttulata*.

MATERIALS AND METHODS

Eggs, larvae, and some juveniles were primarily obtained from California Cooperative Oceanic Fisheries Investigations (CalCOFI) collections. These samples were preserved in a consistent manner as described in Kramer et al. (1972). Additional material was obtained from bay, estuarine, and coastal collections of Occidental College; Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service; California State University at Fullerton; Scripps Institution of Oceanography; Oregon State University; and Humboldt State University. Specimens of *P. ritteri*, *P. verticalis*, and *H. guttulata* reared at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, were also utilized.

Egg and oil globule diameters were measured using an ocular micrometer in a stereomicroscope. For eggs that were not perfectly round, the greatest diameter was recorded. Scanning electronmicrographs were made for four kinds of *Pleuronichthys* eggs and for eggs of *Synodus lucioceps* (Synodontidae). The greatest diameter of 10 randomly selected polygonal facets of the chorion of *Pleuronichthys* and *Synodus* eggs were measured using an ocular micrometer in a compound microscope. To do this the chorion was cut into pieces that were laid flat on a glass slide with a cover slip over them.

The number of specimens examined varied by species, depending on their availability and abundance, ranging from several hundred larvae of *P. verticalis*, the most abundant species, to two larvae of *P. ocellatus*. For most species, the minimum number of specimens studied is indicated in the morphometric tables with usually twice as much material looked at for pigmentation development. A developmental series of larvae through juveniles was assembled for each species. Measurements of selected body parts were taken to provide descriptive and comparative morphometric data. Measurements were made on the right side of each pleuronectid specimen, and on the left side of the bothid, *Hippoglossina stomata*, using an ocular micrometer in a stereomicroscope. Terminology used in the morphometric tables is as follows:

Body length = In preflexion and flexion stages, horizontal distance from tip of snout to tip of notochord, referred to as notochord length (NL); in postflexion stages, from tip of snout to posterior margin of hypural elements, i.e., standard length (SL).

Snout to anus = Horizontal distance from tip of snout through midline of body to vertical through anus.

Head length = Horizontal distance from tip of snout through midline of head to margin of cleithrum preceding the pectoral fin base.

Snout length = Horizontal distance from tip of snout to anterior margin of pigmented region of eye.

Eye width = Horizontal distance through midline of pigmented eye.

Eye height = Vertical distance through center of pigmented eye.

Body depth at pectoral base = Vertical distance across body at pectoral fin base prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement in the morphometric tables when it includes the depth of dorsal fin pterygiophores.

Body depth at anus = Vertical distance across body at anus prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement when it includes the depth of the dorsal fin pterygiophores.

Caudal peduncle depth = Vertical distance across tail immediately posterior to terminal dorsal and anal fin rays.

Caudal peduncle length = Medial horizontal distance from vertical through terminal dorsal and anal fin rays to posterior margin of hypural elements.

Snout to pelvic fin origin = Horizontal distance from tip of snout to vertical through origin of right pelvic fin (left in *H. stomata*).

Larval specimens for each species were not available in sufficient numbers to clear and stain for complete data on meristics and sequence of ossification of bony elements. However, fin ray counts were made and tabulated on unstained specimens. A partial larval series of *P. verticalis*, our most abundant species, was cleared with KOH and stained with Alizarin Red-S by Hollister's method (1934) to determine the process of axial skeletal development and fin formation. In addition, several larvae of *P. coenosus* and *P. decurrens* were cleared and stained for precaudal and

total vertebral counts which verified identifications and proved that Budd (1940) confused identifications of larvae of these two species. Radiographs of transforming larvae, juveniles, and adults of each species provided additional meristic data.

We divide the larval period into three stages, preflexion, flexion, and postflexion, based on the flexion of the notochord which occurs during caudal fin formation (Moser and Ahlstrom 1970; Ahlstrom et al. 1976; Moser et al. 1977). In *Pleuronichthys* and some other flatfishes the initiation of caudal fin formation begins while the notochord is still straight, in the late preflexion stage; we designate this phase as "early caudal formation." We found it convenient to divide the flexion stage into three substages, early flexion, midflexion, and late flexion, dependent upon the state of flexion of the notochord. In the early flexion stage, the notochord is very slightly flexed upward; in midflexion, it is flexed midway (nearly a 45° angle); and in late flexion, the notochord is approaching a terminal position, except that the caudal rays remain in a slightly oblique position. Transformation from the larval to juvenile stage was marked by eye migration, development of ossified pectoral fin rays, scales, and the lateral line.

MERISTIC COUNTS OF LARVAE

Meristic counts overlap among species considered here, and for discrimination of species it is necessary to use a combination of counts (Table 1). Precaudal and caudal vertebral counts, used in conjunction with dorsal and anal fin counts, are of most use in relating larvae to juveniles or adults. Pelvic fin ray counts are six per side in all seven species and branchiostegal ray counts are seven per side. Pectoral fin counts cannot be made on larvae since ossified pectoral rays form at metamorphosis. Gill rakers are not fully formed during the larval period in the species described.

DESCRIPTION OF EGGS

Pleuronichthys spp.

Eggs of three *Pleuronichthys* species were first described by Budd (1940) who collected them in plankton hauls from Monterey Bay, Calif. Budd noted the hexagonal patterns on the chorions of *Pleuronichthys* eggs. This type of ornamentation of the egg shell is confined to *Pleuronichthys* among flatfishes, but similar polygonal sculpturing is found on eggs of the families Synodontidae (Sanzo 1915; Mito 1961) and Callionymidae (Holt 1893; Ehrenbaum 1905; Mito 1962) and in a more exaggerated form on eggs of the sternoptychid, *Maurolicus muelleri* (Sanzo 1931; Mito 1961), and the macrourid, *Coelorhynchus coelorhynchus* (Sanzo 1933). Eggs of the three species of *Pleuronichthys* described by Budd were strikingly different in size; his largest, *P. coenosus*, averaged 1.88 mm in diameter, his intermediate-sized egg, *P. decurrens*, 1.44 mm, and his smallest, *P. verticalis*, 1.07 mm. All had homogeneous yolk, and lacked an oil globule. Our work shows that Budd misidentified the two larger eggs and corresponding larvae; the one he called *P. coenosus* is *P. decurrens* and vice versa. Orton and Limbaugh (1953) described an egg with an hexagonal pattern on its chorion that possessed a single oil globule; they tentatively, but correctly, assigned it to *P. ritteri*. White (1977) illustrated a developing egg of *P. ritteri* from Newport Bay, Calif.

Information concerning egg diameters, presence or absence of an oil globule, and character of the chorion are given in Table 2 for six of the seven species treated in this paper. Egg diameters do not change noticeably with the duration of preservation, although some shrinkage is known at the initial time of preservation. There is no overlap in egg size for the three species of *Pleuronichthys* that lack an oil globule. Eggs of *P. decurrens* range from 1.84 to 2.08 mm; those of *P. coenosus*, from

TABLE 1.—Meristics of the seven species of flatfishes in the eastern North Pacific that have heavily pigmented larvae [1]

Species	Dorsal rays	Anal rays	Pectoral rays (eyed side)	Vertebrae			Total gill rakers	Caudal rays	
				Precaudal	Caudal	Total		Total	Branched
Pleuronichthys decurrens	67-81	46-55	10-14	14-15	24-26	38-41	9-12	19-21	12-15(13)
P. coenosus	66-78	44-56	9-12	12-13	24-26	37-39	11-15	18-20(19)	12-15(13)
P. verticalis	66-79	44-51	10-12	13	23-25	36-38	9-11	19-20	12-14(13)
P. ocellatus	62-74	44-53	10-12	12-13	22-24	34-36	10-14	19	12-15(13)
P. ritteri	62-72	43-52	9-11	12-13	22-24	34-36	12-17	18-19	13-14
Hypsopsetta guttulata	65-75	47-55	11-13	11-12	22-24	34-36	2+(5-6)	19-20	13
Hippoglossina stomata	63-70	47-55	11-12	11	26-28	37-39	15-21	17-18	11-13

[1]Meristics compiled in Table 1 are derived in part from literature, particularly Fitch (1963), Norman (1934) Townsend (1936) Clothier (1950) and Ginsburg (1952), and in part from our original counts. Where a range is given and one count is predominant, that count is italicized.
[2]Lower limb count only

TABLE 2.—Measurements of eggs of *Pleuronichthys* species, *Hypsopsetta guttulata*, and *Hippoglossina stomata*, including *Synodus lucioceps* for comparative data.

Species	Character of chorion	No. of eggs measured	No. of samples	Egg diameters (mm) Range	Mean	SD	Oil globule diameters (mm) Range	Mean	SD
Pleuronichthys decurrens	Sculptured	41	28	1 84-2 08	1 97	0 058	—	—	—
P. coenosus (CalCOFI)	Sculptured	20	15	1 28-1 56	1 47	0 066	—	—	—
P. coenosus (King Harbor)	Sculptured	287	2	1 20-1 42	1 29	0 047	—	—	—
P. verticalis	Sculptured	188	19	1 00-1 16	1 09	0 040	—	—	—
P. ritteri	Sculptured	82	13	0 94-1 08	1 01	0 029	0 08-0 14	0 10	0 009
Hypsopsetta guttulata	Smooth	35	4	0 78-0 89	0 84	0 027	0 12-0 14	0 13	0 010
Hippoglossina stomata	Smooth	26	9	1 22-1 38	1 29	0 045	0.20-0.26	0 23	0 018
Synodus lucioceps	Sculptured	168	8	1 20-1 48	1 32	0 049	—	—	—

1.20 to 1.56 mm; and those of *P. verticalis*, from 1.00 to 1.16 mm. Although eggs of *P. ritteri*, ranging in diameter from 0.94 to 1.08 mm, fall within the size range of *P. verticalis*, they can be readily distinguished by the presence of a small oil globule, 0.08-0.14 mm in diameter. Eggs of *P. ocellatus* were unavailable.

Differences in mean diameter of *P. coenosus* eggs were noted by locality, with eggs taken in open waters off the coast having a larger mean diameter and standard deviation (Table 2, CalCOFI collections) than eggs sampled from the inlet of a small, shallow, manmade harbor near a power plant discharge (Table 2, King Harbor samples). Except that they are often slightly larger in size, early- and middle-stage eggs of *P. coenosus* are difficult to differentiate from *Synodus lucioceps* eggs. They can be separated, however, by careful examination of the size and arrangement of polygons on the chorion. The mean of the greatest distance across polygons (sample size = 200 polygons) on *P. coenosus* eggs is 0.035 mm in contrast to 0.047 mm for *S. lucioceps* eggs (Table 3). Furthermore, the polygons on *P. coenosus* eggs are more regular in arrangement than on *S. lucioceps* eggs (Figure 1). This more uniform compacting of smaller polygons on *P. coenosus* eggs versus a more random patterning of larger polygons on *S. lucioceps* eggs is visible under a light microscope, and will separate these eggs. Late-stage eggs are easily distinguished by the heavy pigmentation on the embryo of *P. coenosus* compared with the sparse pigment on advanced *S. lucioceps* embryos, which also have a longer gut.

TABLE 3.—Comparison of polygon size on chorion of eggs of *Pleuronichthys* and *Synodus lucioceps*.

Species	No. of eggs measured	No. of polygons measured	Range of diameters (mm)	Mean (mm)	SD (mm)
Synodus lucioceps	20	200	0 038-0 053	0 047	0 0033
Pleuronichthys coenosus	20	200	0 029-0 043	0 035	0 0029
P. decurrens	2	20	0 038-0 046	0 042	0 0021
P. verticalis	2	20	0 037-0 051	0 042	0 0046
P. ritteri	2	20	0 028-0 032	0 030	0 0011

The arrangement of polygons on the chorion of eggs of the other three species of *Pleuronichthys* from the eastern Pacific is similarly uniform (Figure 2). The polygons are somewhat larger on the chorion of eggs of *P. decurrens* and *P. verticalis* than *P. coenosus*, averaging ca. 0.042 mm in both species (Table 3). Interestingly, Budd (1940) gave the identical value, 0.042 mm, for this measurement on eggs of these two species. The polygons are smaller on eggs of *P. ritteri*, averaging 0.030 mm.

The eggs of *P. cornutus* were described by Mito (1963) and Takita and Fujita (1964). Mito gave the egg diameters as 1.16-1.26 mm, the oil globule as 0.016-0.020 mm. Takita and Fujita gave similar measurements for the hexagonal meshes of 0.018 mm, but gave a smaller egg diameter of 1.03-1.11 mm.

Hypsopsetta guttulata

Orton and Limbaugh (1953) obtained running ripe eggs of *H. guttulata* by stripping ripe adults and obtained similar eggs from plankton collections. The eggs were notable in that they contained a conspicuous, moderately large oil globule. This was the first record of an oil globule in eggs of flatfishes of the family Pleuronectidae, subfamily Pleuronectinae. The egg capsule was simple, without polygonal sculpturing or other apparent texture; the yolk was homogenous. Orton (1953) gave a fairly detailed description of pigment development on embryos of *H. guttulata*. Neither of the above papers contained information on egg size. Eldridge (1975) reported a mean egg diameter of 0.80 mm with usually one oil globule of 0.14 mm in mean diameter and numerous other small oil globules in the yolk. Eggs in our samples had a mean diameter of 0.84 mm (range 0.78-0.89 mm) with a single oil globule averaging 0.13 mm in

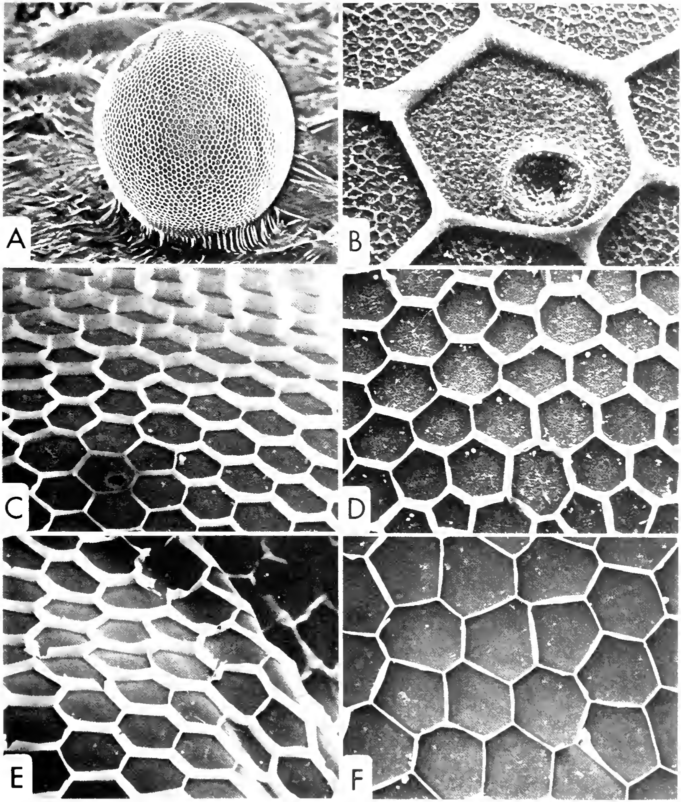


FIGURE 1.—Scanning electronmicrographs of *Pleuronichthys* and *Synodus lucioceps* eggs. A. Entire egg of *P. coenosus*, 40×. B. Single polygon from same egg showing micropyle and texture of chorion surface, 1,880×. C. Side view of same egg showing polygons in perspective and micropyle at lower left, 420×. D. Face view of same egg, 480×. E. Side view of *S. lucioceps* egg showing polygons in perspective, 455×, note delicate nature of polygons. F. Face view of same egg showing irregular nature of polygons and smooth surface of chorion, 490×.

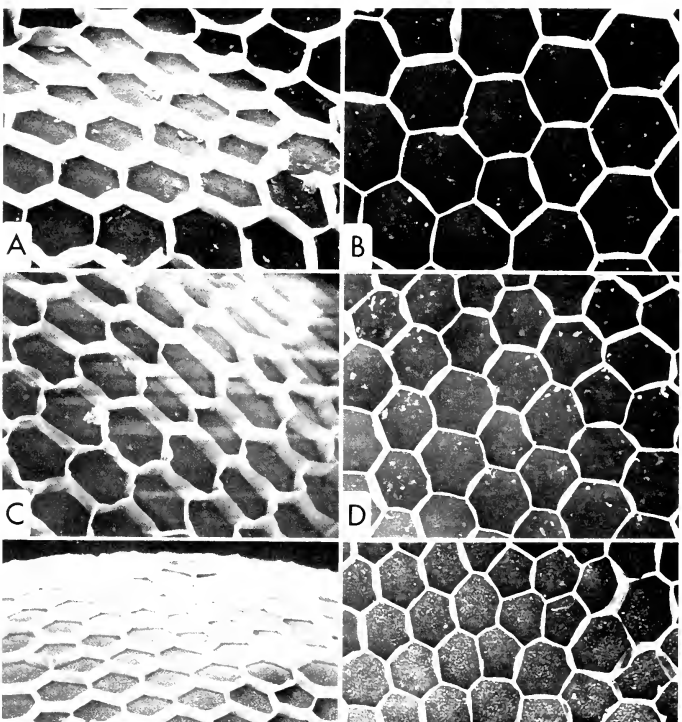


FIGURE 2.—Scanning electromicrographs of *Pleuronichthys* eggs. A, Side view of *P. decurrens* egg, 475×. B, Face view of same egg, 475×. C, Side view of *P. coenosus* egg, 410×. D, Face view of same egg, 450×. E, Side view of *P. ritteri* egg, 460×. F, Face view of same egg, 475×.

diameter (Table 2). There was no evidence of other small oil globules in the yolk, although a few eggs had a damaged oil globule which had separated in two. However, the original oil globule could easily be determined because of surrounding pigment. The oil globule is positioned near the center of the developing embryo in middle-stage eggs. The body of the late-stage embryo is heavily pigmented, similar to the newly hatched larvae.

Hippoglossina stomata

Eggs of *H. stomata* have not been previously described. Eggs are round with a slightly pinkish, unornamented shell and a single oil globule. The egg has a mean diameter of 1.29 mm (range 1.22-1.38 mm) and the oil globule a mean diameter of 0.23 mm (range 0.20-0.26 mm) (Table 2). The oil globule lacks pigment and lies near the tip of the tail of developing embryos in middle-stage eggs. In late-stage eggs the oil globule is in the posterior part of the yolk sac; the embryo is heavily pigmented over the body except for the posteriormost portion of the tail; pigment patches occur on the finfolds in the same places as in early preflexion stage larvae; pigment is widespread over the yolk surface.

DESCRIPTION OF DEVELOPMENTAL STAGES—LARVAL, TRANSFORMING, AND EARLY JUVENILE

Pleuronichthys decurrens Jordan and Gilbert (curlfin turbot)
Figures 3, 4

Literature.—A series of egg stages and two preflexion larvae of *P. decurrens* were described and illustrated by Budd (1940) but incorrectly identified as *P. coenosus*. His larval illustrations were based on a recently hatched specimen, 5.54 mm, and an emaciated specimen, 8 days old, of somewhat smaller size.

Distinguishing characters.—Larvae of this species are unique in the genus *Pleuronichthys* in developing a pterotic spine on each side of the head, in having a higher precaudal vertebral number of 14 or 15, and in having the largest larvae during all stages of development. Larval pigmentation is heaviest in this species with the body and finfold entirely pigmented except for the posteriormost region. Because of their relatively large size and dense pigment, *P. decurrens* larvae cannot be confused with *Hippoglossina stomata* or *Hypsopsetta guttulata*.

Pigmentation.—Newly hatched, preflexion, and early flexion larvae (4.9-9.8 mm NL) are heavily pigmented over the head, trunk, tail, and finfolds with only the pectoral fin and posteriormost tip of the notochord and finfold unpigmented (Figure 3A, B, C). As the first few caudal rays become evident (ca. 9.7 mm NL), several small, discrete melanophores appear on the pectoral fin base (Figure 3C). In late flexion and early postflexion stages during dorsal and anal fin development, the continuous heavy pigment on the finfolds changes to form three to four dorsal and three ventral bands of pigment which extend out from the body margin to part of the rayed fin membrane (Figure 3D). Larvae at this stage have a soft, saccular body with semitransparent and sparsely pigmented areas in the pterygiophore region between the body proper and developing dorsal and anal fins. Larvae >11.2 mm SL have dorsal and anal pterygiophores fully developed; the pterygiophore region is no longer transparent and the specimens become robust (Figure 4).

Morphology.—Larvae of *P. decurrens* are the largest members of the genus at hatching and attain the largest size before transformation. Our smallest specimen is 4.9 mm NL and has yolk remnants (Table 4). The left eye begins to migrate at 10.5 mm SL and has not completed migration in a larva 21.0 mm SL. The smallest available juvenile is 29.4 mm SL.

The gut begins as a tube which diminishes in diameter posteriorly and ends with a free terminal section that diverges from the body in a slight posteriad direction. In 5- to 7-mm NL larvae, the gut increases markedly in diameter and the free terminal section becomes vertical to the body axis. At about 8.0 mm NL, the gut begins to coil and its terminal section begins to slant anteriad. Coiling and the anterior displacement of the anus become more marked as development proceeds. This is reflected in the decreasing relative snout-anus length in postflexion larvae and especially in juveniles (Table 5).

Relative head length increases during larval development whereas relative snout length decreases (Table 5). Relative eye width decreases slightly during the three phases of the larval

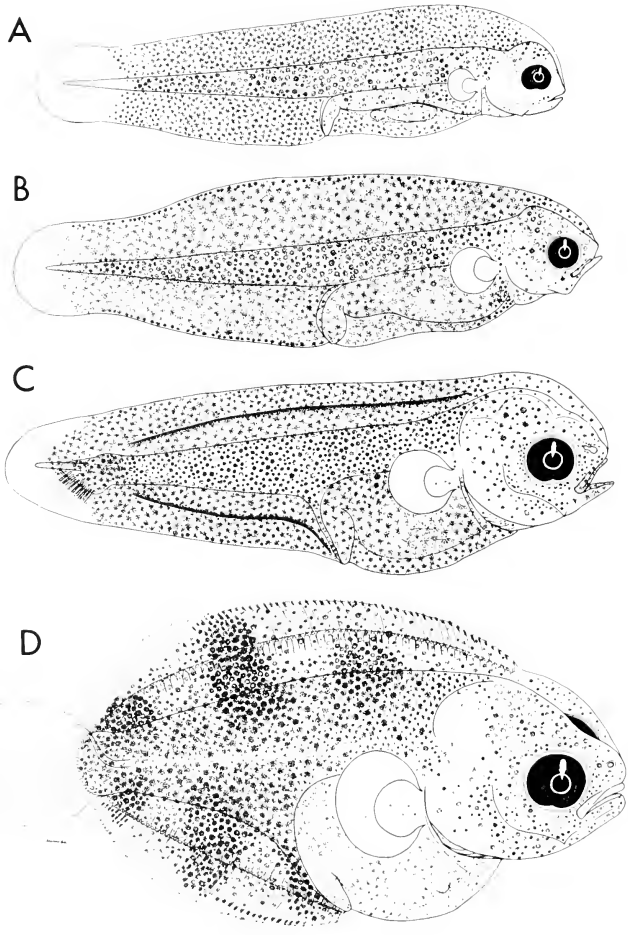

A
B
C
D

FIGURE 3.—Larval stages of *Pleuronichthys decurrens*: A 5.9 mm; B. 6.5 mm; C. 9.7 mm; D 10.0 mm.

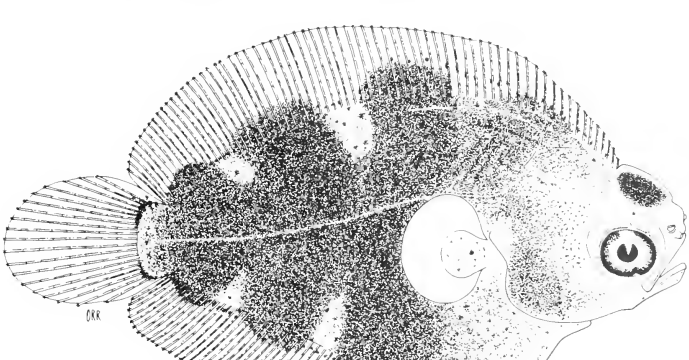


FIGURE 4.—Transforming specimen of *Pleuronichthys decurrens*, 14.4 mm.

TABLE 4.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys decurrens* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5401-90 60	4 9 NL	Sym	Str	2 4	0 80	0 14	0 30	0 24	0 54	0 64	—	—	—
5704-87 50	5 6	Sym	Str	3 0	1 1	0 20	0 40	0 32	0 90	0 96	—	—	—
6501-63 52	6 0	Sym	Str	3 0	1 1	0 20	0 40	0 36	0 90	0 74	—	—	—
5206-70 65	6 5	Sym	Str	3 2	1 2	0 22	0 42	0 40	0 94	1 1	—	—	—
6501-60 70	7 9	Sym	Str	3 9	1 6	0 30	0 50	0 48	1 3	1 3	—	—	—
5003-87 35	8 5	Sym	Str	4 1	1 8	0 32	0 60	0 56	1 7	1 8*	—	—	—
6606-60 65	9 3	Sym	Str	4 3	2 0	0 32	0 66	0 62	1 6	1 8*	—	—	—
6605-80 80	9 8	Sym	Str	4 3	2 2	0 36	0 68	0 64	2 0	2 2*	—	—	—
5706-93 65	7 8	Sym	E fl	3 9	1 9	0 30	0 64	0 64	2 3*	2 3*	—	—	—
5711-87 55	9 1	Sym	E fl	4 7	2 1	0 40	0 70	0 66	2 4*	2 5*	—	—	—
5401-85 60	10 0	Sym	Mid fl	4 4	2 6	0 44	0 80	0 72	2 8*	3 0*	—	—	2 7
6507-87 55	11 0	Sym	L fl	5 8	3 2	0 48	0 98	1 0	4 0*	4 6*	—	—	3 3
5009-47 60	10 2 SL	Sym	Flexed	5 3	3 4	0 60	0 96	0 94	4 5*	4 6*	1 0	0 60	3 4
5407-60 70	10 5	Migr	Flexed	5 5	3 6	0 64	1 1	1 1	4 9*	5 4*	1 0	0 64	3 4
5805-70 80	11 2	Migr	Flexed	5 7	3 9	0 64	1 3	1 2	5 2*	5 9*	1 3	0 68	3 6
7505-90 70	14 5	Migr	Flexed	6 2	5 2	0 66	1 6	0 96	8 1*	8 6*	2 1	0 83	4 6
4903-82 57	15 4	Migr	Flexed	7 0	5 7	0 67	1 8	1 7	9 0*	9 7*	2 1	1 1	4 7
6609-80 60	17 0	Migr	Flexed	8 7	6 4	0 67	1 9	1 5	9 2*	11 4*	2 9	1 2	6 0
5308-73 60	19 2	Migr	Flexed	7 7	6 5	0 91	1 7	1 5	10 0*	11 4*	2 8	1 2	6 4
5004-97 32 Off Santa Cruz Island, Calif	21 0	Migr	Flexed	8 4	6 7	0 66	1 7	1 7	11 7*	12 4*	3 2	1 4	6 2
	29 4	Over	Juv	9 7	9 0	0 66	3 3	2 5	13 9*	14 5*	3 6	2 2	6 8

[1]Sym - symmetrical, Migr - migrating.
[2]Str - straight, E fl - early flexion, Mid fl - midflexion, L fl - late flexion, Juv - juvenile
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement

TABLE 5.—Body proportions of larvae and early juveniles of seven flatfishes with heavily pigmented larvae. (Values given for each body proportion expressed as percentage of body length or head length, mean, standard deviation, and range. Numbers derived from data in morphometric tables for each species.)

Body proportion	*Pleuronichthys decurrens*	*P. coenosus*	*P. verticalis*	*P. ocellatus*	*P. ritteri*	*Hypsopsetta guttulata*	*Hippoglossina stomata*
Snout to anus body length							
Preflexion	48.6 ± 2.9(44-54)	46.2 ± 3.4(39-50)	50.9 ± 1.2(50-53)	—	49.2 ± 3.8(44-57)	50.0 ± 1.2(48-52)	40.1 ± 3.9(36-45)
Flexion	49.8 ± 4.0(44-53)	44.5 ± 3.3(42-51)	50.0 ± 4.7(44-56)	—	49.0 ± 1.4(48-51)	48.5 ± 1.7(46-50)	39.4 ± 1.4(37-41)
Postflexion	46.9 ± 5.3(40-52)	42.4 ± 4.6(37-49)	42.7 ± 4.3(36-45)	47.5 ± 0.7(47-48)	40.7 ± 7.9(31-51)	44.6 ± 5.2(37-52)	40.5 ± 2.6(36-44)
Juvenile	33	31	32.4 ± 0.9(31-33)	32.2 ± 2.2(30-36)	31.2 ± 1.3(30-33)	36.0 ± 1.1(35-38)	33.5 ± 2.1(32-35)
Head length:body length							
Preflexion	19.6 ± 2.1(16-22)	20.0 ± 2.7(15-23)	22.1 ± 1.7(20-25)	—	24.4 ± 2.3(20-28)	21.6 ± 2.8(17-25)	21.5 ± 3.3(17-26)
Flexion	25.5 ± 2.6(23-29)	24.8 ± 3.3(22-31)	27.3 ± 1.9(25-30)	—	27.2 ± 3.9(22-31)	25.8 ± 1.3(24-27)	25.6 ± 1.9(22-28)
Postflexion	34.9 ± 2.0(32-38)	31.1 ± 1.8(28-33)	33.2 ± 2.6(31-37)	30.0	32.8 ± 1.5(31-35)	33.0 ± 1.9(30-36)	31.4 ± 1.7(29-34)
Juvenile	31	28	27.4 ± 1.5(26-30)	27.8 ± 1.2(27-30)	29.0 ± 1.2(28-30)	33.0 ± 0.6(32-34)	34.5 ± 0.7(34-35)
Snout length:head length							
Preflexion	17.6 ± 1.1(16-19)	20.5 ± 3.5(16-27)	22.4 ± 2.8(18-26)	—	18.8 ± 1.8(17-22)	21.9 ± 2.8(18-26)	18.1 ± 4.0(10-24)
Flexion	16.8 ± 1.7(15-19)	18.1 ± 2.4(14-21)	19.7 ± 3.1(15-23)	—	22.0 ± 4.7(17-28)	18.8 ± 1.5(17-20)	20.9 ± 2.2(18-24)
Postflexion	13.9 ± 3.2(10-18)	16.7 ± 2.1(13-19)	14.7 ± 2.9(11-18)	17.0 ± 2.8(15-19)	16.3 ± 1.4(15-18)	17.9 ± 1.6(16-20)	23.1 ± 2.8(19-27)
Juvenile	7	12	6.2 ± 3.0(2-10)	14.2 ± 1.5(12-16)	10.8 ± 1.0(10-12)	14.7 ± 1.8(12-17)	19.5 ± 0.7(19-20)
Eye width:head length							
Preflexion	34.1 ± 2.5(31-38)	36.6 ± 4.1(31-43)	36.4 ± 4.1(31-44)	—	37.2 ± 6.0(31-45)	40.6 ± 3.1(37-45)	35.1 ± 4.9(28-44)
Flexion	32.0 ± 1.5(31-34)	32.0 ± 2.6(28-35)	32.5 ± 1.0(31-34)	—	33.5 ± 6.4(29-43)	31.8 ± 1.0(31-33)	31.9 ± 1.5(30-34)
Postflexion	29.5 ± 2.9(25-33)	29.6 ± 1.7(26-31)	32.5 ± 4.5(29-41)	28.5 ± 2.1(27-30)	30.8 ± 1.2(30-32)	31.5 ± 2.7(28-36)	30.5 ± 2.2(27-34)
Juvenile	37	30	38.4 ± 3.0(34-42)	33.3 ± 2.2(31-37)	36.2 ± 2.9(32-38)	30.7 ± 3.7(28-38)	33.0 ± 2.8(31-35)
Eye height:head length							
Preflexion	30.8 ± 1.6(29-33)	32.1 ± 2.0(29-35)	32.6 ± 4.2(26-39)	—	32.8 ± 3.9(29-40)	33.6 ± 2.6(32-37)	28.6 ± 3.4(26-33)
Flexion	31.0 ± 2.4(28-34)	29.0 ± 3.3(24-34)	30.8 ± 1.7(28-33)	—	32.2 ± 4.6(27-40)	28.8 ± 1.5(27-30)	30.8 ± 3.8(26-37)
Postflexion	26.1 ± 4.7(18-31)	26.7 ± 1.4(25-28)	27.0 ± 2.8(23-30)	27.5 ± 0.7(27-28)	27.2 ± 2.3(25-31)	25.5 ± 1.8(22-28)	29.4 ± 3.7(24-36)
Juvenile	28	—	29.6 ± 4.1(23-33)	33.3 ± 2.2(31-37)	28.3 ± 2.1(26-30)	24.2 ± 3.4(21-30)	—
Body depth at P base before development of D base:body length							
Preflexion	16.1 ± 3.0(11-20)	17.4 ± 4.5(8-22)	16.7 ± 3.7(9-20)	—	20.9 ± 6.4(10-28)	18.6 ± 7.3(8-25)	17.6 ± 4.5(12-23)
Flexion	—	23	—	—	—	23.2 ± 1.0(22-24)	—
Body depth at P base after development of D base:body length							
Preflexion	—	—	—	—	35	—	28.1 ± 6.1(22-34)
Flexion	30.0 ± 4.3(26-36)	27.4 ± 4.0(22-33)	29.8 ± 3.1(25-33)	—	33.8 ± 2.6(31-36)	—	30.6 ± 2.1(28-33)
Postflexion	51.6 ± 5.3(44-58)	39.9 ± 5.9(31-45)	39.7 ± 5.0(31-46)	33.0	40.7 ± 1.5(39-42)	39.2 ± 6.2(33-47)	38.1 ± 2.0(36-41)
Juvenile	47	46	40.4 ± 0.9(39-41)	42.0 ± 1.6(39-43)	39.5 ± 2.1(37-42)	52.8 ± 1.5(51-54)	37.0
Body depth at anus before development of D&A bases:body length							
Preflexion	15.0 ± 2.4(12-17)	15.7 ± 2.9(12-19)	14.3 ± 0.8(13-15)	—	18.0 ± 2.4(14-20)	18.4 ± 3.4(13-22)	14.6 ± 3.9(9-21)
Flexion	—	—	—	—	—	22.2 ± 0.5(22-23)	—
Body depth at anus after development of D&A bases:body length							
Preflexion	20.7 ± 1.5(19-22)	—	—	—	27.7 ± 5.5(22-33)	—	26
Flexion	32.5 ± 6.4(28-42)	28.3 ± 4.2(24-35)	27.7 ± 4.1(21-32)	—	33.2 ± 4.4(27-36)	—	26.6 ± 2.6(24-31)
Postflexion	57.0 ± 7.0(45-67)	44.1 ± 7.1(32-50)	41.7 ± 5.8(31-46)	33.0	42.2 ± 1.6(40-45)	41.2 ± 6.1(35-48)	38.0 ± 4.4(33-45)
Juvenile	49	49	42.2 ± 0.8(41-43)	44.8 ± 1.7(42-47)	40.8 ± 1.9(38-42)	54.7 ± 1.2(54-57)	36.0
Caudal peduncle depth:body length							
Postflexion	13.4 ± 2.5(10-17)	12.4 ± 2.4(9-16)	11.8 ± 1.9(8-13)	7.5 ± 0.7(7-8)	12.0 ± 1.8(9-14)	9.1 ± 1.4(8-11)	8.9 ± 0.8(8-10)
Juvenile	12	14	13.2 ± 0.8(12-14)	12.5 ± 0.6(12-13)	11.5 ± 0.6(11-12)	11.5 ± 0.6(11-12)	9.5 ± 0.7(9-10)
Caudal peduncle length:body length							
Postflexion	6.4 ± 0.5(6-7)	5.1 ± 0.4(5-6)	6.5 ± 1.2(5-8)	6.5 ± 0.7(6-7)	5.8 ± 0.8(5-7)	8.5 ± 0.5(8-9)	8.5 ± 0.5(8-9)
Juvenile	7	6	6.6 ± 0.6(6-7)	6.3 ± 0.5(6-7)	6.2 ± 1.0(5-7)	8.0 ± 1.1(6-9)	8.5 ± 0.7(8-9)
Snout to pelvic base:body length							
Preflexion	—	—	—	—	26	—	—
Flexion	28.5 ± 2.1(27-30)	22.8 ± 2.4(20-27)	26.2 ± 1.8(25-29)	—	27.5 ± 1.9(25-29)	—	24.4 ± 1.8(22-27)
Postflexion	32.1 ± 1.6(30-35)	28.6 ± 0.8(28-30)	28.6 ± 3.1(24-32)	29.5 ± 0.7(29-30)	29.3 ± 3.9(26-36)	29.8 ± 1.9(26-32)	28.0 ± 2.6(24-30)
Juvenile	23	22	24.4 ± 1.1(23-26)	23.8 ± 1.3(22-26)	25.0 ± 2.2(22-27)	27.8 ± 0.8(27-29)	29.5 ± 0.7(29-30)

period and then increases sharply in juveniles (Table 5). Relative eye height is consistently less than eye width; this is the usual pattern among all species being dealt with in this report.

The spine on each pterotic bone first appears on larvae about 6.0 mm NL and achieves maximum development in flexion larvae. It begins to regress near the end of the larval period and is a rugose bump in newly transformed juveniles. No other species of *Pleuronichthys* develops pterotic spines during the larval period, although they are present on larvae of *H. guttulata*.

Another distinctive feature of *P. decurrens* larvae is body depth. As in other species of *Pleuronichthys*, early larvae are slender. Relative body depth increases markedly during the postflexion stage with the result that larvae of this species become strikingly deeper bodied than those of the other six flatfishes with heavily pigmented larvae (Table 5).

Fin and axial skeleton formation.—Because this species is larger at corresponding stages of development than the other six flatfishes considered, fin formation occurs at comparatively larger larval sizes. Caudal fin development occurs between 7.9 and 11.0 mm NL; the smallest postflexion specimen, 10.2 mm SL, has the full count of 19 caudal rays (Table 6). The dorsal and anal fins begin forming simultaneously with the caudal, but obtain their full complement of rays later, by 14.5 mm SL. Pelvic buds are evident on most specimens undergoing flexion, but the full count of fin rays was first obtained on a 15.4-mm SL specimen. The axial skelton is ossified on specimens as small as 11.2 mm SL, as determined by radiographs. Counts of 14 precaudal and 24-27 caudal vertebrae were recorded on five postflexion specimens.

Transformation.—Flatfish larvae are normally symmetrical larvae with eyes opposite each other on either side of the head during their preflexion to flexion stages and into the postflexion stage. Some flatfish larvae remain symmetrical with regard to eye placement until attaining quite large sizes, i.e., 50-120 mm (Hubbs and Chu 1934; Bruun 1937; Nielsen 1963; Amaoka 1970, 1971, 1972, 1973). However, in the flatfishes being studied the migration of one eye (left in dextral flounders, right in sinistral flounders) begins early in the postflexion stage. It can require some time to move completely over. Thus, the left eye was migrating on a 10.5-mm larva of *P. decurrens*, but was not completely over on a 21.0-mm specimen. Ossified rays are not formed in the pectoral fin until after eye migration is completed. On first formation the rays are spaced some distance apart in the blade of the pectoral fin. The pectoral fin rapidly changes form with the structure of the larval pectoral (base and blade) disappearing, to be replaced by a group of ossified, closely spaced rays. Metamorphosis is

TABLE 6.—Meristics of larvae and a juvenile of *Pleuronichthys decurrens*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5401-90 60	4 9 NL	Prefl	0	0	0	0	LP[2]				
5704-87 50	5 6	Prefl	0	0	0	0	LP[2]				
6501-63 52	6 0	Prefl	0	0	0	0	LP[2]				
5206-70 65	6 5	Prefl	0	0	0	0	LP[2]				
6501-60 70	7 9	Prefl	0	0	0	0	LP[2]				
5003-87 35	8 5	Prefl	Forming	Forming	Forming	0	LP[2]				
6606-60 65	9 3	Prefl	Forming	Forming	4	0	LP[2]				
6605-80 80	9 8	Prefl	Forming	Forming	ca 8	0	LP[2]				
5706-93 65	7 8	E fl	Forming	Forming	ca 8	Bud	LP[2]				
5711-87 55	9 1	E fl	Forming	Forming	ca 12	0	LP[2]				
5401-85 60	10 0	Midfl	Forming	Forming	ca 12	Bud	LP[2]				
6507-87 55	11 0	L fl	ca 50	ca 42	17	Bud	LP[2]				
5009-47 60	10 2 SL	Postfl	50	46	19	Bud	LP[2]				
5407-60 70	10 5	Postfl	ca 64	45	19	5 5	LP[2]				
5805-70 80	11 2	Postfl	71	46	19	5 5	LP[2]	14	25	39	X-ray
7505-90 70	14 5	Postfl	74	52	19	5 5	LP[2]				
4903-82 57	15 4	Postfl	72	48	19	6 6	LP[2]	14	25	39	X-ray
6609-80 60	17 0	Postfl	77	48	19	6 6	LP[2]	14	24	38	X-ray
5308-73 60	19 2	Postfl	75	52	19	6 6	LP[2]	14	27	41	X-ray
5004-97 32	21 0	Postfl	74	48	19	6 6	LP[2]	14	25	39	X-ray
Off Santa Cruz Island, Calif	29 4	Juv	78	52	19	6 6	11/11	14	26	40	X-ray

[1]Prefl - preflexion, E fl - early flexion, Midfl - midflexion, L fl - late flexion, Postfl - postflexion, Juv - juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays

considered complete when the lateral line can be discerned and scale formation has begun.

Distribution.—Fitch (1963) reported that the range for this species was from Alaska to San Quintin, Baja California. Miller and Lea (1976) gave an extended southern range limit to 25 mi north-northeast of Cedros Island (lat. 28°47.5'N, long. 114°57.0'W). Egg and larval material in our collections was taken off the entire coast of California over a broad band of stations, from nearshore to 150 or more miles offshore (Figure 5). Lack of egg and larval material off Baja California, despite the intensive coverage of these waters by CalCOFI surveys, indicates a more northerly distribution for young stages than for adults.

Pleuronichthys coenosus Girard
(C-O turbot)
Figures 6, 7

Literature.—Budd (1940) described and illustrated a series of eggs and four reared larvae of *P. coenosus* which he mistakenly identified as *P. decurrens*. The larvae illustrated were newly hatched to 9 days old, ranging in size from 3.88 to 4.72 mm.

Distinguishing characters.—This species is distinguished by having 13 (rarely 12) precaudal vertebrae and a total of 37-39 vertebrae. The larvae are larger than comparable stages of *H. guttulata* and other species of *Pleuronichthys* except *P. decurrens*. Pigmentation patterns discussed below will also separate *P. coenosus* from other species treated in this work.

Pigmentation.—Preflexion larvae are characterized by having opposing, similar appearing, pigment clusters on the dorsal and ventral finfolds posterior to the anus, and by small melanophores dotting the margin of the otherwise unpigmented posterior tip of the tail (Figure 6A, B). The rest of the body is heavily pigmented, with the exclusion of the undifferentiated pectoral fin and the ventral half of the head.

Flexion (6.2-7.8 mm NL) and postflexion larvae (7.1-11.4 mm SL) show an increase anteriorly of the finfold pigment and an increase in pigmentation on the lower region of the head (Figure 6C, D, E). A distinctively narrow, unpigmented zone along the hypurals persists through late flexion specimens, but is subsequently pigmented in

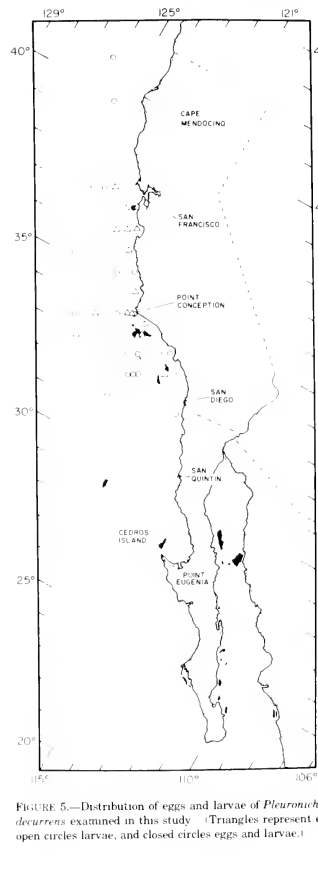
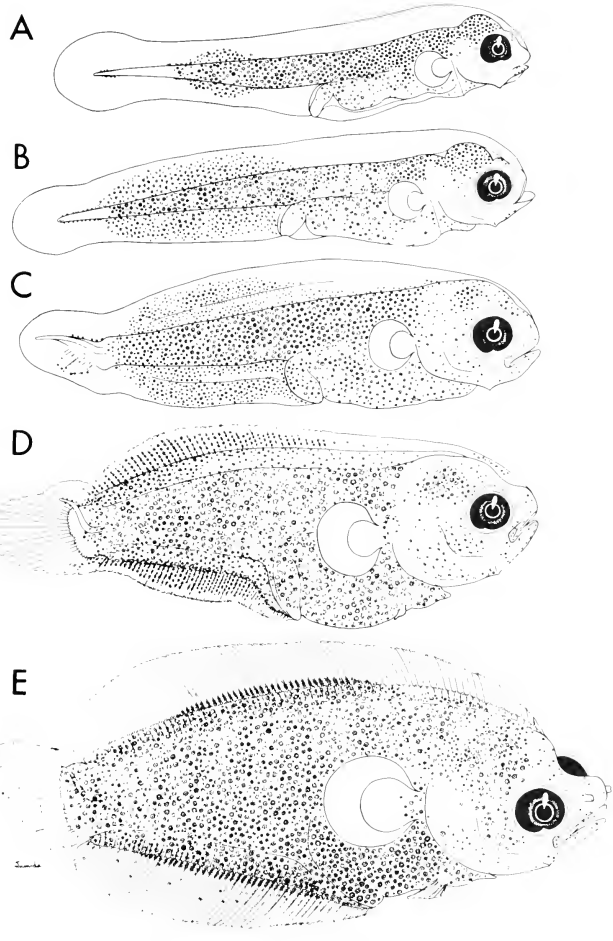


FIGURE 5.—Distribution of eggs and larvae of *Pleuronichthys decurrens* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

FIGURE 6.—Larval stages of *Pleuronichthys coenosus*. A 3.7 mm; B 5.9 mm; C 6.1 mm; D 7.8 mm; E 8.9 mm.


A
B
C
D
E

postflexion specimens (Figure 6E). A few pigment spots dot the anterior margin of the pectoral fin base in postflexion specimens, and extend farther onto the fin base in larger specimens. At dorsal and anal fin formation, pigment clustered in the finfold aligns along the dorsal and anal fin rays, and later in postflexion specimens becomes compacted into a narrow band adjacent to the fin bases. Pigment over the pterygiophores, however, is as dense as on the body (Figure 7).

Morphology.—Larvae of *P. coenosus* are larger at hatching and at transformation than all other species of *Pleuronichthys* except *P. decurrens*. A 3.9-mm NL specimen has much of its yolk sac remaining (Table 7). The smallest specimen in which the left eye begins to migrate is 8.2 mm SL; eye migration is almost complete in our largest transforming specimen, 11.4 mm SL.

The gut begins to coil and the free section becomes vertical to the body axis in larvae between 5.5 and 6.0 mm NL. Snout-anus distance has a moderate decrease relative to body length in all larval phases and decreases markedly after transformation (Table 5).

As in the other species, relative head length increases during larval development through the postflexion stage, but decreases moderately in juveniles. Both relative snout length and eye size decrease during the three larval phases (Table 5).

As in other species of *Pleuronichthys*, body depth increases during each larval stage (Table 5). Relative body depths for larvae of *P. coenosus* are in the intermediate range compared with other species in the genus. Body depth in juveniles is comparable with that in the relatively deep-bodied *P. decurrens*.

Fin and axial skeleton formation.—Fin formation in *P. coenosus* takes place at smaller sizes than in *P. decurrens* but at larger sizes than in other species of *Pleuronichthys*. Larvae undergoing caudal fin formation range from 6.2 to 8.5 mm NL. The smallest fully flexed larva is 7.1 mm SL. The full count of caudal rays is developed on a postflexion specimen 8.2 mm SL (Table 8). Dorsal and anal fin formation takes place at the same size as caudal fin formation; rays are mostly formed on late flexion specimens and fully formed on the 8.2-mm SL postflexion larva. Pelvic buds are present on all specimens undergoing notochord flexion except the smallest (6.2 mm NL), and the full count of six rays per fin is developed on the 9.6-mm SL postflexion specimen. Vertebral counts from two cleared and stained larvae, 8.6 and 10.0 mm SL, are 13+24.

Distribution.—Fitch (1963) denoted the distribution of *P. coenosus* as Alaska to Cape Colnett, Baja California. Collections of our egg and larval mate-

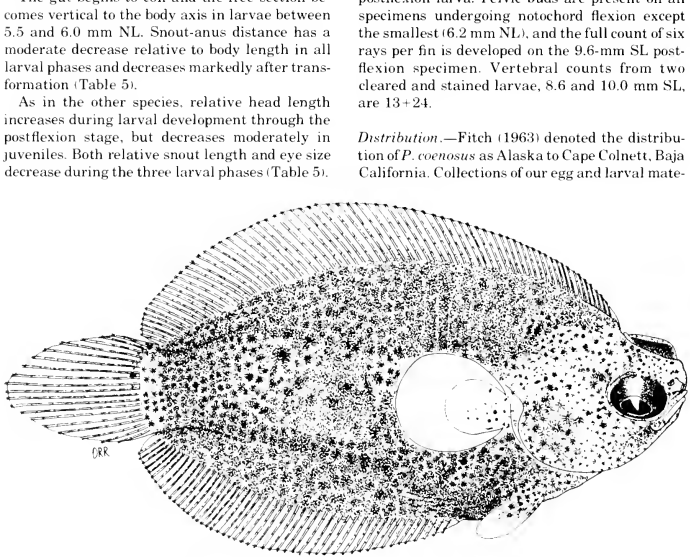


FIGURE 7.—Transforming specimen of *Pleuronichthys coenosus*, 10.0 mm

TABLE 7.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys coenosus* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[1]	Body depth at anus[1]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5902-83 43	3 9 NL	Sym	Str	1 8	0 60	0 16	0 26	0 20	0 30	0 46	—	—	—
5007-127 50	3 7	Sym	Str	1 8	0 68	0 14	0 26	0 22	0 60	0 52	—	—	—
5005-120 45 Off La Jolla, Calif	4 2	Sym	Str	2 1	0 80	0 16	0 32	0 24	0 70	0 56	—	—	—
	5 1	Sym	Str	2 5	1 1	0 20	0 40	0 38	1 1	0 90	—	—	—
5704-82 47	5 6	Sym	Str	2 6	1 1	0 26	0 40	0 36	0 90	0 84	—	—	—
6304-93 40	6 9	Sym	Str	3 1	1 6	0 30	0 50	0 46	1 3	1 3	—	—	—
6304-120 70	6 5	Sym	Str	3 0	1 5	0 28	0 46	0 46	1 4	1 6*	—	—	—
5206-90 41	8 5	Sym	Str	3 3	1 7	0 28	0 64	0 60	1 6	1 6	—	—	—
5110-97 30	6 2	Sym	E fl	2 7	1 4	0 30	0 48	0 42	1 4	1 5*	—	—	—
7207-93 45	7 2	Sym	E fl	3 1	1 6	0 30	0 56	0 54	1 6	1 8*	—	—	1 6
5705-93 27	7 4	Sym	Midfl	3 3	1 8	0 26	0 60	0 54	2 0*	1 9*	—	—	1 6
5304-85 50	8 3	Sym	Midfl	3 5	1 9	0 36	0 60	0 54	2 2*	2 4*	—	—	1 7
1941-25 45	7 2	Sym	L fl	3 1	1 9	0 36	0 58	0 54	2 1*	2 2*	—	—	1 6
4908-72 56	7 8	Sym	L fl	4 0	2 4	0 40	0 68	0 58	2 6*	2 7*	—	—	2 1
5007-90 53	7 1 SL	Sym	Flexed	3 3	2 0	0 38	0 62	0 56	2 2*	2 3*	0 62	0 36	2 0
5004-100 60	8 2	Migr	Flexed	3 4	2 5	0 40	0 74	0 70	3 1*	3 4*	0 98	0 50	2 3
6606-70 70	8 8	Migr	Flexed	4 0	2 7	0 48	0 80	0 74	2 9*	3 3*	0 84	0 42	2 6
5304-85 50	9 6	Migr	Flexed	4 7	3 0	0 60	0 92	0 80	4 2*	4 8*	1 2	0 52	2 8
5206-90 41	9 9	A over	Flexed	3 9	3 2	0 56	0 84	0 80	4 4*	4 9*	1 4	0 48	2 8
5407-83 51	10 2	A over	Flexed	3 8	3 4	0 52	1 0	0 84	4 6*	5 1*	1 6	0 52	3 0
5304-100 29 Off Coronados Islands, B C	11 4	Over	Flexed	4 3	3 4	0 60	1 0	0 88	5 0*	5 4*	1 6	0 60	3 2
	17 0	Over	Juv	5 2	4 7	0 58	1 4	—	7 9*	8 3*	2 4	1 0	3 8

[1]Sym = symmetrical, Migr = migrating, A over = About over
[2]Str = straight, E fl = early flexion, Midfl = midflexion, L fl = late flexion, Juv = juvenile
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement

TABLE 8.—Meristics of larvae and a juvenile of *Pleuronichthys coenosus* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5902-83 43	3 9 NL	Yolk-sac	0	0	0	0	LP[2]				
5007-127 50	3 7	Prefl	0	0	0	0	LP[2]				
5005-120 45 Off La Jolla, Calif	4 2	Prefl	0	0	0	0	LP[2]				
	5 1	Prefl	0	0	0	0	LP[2]				
5704-82 47	5 6	Prefl	0	0	0	0	LP[2]				
6304-93 40	6 9	Prefl	0	0	0	0	LP[2]				
6304-120 70	6 5	Prefl	Forming	Forming	4	0	LP[2]				
5206-90 41	8 5	Prefl	Forming	Forming	ca. 8	0	LP[2]				
5110-97 30	6 2	E fl	Forming	Forming	ca. 8	0	LP[2]				
7207-93 45	7 2	E fl	Forming	Forming	12	Bud	LP[2]				
5705-93 27	7 4	Midfl	Forming	Forming	12	Bud	LP[2]				
5304-85 50	8 3	Midfl	Forming	30	12	Bud	LP[2]				
1941-25 45	7 2	L fl	ca. 55	ca. 44	ca. 14	Bud	LP[2]				
4908-72 56	7 8	L fl	ca. 60	ca. 45	16	Bud	LP[2]				
5007-90 53	7 1 SL	Postfl	ca. 70	ca. 50	16	Bud	LP[2]				
5004-100 60	8 2	Postfl	74	55	19	ca. 4 4	LP[2]				
6606-77 55	8 6	Postfl	72	54	19	ca. 5 5	LP[2]	13	24	37	C&S[3]
6606-70 70	8 8	Postfl	76	50	19	ca. 4 4	LP[2]				
5304-85 50	9 6	Postfl	73	ca. 52	19	6 6	LP[2]				
5206-90 41	9 9	Postfl	69	50	19	6 6	LP[2]				
5206-87 45	10 0	Postfl	71	53	19	—	LP[2]	13	24	37	C&S[3]
5407-83 51	10 2	Postfl	69	49	19	6 6	LP[2]				
5304-100 29 Off Coronados Islands, B C	11 4	Postfl	72	50	19	6 6	LP[2]				
	17 0	Juv	75	53	19	6 6	9 9	13	25	38	X-ray

[1]Prefl = preflexion, E fl = early flexion, Midfl = midflexion, L fl = late flexion, Postfl = postflexion, Juv = juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays
[3]Cleared and stained

rial range from northern California south to Point Abreojos, Baja California (Figure 8). Our records extend the range considerably southward for the species. Larval specimens range widely from nearshore to about 200 mi offshore, but most occurrences are between 50 and 200 mi offshore.

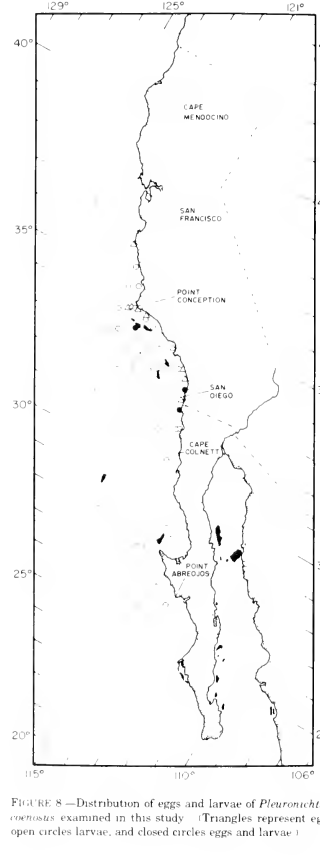


FIGURE 8.—Distribution of eggs and larvae of *Pleuronichthys coenosus* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

Pleuronichthys verticalis Jordan and Gilbert (hornyhead turbot) Figures 9, 10

Literature.—The eggs and two early larvae (3.16 and 3.35 mm) were described and illustrated by Budd (1940). Four illustrations of larvae, between 4.4 and 8.7 mm SL, are contained in CalCOFI Atlas No. 23 (Ahlstrom and Moser 1975).

Distinguishing characters.—Preflexion and early flexion larvae of this species are recognizable by the triangular patches of pigment, one each on the dorsal and ventral finfold posterior to the anus; these form late in the yolk-sac stage and persist through the notochord flexion stage. No other species of *Pleuronichthys* develops this distinctive pigmentation character.

Late flexion and postflexion larvae are distinguished by size (i.e., larger than *H. guttulata*, *P. ritteri*, and *P. ocellatus*, but smaller than *P. coenosus* and *P. decurrens*), and by sparse pigment on the head and on the dorsal and anal fin pterygiophores. This is in sharp contrast to the heavy pigment in these areas for the other species discussed.

Newly transformed specimens are difficult to distinguish from comparable stages of *P. ritteri*. However, pigment on the body tends to be mottled on *P. verticalis* rather than evenly distributed as on *P. ritteri* at this stage. Small juveniles are easily separable from *P. ritteri* because *P. verticalis* lacks the anterior prolongation of the supratemporal branch of the lateral line found on *P. ritteri* juveniles.

Pigmentation.—Pigment on yolk-sac and older preflexion larvae of *P. verticalis* is heavy on the head, trunk, and tail and ends anterior to the last three to five myomeres (Figure 9A, B). As the last remnant of yolk is absorbed, scattered finfold pigment differentiates into triangular-shaped clusters posterior to the anus, the dorsal patch being situated slightly anterior of the ventral patch. The head region below and on each side of the eye is only sparsely pigmented which is typical of most early preflexion larvae of several species of *Pleuronichthys*. The top of the head to the shoulder region is unpigmented, a character shared with preflexion larvae of *P. ritteri*. Small pigment spots dot the margin of the tip of the tail, but do not persist beyond the flexion stage (Figure 9C, D).

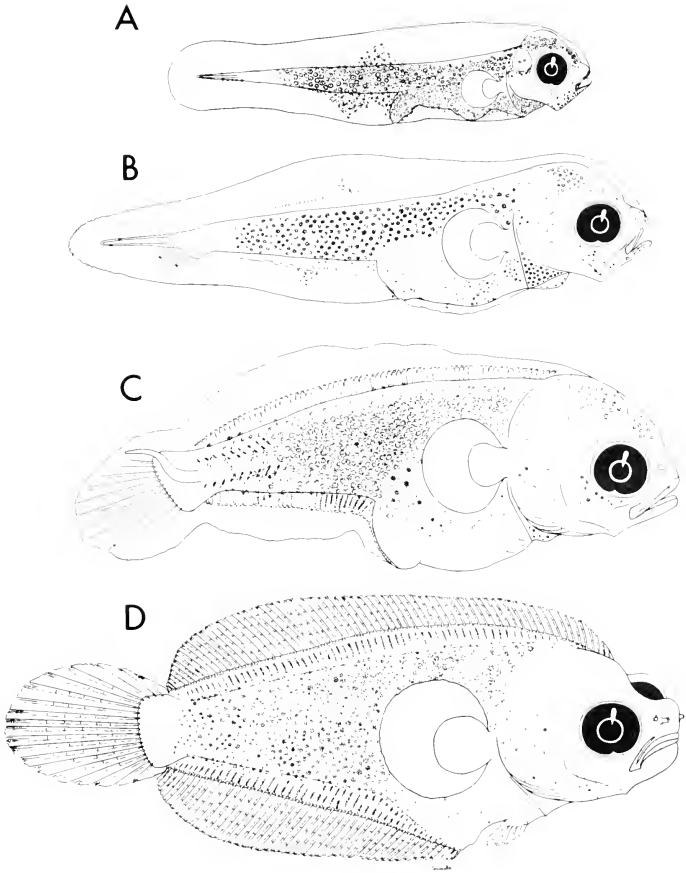


FIGURE 9.—Larval stages of *Pleuronichthys verticalis* A 4.4 mm, B 6.5 mm, C 7.1 mm, D 8.7 mm

Flexion larvae undergo little change in pigment pattern from earlier stages. The triangular patches of finfold pigment are diminished in size and pigment intensity, but are visible by careful examination in specimens through notochord flexion.

Following the completion of notochord flexion, pigment on the tail spreads posteriad leaving only the caudal peduncle unpigmented (Figure 9D). The outlying regions of the head and body, particularly the pterygiophore region, are sparsely pigmented compared with late larvae of other *Pleuronichthys* species and *H. guttulata*.

Transformed specimens develop heavy pigment over the body giving them a mottled appearance. Dark blotches appear along bases of the dorsal and anal fins (Figure 10).

Morphology.—Larvae of *P. verticalis* attain a size intermediate between the large species, *P. decurrens* and *P. coenosus*, and the smaller *P. ritteri*. A specimen with most of its yolk sac remaining is 2.4 mm NL (Table 9). The left eye is beginning to migrate in a specimen as small as 7.3 mm SL and transformation is almost complete at 9.2 mm SL. The smallest available juvenile is 12.2 mm SL, reared from eggs collected off San Diego, Calif.

Gut development follows the course of other *Pleuronichthys*. Snout-anus length is about 50% of body length in preflexion and flexion stages and then is reduced in postflexion and early juvenile stages. The gut begins to coil at about 4.0 mm NL but the free terminal section does not become vertical until at least 5.0 mm NL.

As in the other species, relative head length increases throughout the larval period and then decreases at transformation. Snout length and eye size undergo a gradual relative diminution during the larval stages; however, relative eye width increases sharply at transformation (Table 5).

Larvae of *P. verticalis* are intermediate in body depth when compared with other species of *Pleuronichthys* (Table 5).

Fin and structural development.—*P. verticalis* is the only species for which we could clear and stain a series of larvae (Tables 10, 11). The sequence of fin formation was followed more precisely in this species as was the sequence of ossification of other structures including the vertebral column, supporting bones of the caudal fin, branchiostegal rays, gill rakers, and teeth.

The caudal fin begins to form on the under side of the body a short distance anterior to the tip of the notochord on specimens of about 5.0 mm NL. Some caudal rays form before flexion begins (Figure 11A). Rays initially form at midcaudal and those that will be associated with superior hypural bones differentiate posteriorward, while those that will be associated with inferior hypural bones

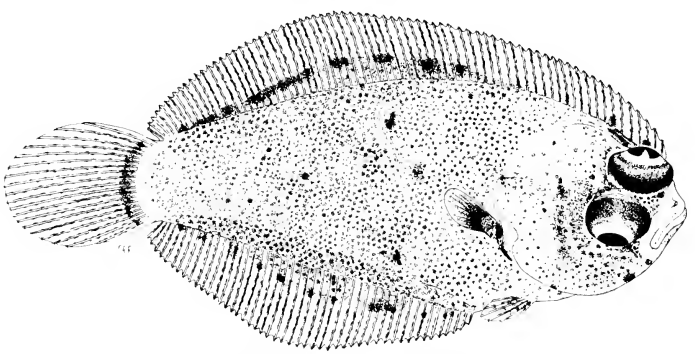


FIGURE 10.—Reared transforming specimen of *Pleuronichthys verticalis*, 11.0 mm

TABLE 9.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys verticalis*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7501-120 26 Off La Jolla, Calif.	2 4 NL	Sym	Str	1 2	0 56	0 10	0 22	0 20	0 22	0 34	—	—	—
SCBS-2-203	3 0	Sym	Str	1 5	0 64	0 16	0 22	0 20	0 48	0 40	—	—	—
7203-103 30	3 8	Sym	Str	2 0	0 86	0 20	0 30	0 26	0 70	0 54	—	—	—
7203-103 30	4 3	Sym	Str	2 2	0 94	0 24	0 34	0 32	0 84	0 62	—	—	—
7203-103 30	4 8	Sym	Str	2 4	1 0	0 20	0 36	0 32	0 90	0 70	—	—	—
7501-120 26	5 2	Sym	Str	2 6	1 3	0 30	0 40	0 34	1 0	0 80	—	—	—
5708-110 33	5 0	Sym	E fl	2 8	1 5	0 34	0 50	0 42	1 6*	1 4*	—	—	—
7203-103 30	5 6	Sym	E fl	2 7	1 4	0 30	0 48	0 46	1 4*	1 2*	—	—	1 5
7503-90 27 6	5 6	Sym	Midfl	2 9	1 5	0 30	0 48	0 46	1 8*	1 8*	—	—	1 4
5610-117 26	5 9	Sym	Midfl	2 7	1 6	0 24	0 50	0 52	1 7*	1 6*	—	—	1 5
7503-120 26	7 2	Sym	Midfl	3 2	1 9	0 32	0 60	0 56	2 1*	2 0*	—	—	1 8
5708-110 33	6 3	Sym	L fl	3 2	1 9	0 32	0 60	0 56	2 1*	2 0*	—	—	1 8
7505-120 30	6 5 SL	Sym	Flexed	3 2	2 0	0 36	0 64	0 60	2 0*	2 0*	0 54	0 50	?
SCBS-4-303	7 3	Migr	Flexed	3 3	2 6	0 40	0 76	0 68	3 1*	3 3*	0 96	0 40	2 2
5506-120 45	7 9	Migr	Flexed	3 3	2 9	0 40	0 84	0 68	3 6*	3 6*	1 0	0 44	2 4
6606-103 29	8 3	Migr	Flexed	3 5	2 7	0 48	0 84	0 68	3 2*	3 5*	1 0	0 44	2 7
6504-137 30	9 2	Migr	Flexed	3 9	2 9	0 36	0 96	0 84	3 8*	4 2*	1 1	0 60	2 5
Reared	11 0	Over	Flexed	4 0	3 4	0 36	1 4	1 0	4 3*	4 4*	1 4	0 76	2 7
Reared	12 2	Over	Juv	4 0	3 6	0 36	1 4	1 2	5 0*	5 1*	1 6	0 80	3 2
Reared	15 9	Over	Juv	5 2	4 3	0 32	1 8	1 4	6 5*	6 6*	2 2	1 0	3 6
Reared	16 9	Over	Juv	5 3	4 5	0 32	1 8	1 3	6 6*	6 9*	2 3	1 0	4 2
Santo Tomas Bay, B C	19 5	Over	Juv	6 4	5 3	0 08	1 8	1 2	7 8*	8 4*	2 5	1 3	4 7
	26 5	Over	Juv	8 4	7 0	0 33	2 6	2 1	10 9*	11 4*	3 3	1 9	6 5

[1]Sym - symmetrical; Migr - migrating
[2]Str - straight, E fl - early flexion, Midfl - midflexion, L fl - late flexion, Juv - juvenile
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement

TABLE 10.—Meristics of larvae and juveniles of *Pleuronichthys verticalis*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin ray					Gill rakers	Teeth			
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left		Upper jaw R	Upper jaw L	Lower jaw R	Lower jaw L
6609-97 29	5 3 NL	Prefl	Forming	Forming	4	0	LP[2]	—				
7503-90 27 6	5 6	Prefl	Forming	Forming	4	0	LP[2]	—				
—	5 5	Prefl	Forming	Forming	6	0	LP[2]	—				
6507-107 30	5 8	Prefl	Forming	Forming	6	0	LP[2]	—				
5708-117 26	5 7	Prefl	Forming	Forming	6	0	LP[2]	—				
5708-117 26	5 8	Prefl	Forming	Forming	6	0	LP[2]	—				
5708-117 26	6 1	E fl	Forming	Forming	8	Bud	LP[2]	—				
—	7 0	L fl	43	37	16	Bud	LP[2]	0 + 2	1	2	3	3
6606-97 29	6 9	L fl	43	43	18	4 4	LP[2]	0 + 3	1	2	0	3
—	7 0	Postfl	67	47	19	5 5	LP[2]	0 + 6	1	3	3	5
6407-83 43	7 1	Postfl	64	44	19	3 3	LP[2]	Not taken	1	4	3	5
5110-100 40	7 3	Postfl	67	47	19	5 5	LP[2]	0 + 5	?	6	5	6
6606-97 29	8 3	Postfl	65	46	19	6 6	LP[2]	0 + 5	0	5	5	7
6504-137 30	9 2	Postfl	65	44	19	6 6	LP[2]	Not taken		Not taken		
Reared	11 0	Postfl	72	49	19	6 6	11 ?	2 + 9		Not taken		
Reared	12 2	Juv	72	47	19	6 6	11 11	3 + 7		Not taken		
Reared	15 9	Juv	74	49	20	6 6	12 12	3 + 8		Not taken		
Reared	16 9	Juv	72	48	19	6 6	10 11	3 + 7		Not taken		
Santo Tomas Bay, B C	19 5	Juv	67	47	19	6 6	10 10	2 + 7		Not taken		
	26 5	Juv	70	49	19	6 6	11 11	3 + 7		Not taken		

[1]Prefl - preflexion, E fl - early flexion, L fl - late flexion, Postfl - postflexion, Juv - juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays

differentiate progressively anteriorward. A number of specimens, 5.3-5.8 mm NL with the notochord still straight, possess 2+2 or 3+3 caudal rays. The complete complement of 10+9 caudal rays is present on specimens 7.0 mm NL and larger. Flexion occurs in larvae between 6.1 and 7.0 mm NL (Figure 11B). By the time the caudal ray complement is fully formed, the rays are aligned in a terminal position (Figure 11C). The hypurals are observed as cartilaginous plates before they ossify. There are two superior and two inferior hypurals[3] in pleuronectid flatfishes. The

[3]We include the "parhypural" as a hypural bone. In flatfishes it is a splinter bone without remnant of a haemal arch

TABLE 11.—Development of vertebral column, caudal fin rays, and caudal fin supporting bones in larvae of *Pleuronichthys verticalis*.

Station	Body length	Stage[1]	Precaudal vertebrae[2] n pr	centra	Caudal vertebrae[2] n pr	h pr	centra	Ural centrum	Total vert[3]	C fin rays	Ural bones[2] Sup hyp Upper	Mid	Inf hyp Mid	Lower	Epural
6609-97 29	5.3 NL	Prefl	0	0	0	0	0	0	0	2+2	0	0	0	0	0
7503-90 27 6	5.6	Prefl	0	0	0	7	0	0	7*	2+2	0	0	0	0	0
—	5.5	Prefl	4+2	0	14	14	0	0	20*	3+3	0	0	0	0	0
6507-107 30	5.8	Prefl	6+3	0	15	15	0	0	24*	3+3	0	0	0	0	0
5708-117 26	5.7	Prefl	7+5	0	16	16	0	0	28*	3+3	0	0	0	0	0
6507-107 30	5.8	Prefl	7+4	0	17	17	0	0	28*	3+3	0	0	0	0	0
5708-117 26	6.1	E fl	13	0	19	20	0	0	33*	4+4	0	0	0	0	0
—	7.0	L fl	13	0	22	22	0	0	35*	8+8	0	0	0	0	0
6606-97 29	6.9	L fl	13	13	22	22	20	1	36	9+9	0	x	x	x	0
—	7.0 SL	Postfl	13	13	23	23	23	1	37	10+9	0	x	x	x	x
6407-83 43	7.1	Postfl	13	13	22	22	22	1	36	10+9	0	x	x	x	x
5110-100 40	7.3	Postfl	13	13	22	22	22	1	36	10+9	x	x	x	x	x
6606-97 29	8.3	Postfl	13	13	22	22	22	1	36	10+9	x	x	x	x	x
Reared	11.0	Postfl	13	13	24	23	23	1	37	10+9	x	x	x	x	x
Reared	12.2	Juv	13	13	22	22	22	1	36	10+9	x	x	x	x	x
Reared	15.9	Juv	13	13	22	22	22	1	36	10+10	x	x	x	x	x
Reared	16.9	Juv	13	13	22	22	22	1	36	10+9	x	x	x	x	x
Santo Tomas Bay, B C	26.5	Juv	13	13	23	23	23	1	37	10+9	x	x	x	x	x

[1]Prefl = preflexion, E fl = early flexion, L fl = late flexion, Postfl = postflexion, Juv = juvenile
[2]Abbreviations in heading: n pr = neural process, h pr = haemal process, vert = vertebrae, Sup hyp = Superior hypurals, Inf hyp = Inferior hypurals
[3]Asterisk indicates incomplete count

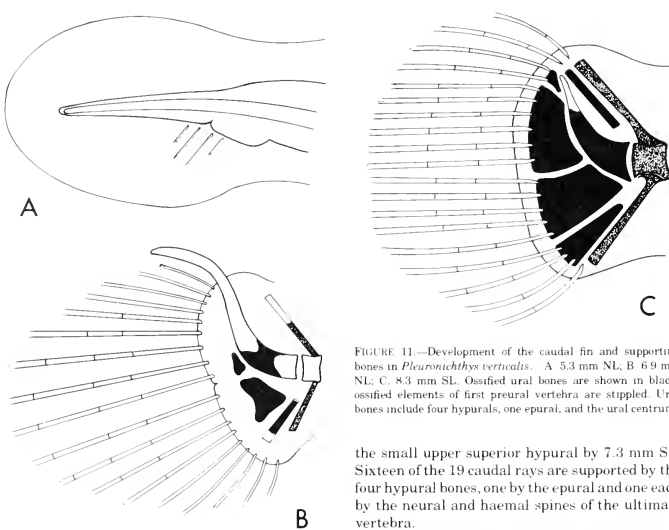


FIGURE 11.—Development of the caudal fin and supporting bones in *Pleuronichthys verticalis*. A 5.3 mm NL; B 6.9 mm NL; C, 8.3 mm SL. Ossified ural bones are shown in black, ossified elements of first preural vertebra are stippled. Ural bones include four hypurals, one epural, and the ural centrum.

main superior hypural and the two inferior hypurals are ossifying in specimens 6.9 mm NL and larger, the single epural by 7.0 mm SL, and the small upper superior hypural by 7.3 mm SL. Sixteen of the 19 caudal rays are supported by the four hypural bones, one by the epural and one each by the neural and haemal spines of the ultimate vertebra.

The vertebral column begins to ossify at about the same time rays begin forming in the caudal fin (Table 11). A 5.6-mm NL specimen which has 2+2 caudal rays has the first seven haemal processes of

the caudal group of vertebrae forming. A slightly more advanced 5.5-mm NL specimen has 14 opposing neural and haemal processes of caudal vertebrae formed as well as the four anteriormost and last two precaudal neural processes. A neural or haemal process consists of two portions—a divided basal portion that forms the neural or haemal arch ending in the second portion as a terminal spine. On the 5.5-mm NL specimen, only the tips of the neural spines of the caudal group are ossified. Of the precaudal group, ossification first occurs in the arched portion of the anterior four neural processes and on the tips only of the last two precaudal neural spines. On a 5.8-mm NL specimen with the first 7 and last 4 precaudal neural processes and 17 pairs of neural and haemal processes in the caudal group ossifying, all of the neural processes except those of the 7 anterior precaudal vertebrae were ossifying initially from both ends, i.e., from the distal tips of the neural spines and from the basal portion of the neural arches, with ossification from both ends proceeding medially (Figure 12A). In a 6.1-mm NL specimen all 13 precaudal neural processes and 19 neural and haemal processes in the caudal group are ossified (Figure 12B). A 7.0-mm NL late flexion specimen has all neural and haemal processes ossified except those on the terminal preural vertebra, but no centra are ossified. A 6.9-mm NL specimen, with all neural and haemal processes ossifying, has various stages of vertebral centra ossification with initial ossification of centra occurring below the bases of the neural and haemal arches and then filling in medially; only the two vertebral centra adjacent to the urostyle lack any ossification; the six vertebrae immediately forward of these have the best ossified centra. A 7.0-mm SL specimen has all centra ossified.

The bases of the dorsal and anal fins are present on larvae as small as 5.3 mm NL and rays begin to form by late flexion. Full complements of dorsal and anal fin rays are present on most postflexion specimens. Buds of the pelvic fins were first seen on a 6.1-mm NL specimen, and the complete count of six rays per fin is developed by 8.3 mm SL. Pectoral rays form only toward the end of the transformation stage after the left eye has nearly completed its migration to the right side.

Branchiostegal rays form progressively anteriorward during the period of caudal fin forma-

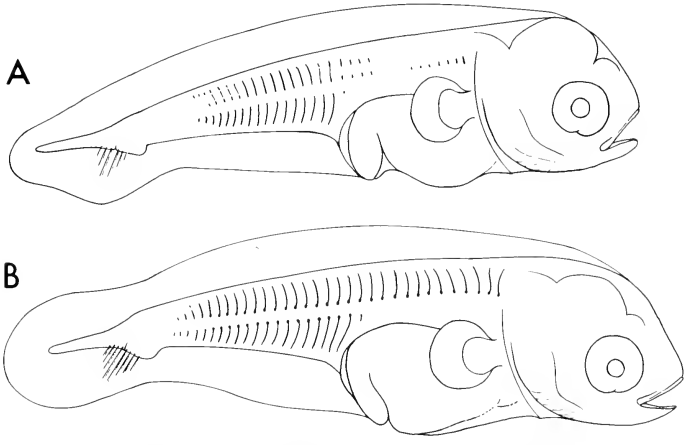


FIGURE 12.—Ossification pattern of the axial skeleton of *Pleuronichthys verticalis*: A 5.8 mm; B 6.1 mm

tion between 5.6 and 6.9 mm NL, and the full count of seven rays per side is present on late flexion specimens. Gill rakers begin to develop by late flexion, but the full count is not obtained until the early juvenile stage. Few teeth form during the larval period. Only a single tooth is developed on the right side of the upper jaw in postflexion larvae, compared with 3-6 on the left side of this jaw. The disproportion is less marked in the lower jaw, with 3-5 teeth on the right side compared with 5-7 on the left side.

Distribution.—This species ranges from Point Reyes, Calif., south to Magdalena Bay, Baja California, with an isolated population at the northern end of the Gulf of California (Norman 1934; Fitch 1963). Eggs and larvae are common in our collections, particularly at inshore stations located over the continental shelf, with only an occasional specimen being taken more than 60 mi from the coast (Figure 13).

Pleuronichthys ocellatus Starks and Thompson (Gulf turbot) Figure 14

Literature.—Neither eggs nor larvae have been described previously.

Distinguishing characters.—This species may only be confused with *P. verticalis* or *H. guttulata* which cooccur with it in the upper Gulf of California. Larvae may be distinguished from *P. verticalis* by the lower total vertebral number of 34 or 35 and pigmentation differences. The larger size of larvae, lack of pterotic spines, and different pigment pattern separate it from *H. guttulata*. Meristics of the larvae and juveniles, given in Table 12, are distinctive for the species.

Pigmentation.—Only two postflexion larvae (6.6 mm SL and 7.0 mm SL) were available. Both specimens are heavily pigmented and somewhat resemble similar stages of *P. verticalis* larvae (Figure 14 vs. Figure 9D). However, smaller sized larvae of *P. ocellatus* are heavier in pigment than *P. verticalis* in regions of the head and dorsal and anal fin pterygiophores. Only the margin of the opercle, otic region, pectoral fin, and caudal peduncle remain unpigmented.

Morphology.—Larvae of *P. ocellatus* are intermediate in size between comparable stages of *P. ritteri* and *P. verticalis* (Table 13). It is the most slender-bodied species having the smallest body depth ratios in the postflexion larval stage within its genus (Table 5).

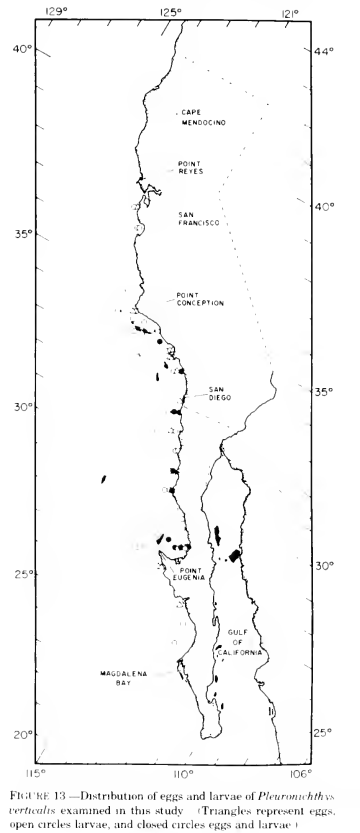


FIGURE 13.—Distribution of eggs and larvae of *Pleuronichthys verticalis* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

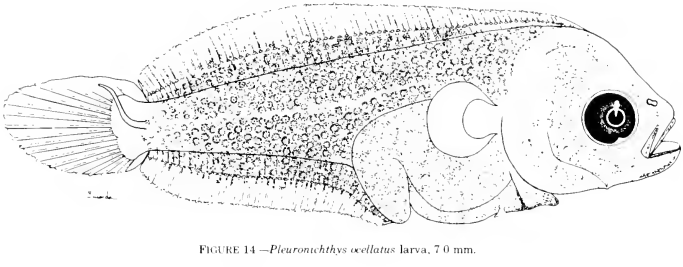


FIGURE 14.—*Pleuronichthys ocellatus* larva, 7.0 mm.

TABLE 12.—Meristics of larvae and juveniles of *Pleuronichthys ocellatus*

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right left	Precaudal	Caudal	Total	
5604-111 G 14	6.6 SL	Postfl	65	49	19	ca. 4-4	LP[2]				
5604-109 G 25	7.0	Postfl	73	50	19	ca. 3-3	LP[2]				
Upper Gulf of California	19.2	Juv	64	46	19	6.6	10/11	12	22	34	X-ray
	22.0	Juv	73	49	19	6.6	10/10	12	24	36	X-ray
	24.0	Juv	67	48	19	6.6	— 11	12	22	34	X-ray
	24.5	Juv	71	51	19	6.6	11/10	12	23	35	X-ray
	25.0	Juv	70	50	19	6.6	11/10	12	22	34	X-ray
	25.5	Juv	68	46	19	6.6	10/10	12	23	35	X-ray

[1]Postfl. - postflexion; Juv. - juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays

TABLE 13.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ocellatus*

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base	Body depth at anus	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5604-111 G 14	6.6 SL	Sym.	Flexed	3.2	2.0	0.30	0.54	0.56	2.2	2.2	0.50	0.40	1.9
5604-109 G 25	7.0	Sym.	Flexed	3.3	2.1	0.40	0.62	0.56	2.3	2.3	0.52	0.50	2.1
Upper Gulf of California	19.2	Over	Juv.	7.0	5.7	0.83	1.8	—	8.2	9.0	2.4	1.2	5.0
	22.0	Over	Juv.	7.0	6.2	0.91	1.9	—	9.4	9.8	2.8	1.4	5.2
	24.0	Over	Juv.	7.7	6.5	0.91	2.1	—	9.4	10.2	2.8	1.4	5.7
	24.5	Over	Juv.	7.4	6.8	1.1	2.3	—	10.5	11.0	3.2	1.5	5.5
	25.0	Over	Juv.	7.5	6.7	0.83	2.5	—	10.4	11.2	3.2	1.7	5.7
	25.5	Over	Juv.	8.5	6.8	0.91	2.3	—	10.7	11.7	3.1	1.8	6.0

[1]Sym. - symmetrical
[2]Juv. - juvenile

Distribution.—This species is restricted to the northern half of the Gulf of California (Norman 1934; Fitch 1963). Larvae were collected at two stations in the upper Gulf.

Pleuronichthys ritteri Starks and Morris (spotted turbot) Figures 15-17

Literature.—The egg of *P. ritteri* was described by Orton and Limbaugh (1953) and illustrated by White (1977). Larvae of this species have not been described previously.

Distinguishing characters.—Larval stages of this species may be confused with *P. verticalis* and *H. guttulata*. Characters of preflexion and flexion larvae which separate it from *P. verticalis* include the lack of triangular clusters of pigment on the finfold, less pigment on the tail with 8 or 9 unpigmented myomeres compared with 3-5 in *P. verticalis*, and a more robust body. Postflexion larvae are more heavily pigmented, particularly on the dorsal and anal fin pterygiophores, and are smaller than comparable stages of *P. verticalis*. Distinguishing characters for newly transformed and early juvenile stages have been discussed earlier under *P. verticalis*.

Characters for distinguishing yolk-sac larvae of *P. ritteri* from *H. guttulata* include the presence of

pigment on the finfolds of *P. ritteri*, a smaller oil globule (average 0.10 vs. 0.14 mm), lack of pigment on the oil globule, and presence of pigment ventrally near the tip of the notochord. Distinctive characters of preflexion and flexion larvae of *P. ritteri* include the lack of pterotic spines on the head which is more rounded than on preflexion *H. guttulata*, the lack of pigment from the top of the head posteriorly to the nape, a more robust head and trunk (compare Figure 15D with Figure 19D), and the presence of small pigment spots on the pectoral fin blade along its margin or base. Postflexion and early transforming specimens can be distinguished by a deeper and shorter caudal peduncle, a more robust body, and the origin of the dorsal fin on the future blind side of the head instead of on the medial line of the head as found in *H. guttulata*.

Pigmentation.—Yolk-sac larvae are heavily pigmented with the exception of the last 8 or 9 myomeres. Pigment is also scattered on the remnant of the yolk sac, on the dorsal and ventral finfolds, and ventrally on the tail near the tip of the notochord (Figure 15A). Except for the appearance of pigment along the margins of the pectoral fin blade, no significant changes in pigmentation occur in early preflexion larvae of ca. 3.0 mm NL (Figure 15B).

By 4.0 mm NL, pigment found earlier along the top of the head posterior to the nape is lost, leaving an unpigmented streak which persists until flexion of the notochord is complete at 5.5 mm NL (Figures 15C, D; 16A, B). Ventral pigment is similarly lost on the abdominal region, resulting in an unpigmented lower abdomen in late preflexion and flexion specimens. Marginal pectoral fin pigment present on larvae to about 3.3 mm NL, changes to small, discrete spots on the fin membrane along its base. These melanophores persist through postflexion larvae until the pectoral fin differentiates into a small, rayed fin by ca. 10.0 mm SL (Figures 16C, 17).

Pigment on the tail extends posteriad the same distance in flexion larvae as in preflexion larvae, but in postflexion larvae the tail pigment fills in posteriorly to the terminal dorsal and anal fin rays. In later postflexion and transformation stages, the head, trunk, and tail, except the caudal peduncle, are completely covered with pigment which extends over the dorsal and anal fin pterygiophores (Figures 16C, 17).

At 10.0 mm SL, a dark circular blotch of pigment develops on the middle section of the body, with a heavy band of pigment at the posterior extreme of body pigment. Several triangular patches are clustered on the dorsal and anal fin rays above the pterygiophores. The caudal peduncle area remains unpigmented (Figure 17).

Morphology.—Larvae of *P. ritteri* are the smallest among species of *Pleuronichthys* in comparable stages of development. Our smallest specimen has a large yolk sac and is 2.1 mm NL (Figure 15A). The oil globule is positioned posteriorly in the yolk mass and measures 0.11 mm in diameter. The left eye begins to migrate at about 6.0 mm SL and migration of the eye is completed before 10.0 mm SL (Table 14). The smallest available juvenile was 12.7 mm SL.

The gut develops as in other *Pleuronichthys* but coiling begins earlier, at about 3.0 mm NL, and the terminal section of the gut is in a vertical position in most specimens >4.0 mm NL.

The head is relatively larger in preflexion larvae of *P. ritteri* than in the other species (Table 5). Relative head length increases throughout the larval period, then is moderately reduced at transformation. Mean relative snout length increases in *P. ritteri* larvae undergoing notochord flexion and decreases during subsequent stages, but in other species of *Pleuronichthys* it decreases during all major phases of larval development. Relative eye size is largest in preflexion larvae, becomes reduced in later larval stages, and increases at transformation.

The early larvae of *P. ritteri* are the deepest bodied species of *Pleuronichthys*. Mean relative body depth measured at the base of the pectoral fin is greater during preflexion and flexion stages of the notochord than in any other species. In postflexion larvae, however, mean relative body depth is markedly less than in *P. decurrens* and about equal to that in *P. coenosus* and *P. verticalis* (Table 5).

Fin and axial skeleton formation.—Early caudal formation involving thickening in the hypural area of the developing caudal fin occurs on larvae 4.3-5.1 mm NL (Table 15). Caudal rays are forming on larvae as small as 4.5 mm NL, with a simultaneous initiation of flexion of the notochord. Specimens between 4.5 and 5.6 mm NL undergo notochord flexion. Our smallest specimen with a fully flexed notochord is 5.3 mm SL. The full

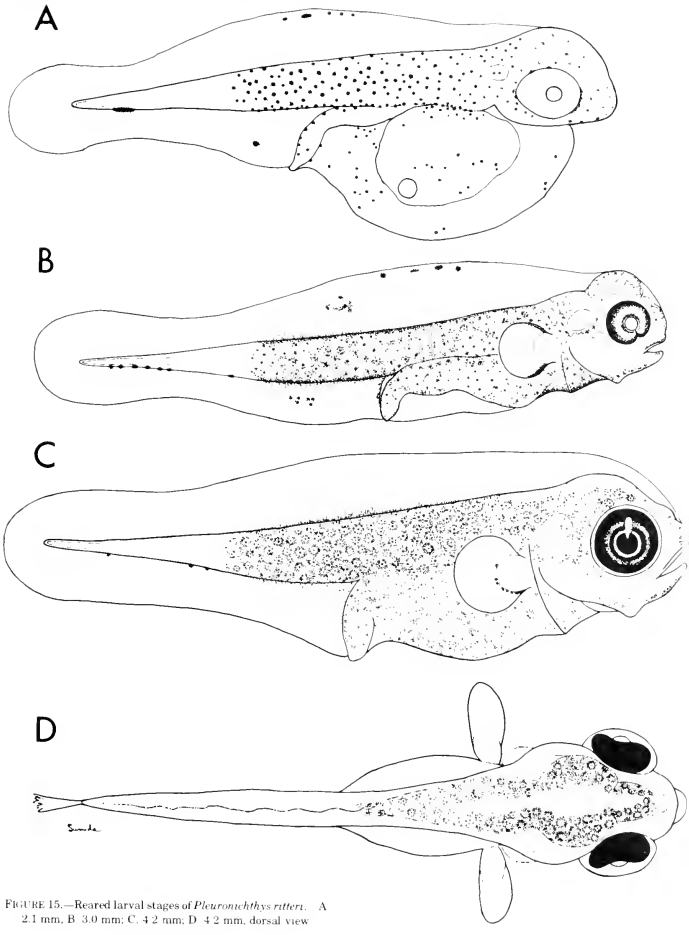


FIGURE 15.—Reared larval stages of *Pleuronichthys ritteri*. A 2.1 mm, B 3.0 mm; C, 4.2 mm; D 4.2 mm, dorsal view

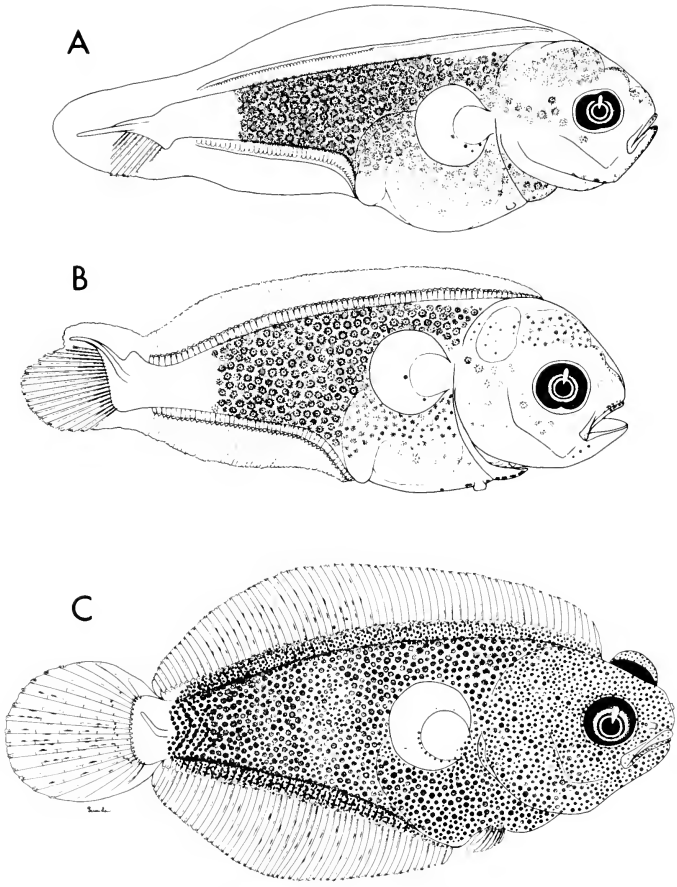


FIGURE 16.—Larval stages of *Pleuronichthys ritteri*—A 5.6 mm; B 5.5 mm; C 6.4 mm

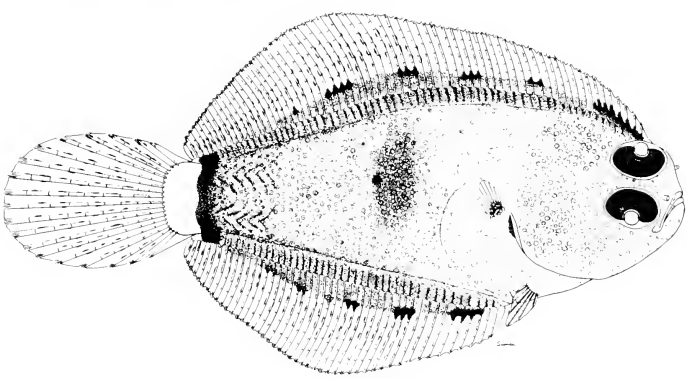


FIGURE 17.—Transforming specimen of *Pleuronichthys ritteri*, 10.0 mm

TABLE 14.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ritteri*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[2]	Body depth at anus[2]	Caudal peduncle depth	Caudal peduncle to length	Snout to origin pelvic fin
Off La Jolla, Calif	2.1 NL	Sym	Str	1.2	0.50	0.10	0.24	0.20	0.20	0.38	—	—	—
	3.0	Sym	Str	1.4	0.60	0.12	0.26	0.22	0.42	0.42	—	—	—
7412-123 36	3.3	Sym	Str	1.6	0.80	0.14	0.28	0.24	0.78	0.58	—	—	—
Off La Jolla	4.2	Sym	Str	2.2	1.0	0.18	0.40	0.32	0.96	0.86	—	—	—
5709-117 26	4.3	Sym	Str	2.1	1.1	0.20	0.40	0.36	1.2	1.2*	—	—	—
7207-123 36	4.4	Sym	Str	2.1	1.1	0.24	0.34	0.32	1.0	0.9	—	—	—
6204-120 25	5.0	Sym	Str	2.2	1.2	0.20	0.38	0.38	1.2	1.1*	—	—	—
5708-120 25	5.1	Sym	Str	2.5	1.4	0.24	0.46	0.40	1.8*	1.7*	—	—	1.3
6507-120 35	4.5	Sym	E.fl	2.3	1.4	0.32	0.44	0.42	1.6*	1.6*	—	—	1.2
5506-120 40	4.8	Sym	E.fl	2.3	1.4	0.28	0.40	0.38	1.5*	1.7*	—	—	1.4
5510-117 26	5.5	Sym	Midfl	2.7	1.2	0.34	0.52	0.48	2.0*	1.9*	—	—	1.6
7501-120 25	5.6	Sym	Midfl	2.7	1.5	0.26	0.46	0.40	1.8*	1.5*	—	—	1.4
5112-120 35	5.3 SL	Sym	Flexed	2.7	1.7	0.30	0.52	0.52	2.2*	2.2*	0.50	0.36	1.4
5802-137 23	6.0	Migr	Flexed	2.9	2.0	0.32	0.60	0.54	2.4*	2.7*	0.66	0.30	1.8
Off La Jolla	6.4	Migr	Flexed	2.6	2.2	0.40	0.64	0.60	2.5*	2.7*	0.76	0.38	2.0
Sebastian Viscaino Bay, B.C.	7.5	A. over	Flexed	3.0	2.6	0.40	0.80	0.64	2.9*	3.0*	1.0	0.48	2.7
7501-120 22 4	8.5	A. over	Flexed	2.8	2.7	0.40	0.86	?	3.6*	3.6*	1.1	0.44	2.3
Off La Jolla	10.0	Over	Flexed	3.1	3.1	0.48	1.0	0.80	4.2*	4.2*	1.4	0.60	2.6
Reared	12.7	Over	Juv	4.2	3.8	0.36	1.4	1.0	5.1*	5.4*	1.4	0.76	3.4
Reared	15.0	Over	Juv	4.5	4.2	0.48	1.6	1.2	5.9*	6.1*	1.8	1.0	3.9
Reared	16.7	Over	Juv	5.2	4.7	0.48	1.8	1.4	6.2*	6.4*	2.0	1.1	4.2
Off San Juanico, B.C.	23.0	Over	Juv	7.2	6.8	0.83	2.2	?	9.7*	9.7*	2.6	1.2	5.8

[1]Sym - symmetrical, Migr - migrating, A. over - About over
[2]Str - straight, E.fl - early flexion, Midfl - midflexion, Juv - juvenile
[3]Asterisk indicates inclusion of dorsal-fin pterygiophores in body depth measurement

caudal count of 19 rays was observed on a 6.0-mm SL postflexion specimen.

Dorsal and anal fin bases are forming in the finfold on larvae 4.3 mm NL, and the full complement of rays develops by 6.0 mm SL. Pelvic fin buds are evident during early caudal formation but rays are first observed on a 6.0-mm specimen. Pectoral rays were fully formed on a 10.0-mm

TABLE 15.—Meristics of larvae and juveniles of *Pleuronichthys ritteri*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right,left	Precaudal	Caudal	Total	
Off La Jolla, Calif	2.1 NL	Yolk-sac	0	0	0	0	LP[2]				
	3.0	Prefl	0	0	0	0	LP[2]				
7412-123 36	3.3	Prefl	0	0	0	0	LP[2]				
Off La Jolla	4.2	Prefl	0	0	0	0	LP[2]				
5709-117 26	4.3	Prefl	Forming	Forming	Forming	0	LP[2]				
7207-23 36	4.4	Prefl	Forming	Forming	Forming	0	LP[2]				
6204-120 25	5.0	Prefl	Forming	Forming	Forming	0	LP[2]				
5708-120 25	5.1	Prefl	Forming	Forming	Forming	Bud	LP[2]				
6507-120 35	4.5	E fl	Forming	Forming	ca. 6	Bud	LP[2]				
5506-120 40	4.8	E fl	Forming	Forming	ca. 4	Bud	LP[2]				
5510-117 26	5.5	Midfl	Forming	Forming	ca. 8	Bud	LP[2]				
7501-120 25	5.6	Midfl	Forming	Forming	ca. 8	Bud	LP[2]				
5112-120 35	5.3 SL	Postfl	ca. 60	ca. 45	16	Bud	LP[2]				
5802-137 23	6.0	Postfl	72	49	19	6.6	LP[2]				
Off La Jolla	6.4	Postfl	65	45	19	6.6	LP[2]				
Sebastian Viscaino Bay, B.C.	7.5	Postfl	70	48	19	6.6	LP[2]				
7501-120 22 4	8.5	Postfl	69	51	19	6.6	LP[2]				
Off La Jolla	10.0	Postfl	68	47	19	6.6	9.9	12	23	35	X-ray
Reared	12.7	Juv	69	47	19	6.6	10.11	12	23	35	X-ray
Reared	15.0	Juv	64	44	19	6.6	10.11	12	23	35	X-ray
Reared	16.7	Juv	65	44	19	6.6	11.11	12	22	34	X-ray
Off San Juanico, B.C.	23.0	Juv	68	49	Damaged	6.6	9.9	12	23	35	X-ray

[1]Prefl = preflexion, E fl = early flexion, Midfl = midflexion, Postfl = postflexion, Juv = juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays.

larva. A radiograph of this specimen showed 12 precaudal and 23 caudal vertebrae, the typical count for this species.

Distribution.—This species ranges from Morro Bay, Calif., to Magdalena Bay, Baja California (Fitch 1963; Miller and Lea 1972; Fierstine et al. 1973). Our egg and larval material, which was collected between southern California and Magdalena Bay, Baja California, shows a markedly coastal, inshore distribution for *P. ritteri*, with a majority of collections made over or near the continental shelf (Figure 18).

Hypsopsetta guttulata Girard (diamond turbot) Figures 19-22

Literature.—Orton and Limbaugh (1953) and Orton (1953) briefly described the eggs of *H. guttulata*. Eldridge (1975) described and illustrated larvae of this species, and noted the average size of its egg and oil globule. Although the larval series is quite well described in Eldridge (1975) (except for the omission of the pterotic spine on the head), we are including information about distinguishing characters, pigmentation, etc. to facilitate identification.

Distinguishing characters.—Larvae of *H. guttulata* are distinguishable from species of *Pleuronichthys*, except for *P. ritteri*, by their lower total vertebral number, by attaining comparable stages of development at smaller sizes, and by the presence of a pterotic spine on each side of the head in yolk-sac larvae to midflexion larvae. In the genus *Pleuronichthys*, only *P. decurrens* develops pterotic spines. (See Distinguishing characters for *P. decurrens*.)

The only species with which larval *H. guttulata* may be confused is *P. ritteri* because of its relatively small size and somewhat similar pigment pattern. (See Distinguishing characters for separating larvae of the two species discussed under *P. ritteri*.)

Pigmentation.—Yolk-sac larvae are heavily pigmented on the head, trunk, and for a short distance on the tail, with the posteriormost 9 or 10 myomeres remaining unpigmented (Figure 19A). Pigment spots are scattered over the ventral and posterior surfaces of the yolk sac and oil globule, and over the terminus of the gut.

Preflexion larvae show little change in pigment pattern. One or two melanophores develop on the pectoral fin base. The isthmus has a line of pigment spots, and the entire abdominal area is covered with pigment (Figure 19B).

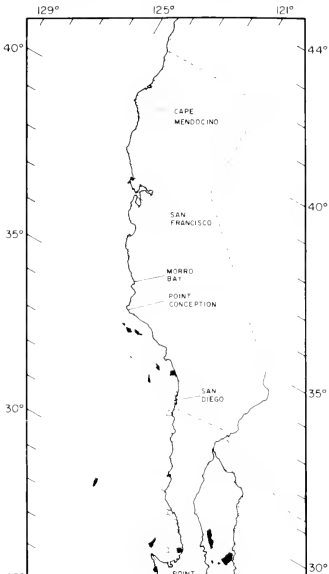


FIGURE 18.—Distribution of eggs and larvae of *Pleuronichthys ritteri* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

At the initiation of dorsal and anal fin formation, the tail pigment spreads out dorsally and ventrally onto the finfold, resulting in conspicuous dark mounds of pigment opposing each other in the area between the body and the dorsal and anal fin bases (Figure 19C). The tops of the head, nape, and shoulder area are pigmented in contrast to *P. ritteri*, which has an unpigmented streak dorsally (Figure 19D). Flexion, postflexion, and early transforming specimens maintain the earlier pigment pattern and the only obvious change is a slight posteriad extension of trunk pigment, leaving 5 or 6 unpigmented myomeres posteriorly compared with 9 or 10 in earlier stages (Figure 20). The base of the pectoral fin acquires more pigment spots in postflexion larvae, and pigment on the head similarly increases in density (Figure 20B).

Preserved small juveniles are brownish-black with numerous small, dark spots scattered over the body and pterygiophores, giving them a mottled appearance (Figure 21).

Morphology.—Our smallest yolk-sac larva is 2.2 mm NL and has a posteriorly positioned oil globule 0.14 mm in diameter (Figure 19A). The left eye is beginning to migrate in a specimen 4.4 mm SL and is complete in a 7.3-mm SL larva (Table 16). The smallest available juvenile was 11.2 mm SL.

A major distinguishing feature of *Hypsopsetta* larvae is the presence of a pterotic spine on each side of the head. The spines are present on the smallest yolk-sac larva and are prominent in most preflexion larvae. The spines begin to regress on late preflexion larvae, and are totally regressed in late flexion specimens. In *P. decurrens* the spines are well developed throughout the larval period and begin to regress late in the postflexion stage.

Although mean relative body depth of *H. guttulata* larvae increases with development, it is slightly less in postflexion specimens than in any species of *Pleuronichthys*, except *P. ocellatus* (Table 5). In newly transformed juveniles, however, relative body depth is greater than in any species of *Pleuronichthys*. As a juvenile, *H. guttulata* assumes a diamond-shaped body form.

Relative body width is useful to separate *Hypsopsetta* larvae from those of *P. ritteri*. As shown in Figures 15D and 19D, larvae of *Hypsopsetta* have narrower bodies.

Fin formation.—The caudal fin forms on larvae between 4.0 and 5.2 mm NL and is complete on some specimens as small as 4.4 mm (Table 17). The dorsal and anal fins form simultaneously with the

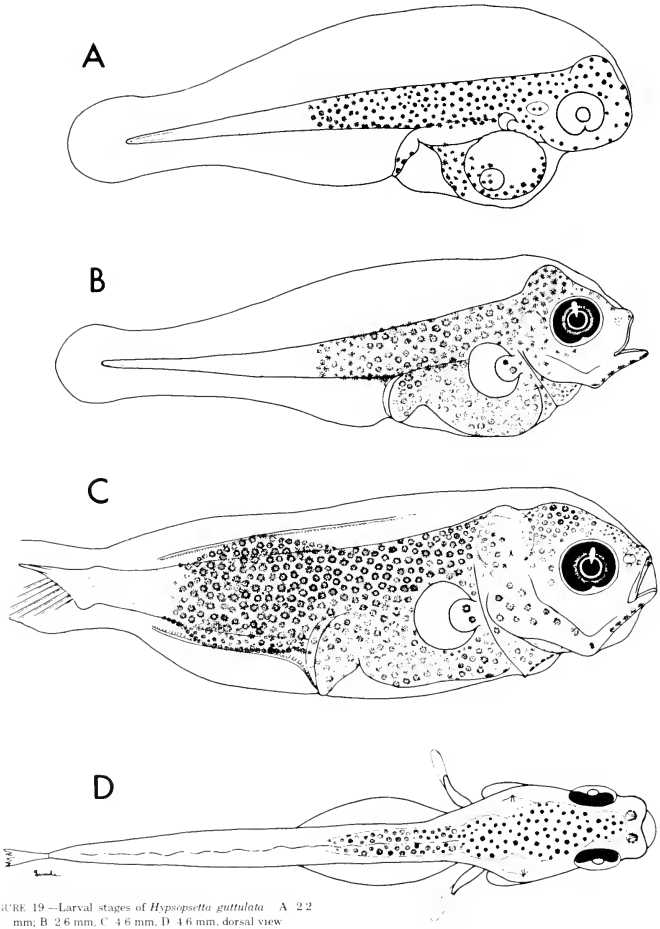


FIGURE 19.—Larval stages of *Hypsopsetta guttulata*. A, 2.2 mm; B, 2.6 mm; C, 4.6 mm; D, 4.6 mm, dorsal view.

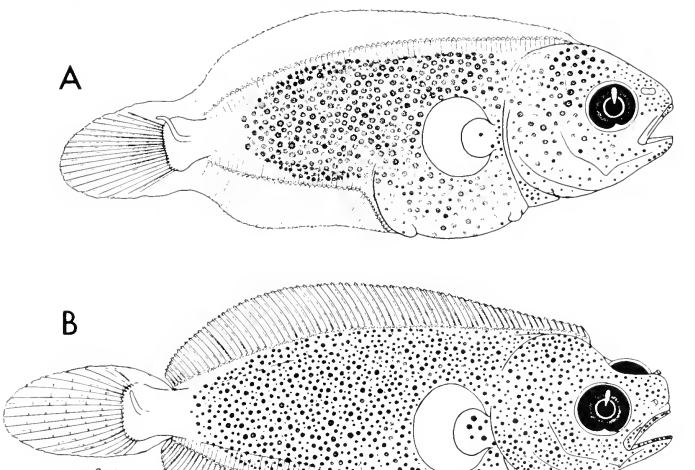


FIGURE 20.—Larval stages of *Hypsopsetta guttulata*. A, 5.9 mm; B, 6.6 mm.

caudal and are complete, or nearly so, on all postflexion specimens (4.4-8.8 mm SL). Pelvic fins are late in forming compared with their developmental pattern in *Pleuronichthys* larvae. Pelvic buds can be observed only after notochord flexion has been completed, and rays are first evident on the 6.6-mm SL specimen.

Distribution.—*Hypsopsetta guttulata* ranges from Cape Mendocino, Calif., to Magdalena Bay, Baja California, with an isolated population in the upper Gulf of California (Norman 1934; Fitch 1963). Egg and larval material examined by us was collected in bays along the coast, or at CalCOFI stations located over the continental shelf, a pattern of distribution similar to the habitat of *P. ritteri* (Figure 22).

Hippoglossina stomata Eigenmann and Eigenmann (bigmouth sole) Figure 23

Literature.—There is no published account of eggs and larvae of this species. However, Leonard (1971) described a larval series of *H. oblonga* from the western North Atlantic. Earlier, Agassiz and Whitman (1885) and Miller and Marak (1962) described the eggs and early-stage larvae of *H. oblonga*. Miller and Marak reported the egg size range as 0.91-1.12 mm (average 1.04 mm) with an oil globule diameter of ca. 0.17 mm. The larval size at hatching was 2.7-3.2 mm.

Distinguishing characters.—Preflexion larvae of *H. stomata* may be confused with early larvae of *P.*

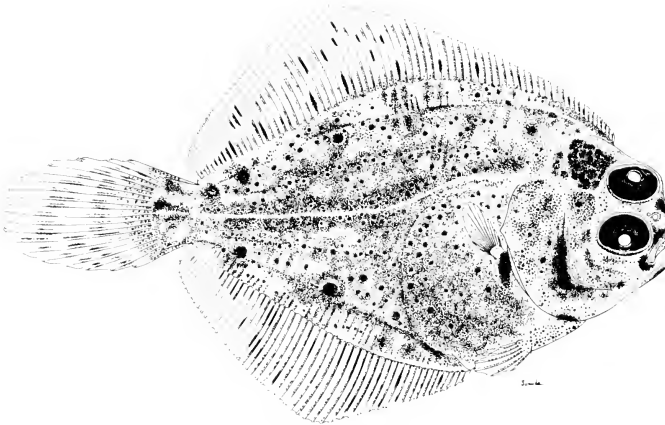


FIGURE 21.—Early juvenile of *Hypsopsetta guttulata*, 13.2 mm.

coenosus and *P. verticalis* due to similarities in size and pigmentation of the larvae, and the presence of pigment on the finfold dorsally and ventrally, posterior to the anus. Characters of *H. stomata* larvae which distinguish them from preflexion *P. coenosus* larvae include the presence of a pigment bar through the eye, heavy pigment on both sides of the pectoral fin base and a sprinkling of pigment on the pectoral blade, a more slender, elongate body, and a significantly smaller patch of dorsal finfold pigment. The same characters help to distinguish *H. stomata* from *P. verticalis*, except for the finfold pigmentation. *Pleuronichthys verticalis* has small, triangular-shaped pigment patches whereas *H. stomata* has a small rounded pigment cluster on the dorsal finfold and a broad patch on the ventral finfold. Larvae of *P. verticalis* are also smaller than *H. stomata* at similar developmental stages.

Larvae in the flexion stage and larger are readily separable from *Pleuronichthys* by the preopercular spines and development of several elongated dorsal rays in the anteriormost part of the dorsal fin. These do not develop on larval *Pleuronichthys* or *Hypsopsetta*.

Pigmentation.—Yolk-sac larvae (ca. 3.7 mm) are heavily pigmented on the trunk and tail except for the posteriormost part of the tail which is pigmented with several small spots dorsally and ventrally (Figure 23A). The upper head and abdominal region have scattered pigment, with a more concentrated bar of pigment on each side of the eye. Both sides of the pectoral fin base are conspicuously pigmented. Finfold pigment consists of a small, rounded patch at the edge of the dorsal finfold, and a broad patch on the ventral finfold, both situated posterior to the anus near the midpoint between the anus and tip of the tail (Figure 23A).

Preflexion larvae, 4.1-7.0 mm NL, undergo little change in pigmentation except to augment pigment in areas of the pectoral fin, abdominal region, and top of the head (Figure 23B).

On larvae forming the dorsal and anal fins, the dorsal finfold pigment spreads to include the area between the fin rudiments and body margin, and the ventral finfold pigment spreads both anteriorly and posteriorly (Figure 23C). Pigment on the pectoral fin base intensifies and also extends out onto the fin blade.

TABLE 16.—Morphometrics, in millimeters, of larvae and juveniles of *Hypsopsetta guttulata* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
San Diego Bay	2.2 NL	Sym	Str	1.1	0.38	0.08	0.17	0.13	0.18	0.28	—	—	—
King Harbor, Calif	2.3	Sym	Str	1.1	0.46	0.12	0.20	0.17	0.18	0.34	—	—	—
7501-120 25	2.8	Sym	Str	1.4	0.68	0.12	0.26	0.22	0.62	0.52	—	—	—
7501-120 29	3.3	Sym	Str	1.7	0.82	0.20	0.30	0.24	0.82	0.72	—	—	—
San Diego Bay	3.6	Sym	Str	1.8	0.84	0.16	0.32	0.28	0.78	0.66	—	—	—
San Diego Bay	4.0	Sym	Str	2.0	0.88	0.20	0.36	0.30	0.88	0.84	—	—	—
7412-127 32 6	4.4	Sym	Str	2.2	0.90	0.20	0.37	0.32	1.0	0.92	—	—	—
7412-127 32 6	4.6	Sym	E fl	2.3	1.2	0.24	0.38	0.32	1.1	1.0	—	—	—
7501-120 22 4	4.9	Sym	E fl	2.4	1.3	0.22	0.40	0.36	1.2	1.1	—	—	—
7501-120 29	5.1	Sym	E fl	2.5	1.2	0.22	0.40	0.36	1.1	1.1	—	—	—
King Harbor	5.2	Sym	L fl	2.4	1.4	0.28	0.44	0.42	1.2	1.2	—	—	—
L.A. Harbor, Calif	4.4 SL	Migr	Flexed	2.2	1.6	0.30	0.48	0.42	1.8*	1.9*	0.40	0.40	1.4
La Jolla, Calif	4.8	Migr	Flexed	2.2	1.5	0.30	0.48	0.40	1.6*	1.7*	0.40	0.36	1.4
San Diego Bay	5.4	Migr	Flexed	2.3	1.8	0.34	0.52	0.40	1.8*	1.9*	0.42	0.42	1.6
7501-120 22 7	5.9	Sym	Flexed	3.1	1.8	0.32	0.50	0.46	2.0*	2.2*	0.44	0.48	1.9
7501-120 24	6.6	Migr	Flexed	3.2	2.1	0.40	0.62	0.52	2.3*	2.4*	0.50	0.60	2.0
Reared	7.3	Over	Flexed	2.9	2.5	0.40	0.90	0.70	3.3*	3.5*	0.76	0.64	2.1
Reared	7.9	Over	Flexed	2.9	2.7	0.44	0.92	0.68	3.6*	3.8*	0.86	0.70	2.1
Reared	8.8	Over	Flexed	3.6	3.0	0.48	1.0	0.76	4.1*	4.2*	0.96	0.68	2.6
Reared	11.2	Over	Juv	4.2	3.7	0.50	1.4	1.1	5.7*	6.0*	1.4	1.0	3.3
Richardson Bay Calif	12.9	Over	Juv	4.5	4.3	0.52	1.2	0.92	7.0*	7.0*	1.5	1.0	3.6
	13.2	Over	Juv	4.8	4.3	0.75	1.3	1.1	6.7*	7.1*	1.4	1.0	3.6
	14.0	Over	Juv	5.0	4.7	0.75	1.4	1.2	7.5*	7.7*	1.6	1.2	3.8
	14.5	Over	Juv	5.2	4.8	0.72	1.4	1.0	7.7*	7.9*	1.8	0.88	4.1
	18.4	Over	Juv	6.4	5.8	0.80	1.7	1.4	10.0*	10.5*	2.1	1.4	5.1

[1]Sym - symmetrical, Migr - migrating
[2]Str - straight, E fl - early flexion, L fl - late flexion, Juv - juvenile
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement

TABLE 17.—Meristics of larvae and juveniles of *Hypsopsetta guttulata* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right left	Precaudal	Caudal	Total	
7501-120 25	2.8 NL	Prefl	0	0	0	0	LP[2]				
7501-120 29	3.3	Prefl	0	0	0	0	LP[2]				
San Diego Bay	3.6	Prefl	0	0	0	0	LP[2]				
San Diego Bay	4.0	Prefl	Forming	Forming	Forming	0	LP[2]				
7412-127 32 6	4.4	Prefl	Forming	Forming	6	0	LP[2]				
7412-127 32 6	4.5	E fl	Forming	Forming	8	0	LP[2]				
7501-120 22 4	4.9	E fl	Forming	Forming	6	0	LP[2]				
7501-120 29	5.1	E fl	Forming	Forming	4	0	LP[2]				
King Harbor, Calif	5.2	L fl	ca. 50	ca. 35	15	0	LP[2]				
L.A. Harbor, Calif	4.4 SL	Postfl	67	47	19	Bud	LP[2]				
Off La Jolla, Calif	4.8	Postfl	66	49	19	Bud	LP[2]				
San Diego Bay	5.4	Postfl	73	45	19	Bud	LP[2]				
7501-120 22 7	5.9	Postfl	73	46	19	Bud	LP[2]				
7501-120 24	6.6	Postfl	69	50	19	6-6	LP[2]				
Reared	7.3	Postfl	68	47	19	6-6	11-11	11	23	34	X-ray
Reared	7.9	Postfl	67	51	20	6-6	12-12	12	23	35	X-ray
Reared	8.8	Postfl	72	50	19	6-6	13-13	12	23	35	X-ray
Reared	11.2	Juv	73	48	19	4-6	12-12	12	22	34	X-ray
Richardson Bay, Calif	12.9	Juv	66	48	19	6-6	12-11	12	23	35	X-ray
	13.2	Juv	74	53	19	6-6	11-11	12	23	35	X-ray
	14.0	Juv	78	55	19	6-6	11-11	12	23	35	X-ray
	14.5	Juv	71	51	19	6-6	12-12	12	23	35	X-ray
	18.4	Juv	68	51	19	6-6	11-12	12	23	35	X-ray

[1]Prefl - preflexion, E fl - early flexion, L fl - late flexion, Postfl - postflexion, Juv - juvenile
[2]LP refers to functional larval pectoral fins which have no ossified rays

Postflexion and early transforming specimens are less heavily pigmented than earlier stage larvae, with a noticeable diminution of pigment on the dorsal area of the head and body (Figure 23D).

Morphology.—Larvae of *H. stomata* are closest to *P. coenosus* in size at hatching, notochord flexion, and transformation (Table 18). A specimen 3.7 mm NL has a moderate amount of yolk remaining.

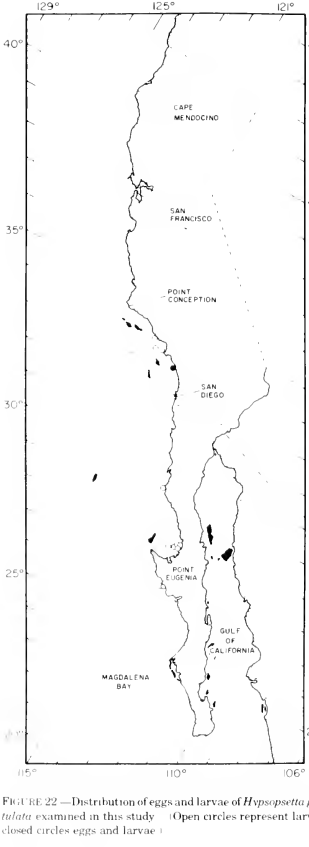


FIGURE 22.—Distribution of eggs and larvae of *Hypsopsetta guttulata* examined in this study. (Open circles represent larvae, closed circles eggs and larvae.)

The right eye is beginning to migrate in a specimen 9.1 mm SL and transformation is almost complete at 11.7 mm SL.

In early preflexion larvae of *Hippoglossina*, the gut is shaped like that in *Pleuronichthys* larvae; however, coiling begins at about 4.5 mm NL and the gut assumes a more compact shape than in *Pleuronichthys*. This is reflected in the relatively shorter snout-anus length. Mean relative snout-anus length remains at about 40% of the body length throughout the larval period, in contrast to *Pleuronichthys* larvae in which there is a gradual decrease in relative gut length during larval development (Table 5). In juveniles, however, there is a decrease in snout-anus length to about 33% of body length, a value comparable with that in *Pleuronichthys* juveniles.

The head is similar in size and shape to that in *Pleuronichthys*. Relative head length increases gradually during larval development. The same is true for relative snout length and is thus opposite to the condition in *Pleuronichthys*; however, it decreases somewhat in juveniles. Relative eye width undergoes a moderate diminution during larval development as in *Pleuronichthys*, but increases moderately in juveniles.

Small preopercular spines develop on larvae from ca. 5.5 mm NL, become most conspicuous on flexion stage larvae, and undergo resorption during transformation from 9.5 mm SL. This spination is distinctive of *H. stomata* when compared with *Pleuronichthys* and *Hypsopsetta*.

Larvae of *Hippoglossina* have a slender appearance compared with some of the deeper bodied species of *Pleuronichthys*. Body depth at the anus is comparatively small in preflexion larvae and remains so in flexion and postflexion larvae and early juveniles (Table 5).

As in *Hypsopsetta*, the caudal peduncle is longer and more slender than in *Pleuronichthys*, except for *P. ocellatus* postflexion larvae.

Fin formation.—Larvae of *Hippoglossina stomata* are comparable with those of *P. coenosus* with regard to size at which the caudal fin develops. Caudal fin formation occurs between 6.2 and 8.8 mm NL (Table 19). Although about six caudal rays are formed on a 7.0-mm NL specimen with a straight notochord, all other specimens with caudal rays have the notochord flexing. The smallest, fully flexed specimen is 7.1 mm SL. Postflexion specimens $\geq$ 9.0 mm SL lack the full complement of 18½ caudal rays. The ural bones supporting the caudal rays are made up of two superior and two inferior hypurals; there is no epural. The lack of an epural bone is a specific

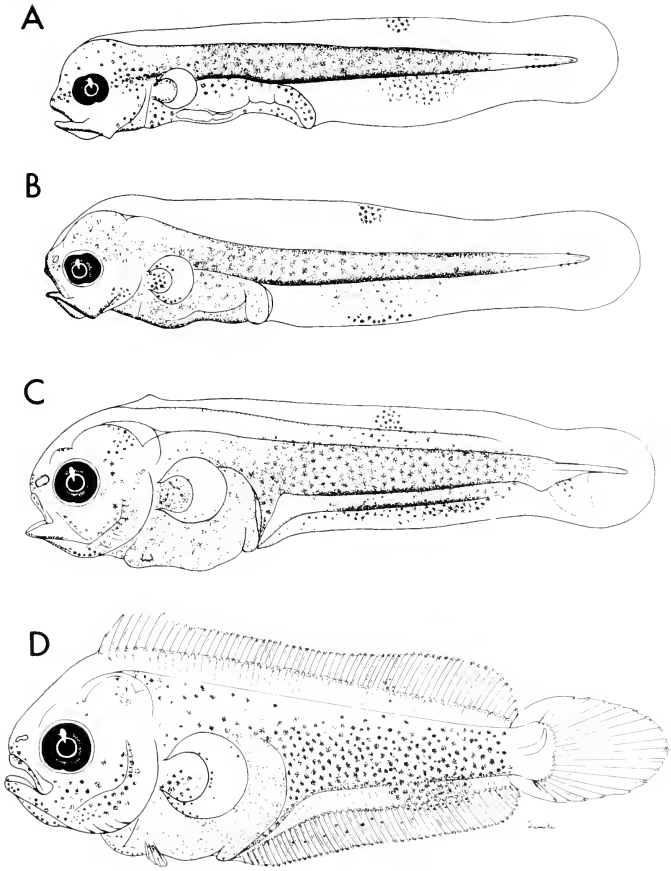


FIGURE 23.—Larval stages of *Hippoglossina stomata*. A, 3.8 mm; B, 4.8 mm; C, 8.3 mm; D, 8.6 mm.

TABLE 18.—Morphometrics, in millimeters, of larvae of *Hippoglossina stomata* (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7201-117 35	3 7 NL	Sym	Str	1 4	0 64	0 10	0 28	0 21	0 50	0 40	—	—	—
7412-103 29	4 1	Sym	Str	1 8	0 72	0 07	0 24	0 24	0 48	0 36	—	—	—
7412-88 5 31	4 8	Sym	Str	2 0	1 0	0 24	0 36	0 28	0 96	0 68	—	—	—
5801-117 35	5 2	Sym	Str	2 2	1 2	0 24	0 48	0 36	1 2	0 82	—	—	—
6310-93 28	6 2	Sym	Str	2 2	1 3	0 26	0 42	0 36	1 2	0 92	—	—	—
6605-123 37	6 4	Sym	Str	2 2	1 3	0 24	0 44	0 36	1 4*	1 0	—	—	—
5910-117 30	6 2	Sym	Str	2 8	1 6	0 30	0 54	0 42	2 1*	1 3	—	—	—
6706-110 50	7 0	Sym	Str	2 8	1 8	0 32	0 50	0 42	2 1*	1 8*	—	—	—
5708-118 5 35	6 6	Sym	E fl	2 7	1 7	0 40	0 54	0 54	2 1*	1 7*	—	—	1 5
5706-127 34	7 5	Sym	E fl	3 0	2 0	0 36	0 66	0 70	2 2*	1 8*	—	—	1 8
6912-83 60	8 3	Sym	E fl	3 2	1 8	0 42	0 60	0 66	2 4*	2 0*	—	—	2 0
5807-130 30	7 6	Sym	Midfl	2 9	1 9	0 38	0 64	0 58	2 2*	2 0*	—	—	1 8
5709-110 30	7 9	Sym	Midfl	2 9	1 9	0 42	0 60	0 52	2 2*	2 0*	—	—	1 7
6706-123 37	8 8	Sym	Midfl	3 4	2 3	0 44	0 68	0 60	2 8*	2 4*	—	—	2 4
5706-123 37	7 6	Sym	L fl	3 1	2 1	0 46	0 66	0 64	2 5*	2 3*	—	—	1 8
6706-123 36	8 5	Sym	L fl	3 4	2 3	0 44	0 70	0 66	2 8*	2 6*	—	—	2 3
6608-120 30	7 1 SL	Sym	Flexed	3 1	2 2	0 46	0 76	0 78	2 6*	2 4*	0 66	0 62	2 1
5708-115 35	8 0	Sym	Flexed	3 3	2 4	0 64	0 72	0 68	2 9*	2 7*	0 62	0 70	2 0
6706-123 37	9 0	Sym	Flexed	3 9	2 7	0 52	0 84	0 84	3 4*	3 0*	0 70	0 82	2 7
6410-83 43	9 4	Sym	Flexed	3 7	2 7	0 56	0 84	0 84	3 6*	3 8*	0 80	0 84	2 3
5701-120 35	9 1	Migr	Flexed	3 8	3 1	0 72	1 0	0 96	3 7*	4 1*	0 92	0 68	2 7
5709-110 33	9 9	Migr	Flexed	4 0	3 2	0 80	0 90	0 86	4 1*	4 3*	0 90	0 76	2 6
6706-123 36	10 5	Migr	Flexed	4 1	3 5	0 80	1 1	0 94	3 8*	3 9*	0 98	0 88	3 0
5507-130 30	11 7	Migr	Flexed	4 2	3 7	0 96	1 0	0 88	4 4*	4 5*	1 2	0 90	3 5
Asuncion Bay	35 8	Over	Juv	12 4	12 2	2 3	4 3	—	13 4*	13 0*	3 2	2 9	10 5
B C	38 2	Over	Juv	12 2	13 5	2 7	4 2	—	14 2*	13 7*	3 8	3 4	11 4

[1]Sym - symmetrical, Migr - migrating.
[2]Str - straight, E fl - early flexion, Midfl - midflexion, L fl - late flexion, Juv - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygophores in body depth measurement.

TABLE 19.—Meristics of larvae and juveniles of *Hippoglossina stomata*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
7201-117 35	3 7 NL	Prefl	0	0	0	0	LP[2]				
7412-103 29	4 1	Prefl	0	0	0	0	LP[2]				
7412-88 5 31	4 8	Prefl	0	0	0	0	LP[2]				
5801-117 35	5 2	Prefl	0	0	0	0	LP[2]				
6310-93 28	6 2	Prefl	0	0	0	0	LP[2]				
6605-123 37	6 4	Prefl	Anterior swelling	0	0	0	LP[2]				
5910-117 30	6 2	Prefl	Forming	0	Forming	0	LP[2]				
6706-110 50	7 0	Prefl	Forming	Forming	ca 6	0	LP[2]				
5708-118 5 35	6 6	E fl	Forming	Forming	ca 6	Bud	LP[2]				
5706-127 34	7 5	E fl	Forming	Forming	ca 10	Bud	LP[2]				
6912-83 60	8 3	E fl	Ant 4	Forming	ca 10	Bud	LP[2]				
5807-130 30	7 6	Midfl	ca 15	ca 15	12	Bud	LP[2]				
5709 110 30	7 9	Midfl	ca 55	ca 45	12	Bud	LP[2]				
6706-123 37	8 8	Midfl	ca 62	ca 50	16	Bud	LP[2]				
5706-123 36	7 6	L fl	ca 63	ca 45	14	Bud	LP[2]				
6706-123 36	8 5	L fl	ca 68	ca 50	14	Bud	LP[2]				
6608-120 30	7 1 SL	Postfl	ca 66	ca 51	16	ca 5 5	LP[2]				
5708 115 35	8 0	Postfl	63	50	ca 18	6 6	LP[2]				
6706-123 37	9 0	Postfl	68	53	18½	5 5	LP[2]				
6410 83 43	9 4	Postfl	68	54	ca 18	6 6	LP[2]				
5701-120 35	9 1	Postfl	67	53	18½	6 6	LP[2]				
5709-110 33	9 9	Postfl	65	50	18½	6 6	LP[2]				
6706-123 36	10 5	Postfl	66	53	18½	6 6	LP[2]				
5507-130 30	11 7	Postfl	64	50	18½	6 6	LP[2]				
Asuncion Bay	35 8	Juv	67	52	18½	6 6	10 10	11	27	38	X-ray
B C	38 2	Juv	65	50	17½	6 6	10 10	11	27	38	X-ray

[1]Prefl - preflexion, E fl - early flexion, Midfl - midflexion, L fl - late flexion, Postfl - postflexion, Juv - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

character in *H. stomata* because other species of *Hippoglossina* possess this bone.

The dorsal fin of *H. stomata* develops quite differently than in *Pleuronichthys*. An anterior group of about five dorsal rays is the first to form in *H. stomata*; these become more elongated than the other rays. The anlage of these is evident on a 6.4-mm NL preflexion specimen and four rays are formed on a 9.3-mm NL early flexion larva. A similar pattern of early forming dorsal fin rays is found in the closely related genera *Paralichthys* (Okiyama 1967; Smith and Fahay 1970; Ahlstrom and Moser 1975) and *Pseudorhombus* (Devi 1969). Although the anterior dorsal rays form early, the pelvic fins do not develop elongated rays, such as in the bothid genera *Svacium* (Aboussouan 1968) and *Cyclopsetta* (Gutherz 1970). The dorsal fin rays differentiate posteriad but most rays form simultaneously and the full complement is developed on a late flexion specimen. The base of the anal fin is evident during early caudal formation, rays are forming on midflexion specimens, and the total number is formed on a late flexion specimen. Pelvic fin buds are evident on early flexion specimens, but rays can be distinguished only on postflexion larvae.

Distribution.—This species ranges from Monterey Bay, Calif., to the Gulf of California, including Guadalupe Island (Miller and Lea 1972). Larvae occurred over a wide band of inshore and offshore stations (Figure 24). The southern limit of *H. stomata* overlaps the northern range of *H. tetrophthalmus* which has different fin counts (Ginsburg 1952). To date, larvae of *H. tetrophthalmus* are not known.

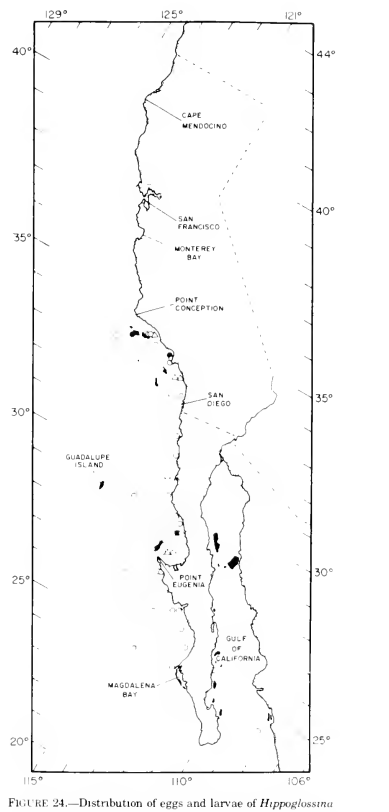


FIGURE 24.—Distribution of eggs and larvae of *Hippoglossina stomata* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

SUMMARY

We used a combination of larval morphology, meristics, and pigmentation to distinguish seven known eastern North Pacific species of flatfishes with heavily pigmented larvae. Table 20 summarizes many pertinent characters for identifying eggs and larvae of these species. Information is given for three characters of eggs: size, ornamentation of the chorion, and presence or absence of an oil globule.

In most instances, the size of a newly hatched larva is directly related to the size of the egg from which it hatched, and such is the case with *Pleuronichthys*. *Pleuronichthys decurrens*, with the largest egg, has the largest larva, with a successive decrease in larval size of the other species corresponding to their smaller sized eggs. This also applies to the yolk-sac larvae of *Hypsopsetta guttulata* and *Hippoglossina stomata*. *Pleuron-*

ichthys decurrens, with the largest yolk-sac larva, is correspondingly large at caudal fin formation (notochord flexion) and at transformation, whereas *Hypsopsetta guttulata*, with the smallest egg, is correspondingly smallest at all stages of larval development with the exception of some overlap with larvae of *P. rittert*.

A larval character that is particularly useful in separating preflexion larvae of *H. guttulata* from those of *P. rittert* is the presence of a pterotic spine on each side of the head of *H. guttulata*. The only species of *Pleuronichthys* with a pterotic spine is *P. decurrens*.

For relating a larval series to its juveniles and adults, and thus substantiating identification of the series, meristic counts, particularly of the precaudal and caudal groups of vertebrae, are indispensible. One can seldom rely on one meristic character alone, but must use a combination of all available counts.

The distribution of pigment, which changes with growth, provides good characters for discriminating among larvae of the several species. It is particularly useful with preflexion larvae, and for this reason we emphasize pigment for this stage in Table 20.

ACKNOWLEDGMENTS

We would like to thank the following individuals for loan of specimens: Gerald McGowen (Occidental College), Joseph Copp and Richard Rosenblatt (Scripps Institution of Oceanography), Maxwell Eldridge (National Marine Fisheries Service, Tiburon), Wayne White (California State University, Fullerton), Robert Behrstock (Humboldt State University), and Sally Richardson (Oregon State University). We are grateful to Dennis Gruber (Scripps Institution of Oceanography) and John Butler (National Marine Fisheries Service, La Jolla) for providing reared specimens. Appreciation is also extended to Susan D'Vincent, Elaine Sandknop, and Betsy Stevens (National Marine Fisheries Service, La Jolla) for their assistance in gathering material from our collections. Henry Orr (National Marine Fisheries Service, La Jolla) deserves thanks for some of the illustrations. Our special thanks go to George Boehlert and Ellen Flentye (Scripps Institution of Oceanography) for providing the scanning electronmicrographs, and to John Fitch (California Department of Fish and Game), Edward Houde (University of Miami), David Kramer (National Marine Fisheries Service, La Jolla), and Sally Richardson for their critical review of the manuscript.

LITERATURE CITED

ABOUSSOUAN, A
1968 Oeufs et larves de Téleosteens de l'Ouest africain VII. Larves de *Syacium guineensis* (Blkr) (Bothidae). Bull Inst Fondam. Afr. Noire, Ser. A Sci Nat 30:1188-1197

AGASSIZ, A., AND C. O. WHITMAN
1885 Studies from the Newport Marine Laboratory XVI The development of osseous fishes I The pelagic stages of young fishes. Mem Mus. Comp. Zool. Harv. Coll. 14, 56 p.

AHLSTROM, E. H., AND H. G. MOSER.
1975 Distributional atlas of fish larvae in the California Current region Flatfishes, 1955 through 1960 Calif Coop Oceanic Fish Invest Atlas 23, text vii-xix, 207 distribution charts

AHLSTROM, E. H., J. L. BUTLER, AND B. Y. SUMIDA
1976 Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific Kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic Bull. Mar. Sci. 26:285-401

AMAOKA, K.
1970 Studies on the larvae and juveniles of the sinistral flounders - I *Taeniopsetta ocellata* (Gunther) Jpn J Ichthyol. 17:95-104
1971 Studies on the larvae and juveniles of the sinistral flounders—II *Chascanopsetta lugubris*. Jpn J Ichthyol 18:25-32
1972 Studies on the larvae and juveniles of the sinistral flounders—III. *Laeops kitaharae*. Jpn J Ichthyol 19:154-165
1973 Studies on the larvae and juveniles of the sinistral flounders—IV *Arnoglossus japonicus*. Jpn J. Ichthyol. 20:145-156

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT
1970 A list of common and scientific names of fishes from the United States and Canada 3d ed Am Fish Soc., Spec Publ 6, 150 p

BELL, R. R
1971 California marine fish landings for 1970 Calif Dep Fish Game, Fish Bull 154:33-34

BRUUN, A. F
1937 *Chascanopsetta* in the Atlantic; a bathypelagic occurrence of a flat-fish, with remarks on distribution and development of certain other forms Vidensk Medd Dan Naturhist Foren Khh 101:125-135

BUDD, P. L
1940 Development of the eggs and early larvae of six California fishes. Calif Div Fish Game, Fish Bull. 56, 50 p

CLOTHIER, C. R
1950 A key to some southern California fishes based on vertebral characters Calif Div Fish Game, Fish Bull 79, 83 p

DEVI, C. B. L
1969 Occurrence of larvae of *Pseudorhombus elevatus* Ogilby (Heterosomata—Pisces) along the south-west coast of India. Proc Indian Acad Sci 70(Sect B):178-186

TABLE 20.—Summary of egg and larval characters useful in identifying flatfishes with heavily pigmented larvae

Characters	*Pleuronichthys decurrens*	*P. coenosus*	*P. verticalis*	*P. ocellatus*	*P. ritteri*	*Hypsopsetta guttulata*	*Hippoglossina stomata*
Eggs							
Diameter	1.84–2.08	1.20–1.56	1.00–1.16	No data	0.94–1.08	0.78–0.89	1.22–1.38
Chorion	Polygonal sculpturing	Polygonal	Polygonal		Polygonal	Smooth	Smooth
Oil globule	0	0	0		1 (0.10 mm)	1 (0.13 mm)	1 (0.23 mm)
Larval morphology							
Size of available yolk-sac larvae (mm NL)	4.9 (5.54-Budd 1940)	3.9 (3.88-Budd 1940)	2.4 (3.16-Budd 1940)	No data	2.1	2.2–2.3 (1.7–2.1-Eldridge 1975)	3.7
Size range of preflexion larvae	4.9–9.8	3.7–8.5	2.4–5.8	No data	2.1–5.1	2.2–4.4	3.7–7.0
Size range at caudal fin formation (mm NL)	7.8–11.0	6.2–8.5	5.0–7.2	No data 6.6	4.3–5.6	4.0–5.2	6.2–8.8
Size range during transformation (mm SL)	10.5–29.4	8.2–17.0	7.3–12.2	No data	6.0–12.7	4.4–11.2	9.1–11.7
Pterotic spines	1 on each side	0	0	0	0	1 on each side	0
Elongated anterior dorsal rays	0	0	0	0	0	0	ca. 5
Meristics							
Precaudal vertebrae	14–15 (14)	12–13 (13)	13	12–13 (12)	12–13 (12)	11–12 (12)	11
Caudal vertebrae	24–26 (25)	24–26 (24–25)	22–25 (23)	22–24 (22–23)	22–24 (23)	22–24 (23)	26–28 (27)
Caudal rays	18–20 (19)	19–21 (19)	19	18–19 (19)	19–20 (19)	19–20 (19)	17^{2}–18^{1} (18^{1},$_{2}$)
Pigmentation							
Finfold of early larvae	Entirely pigmented except for extreme posterior portion of tail	Opposing clusters approx. midway on tail region	Triangular cluster behind anus ventrally; dorsal cluster slightly forward of ventral cluster, persist through notochordal flexion	No data	Few scattered melanophores on distal margins near anus, these do not persist after long preservation. Often with expansion of melanophores along both margins of body posterior to anus	Opposing pigment extending from body posterior of the anus	Small rounded patch dorsally and broad patch ventrally from middle part of tail
Top of head to shoulder region in early larvae	Present	Present	Absent	No data	Absent	Present	Present but sparse
Unpigmented posterior tail region	Extreme tip of notochord only in very early larvae	Tip of notochord followed by narrow posterior band of caudal peduncle in later stages	Last 3 to 5 myomeres through early notochordal flexion, followed by unpigmented caudal peduncle (shorter than in *P. ritteri*)	Caudal peduncle in late larvae	Last 7 or 8 myomeres through notochordal flexion, entire caudal peduncle unpigmented where dorsal & anal fins terminate in transforming sizes	Last 9 to 10 myomeres prior to notochord flexion shortening to 5 or 6 myomeres after flexion	Tip of tail
Pectoral fin base or fin membrane prior to caudal fin formation	Few melanophores scattered on fin base	None	None	No data	Small melanophores along proximal margin of fin membrane	Two to three melanophores on fin base, particularly at symphysis	Dense pigment on fin base, sparse on fin membrane

EHRENBAUM, E
1905 Nordisches Plankton. Zoologischer Teil. Erster Band. Eier und larven von Fischen. 1905 p 1-216 Labridae through Pleuronectidae, 1909 p. 217-414 Gadidae to Amphioxidae. Reprinted 1964 A. Asher and Co., Amsterdam.

ELDRIDGE, M B
1975. Early larvae of the diamond turbot, *Hypsopsetta guttulata*. Calif. Fish Game 61:26-34

FIERSTINE, H. L., K. F. KLINE, AND G. R. GARMAN
1973. Fishes collected in Morro Bay, California between January, 1968 and December, 1970. Calif. Fish Game 59 73-88

FITCH, J. E.
1963. A review of the fishes of the genus *Pleuronichthys*. Los Ang. Cty. Mus. Contrib. Sci. 76, 33 p.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, 148 p

GATES, D. E., AND H. W. FREY.
1974 Designated common names of certain marine organisms of California. Calif. Dep. Fish Game, Fish Bull 161.55-90

GINSBURG, I.
1952 Flounders of the genus *Paralichthys* and related genera in American waters. U.S. Fish Wildl. Serv., Fish. Bull. 52:267-351.

GUTHERZ, E. J
1970 Characteristics of some larval bothid flatfish, and development and distribution of larval spotfin flounder, *Cyclopsetta fimbriata* (Bothidae) U.S. Fish Wildl. Serv., Fish. Bull. 68:261-283

HOLLISTER, G.
1934 Clearing and dyeing fish for bone study. Zoologica (N.Y.) 12:89-101.

HOLT, E. W. L.
1893 Survey of fishing grounds, west coast of Ireland. 1890-91. on the eggs and larval and post-larval stages of teleosteans. Sci. Trans. R. Dublin Soc., Ser. 2, 5, 121 p.

HUBBS, C. L.
1928 A checklist of the marine fishes of Oregon and Washington. J. Pan-Pac. Res. Inst. 3(3):9-16.

HUBBS, C. L., AND Y. T. CHU.
1934 Asiatic fishes (*Diploprion* and *Laeops*) having a greatly elongated dorsal ray in very large postlarvae. Occas. Pap. Mus. Zool., Univ. Mich. 299, 7 p.

KRAMER, D., M. J. KALIN, E. G. STEVENS, J. R. THRAILKILL, AND J. R. ZWEIFEL.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC 370, 38 p.

LEONARD, S. B.
1971 Larvae of the foursport flounder, *Hippoglossina oblonga* (Pisces: Bothidae), from the Chesapeake Bight, western North Atlantic. Copeia 1971:676-681.

MCALLISTER, R.
1975 California marine fish landings for 1973. Calif. Dep. Fish Game, Fish Bull. 163,33.

MILLER, D. J., AND R. N. LEA.
1972 Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p., 1976 addendum, p. 237-249 in reprint edition. Div. Agric. Sci., Univ. Calif., Sale publ. 4065, 249 p.

MILLER, D., AND R. R. MARAK.
1962. Early larval stages of the foursport flounder, *Paralichthys oblongus*. Copeia 1962:454-455

MITO, S.
1961. Pelagic fish eggs from Japanese waters—I. Clupeina, Chanina, Stomiatina, Myctophida, Anguillida, Belonida and Syngnathida. [In Jpn., Engl. summ.] Sci. Bull. Fac. Agric., Kyushu Univ. 18:285-310.
1962. Pelagic fish eggs from Japanese waters—V. Callionymina and Ophidiina. [In Jpn., Engl. summ.] Sci. Bull. Fac. Agric., Kyushu Univ. 19:377-380
1963. Pelagic fish eggs from Japanese waters—IX. Echeneida and Pleuronectida. Jpn. J. Ichthyol. 11:81-102.

MOSER, H. G., AND E. H. AHLSTROM
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.

NIELSEN, J. G.
1963 Description of two large unmetamorphosed flatfish-larvae (*Heterosomata*). Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 125:401-406

NORMAN, J. R.
1934 A systematic monograph of the flatfishes (Heterosomata). Vol. I: Psettodidae, Bothidae, Pleuronectidae. Br. Mus. (Nat. Hist.), Lond., 459 p.

OKIYAMA, M.
1967 Studies on the early life history of a flounder, *Paralichthys olivaceus* (Temminck et Schlegel). 1. Descriptions of postlarvae. Bull. Jpn. Sea Reg. Fish. Res. Lab. 17:1-12.

OLIPHANT, M. S.
1973. California marine fish landings for 1971. Calif. Dep. Fish Game, Fish Bull. 159:32-33.

ORTON, G. L.
1953. Development and migration of pigment cells in some teleost fishes. J. Morphol. 93:69-99

ORTON, G. L., AND C. LIMBAUGH
1953. Occurrence of an oil globule in eggs of pleuronectid flatfishes. Copeia 1953:114-115.

PINKAS, L.
1974 California marine fish landings for 1972. Calif. Dep. Fish Game, Fish Bull. 161:32-33

SANZO, L.
1915. Contributo alla conoscenza dello sviluppo negli Scopelini Muller (*Saurus griseus* Lowe, *Chlorophthalmus agassizii* Bp. ed *Aulopus filamentosus* Cuv.). R. Com. Talassogr. Ital. Mem. 49, 21 p.
1931. Uova, larvae e stadi giovanili di Teleostei Sottordine Stomiatoidei. Fauna Flora Golfo Napoli Monogr. 38:42-92
1933 Uova, larvae e stadi giovanili di Teleostei Famiglia Macruridae. Fauna Flora Golfo Napoli Monogr. 38:255-265.

SMITH, W. G., AND M. P. FAHAY
1970. Description of eggs and larvae of the summer floun-

der, *Paralichthys dentatus*. U.S. Fish Wildl. Serv., Res. Rep. 75, 21 p.

STARKS, E. C., AND W. F. THOMPSON.
1910. A review of the flounders belonging to the genus *Pleuronichthys*. Proc. U.S. Natl. Mus. 38:277-287.

TAKITA, T., AND S. FUJITA.
1964. Egg development and prolarval stages of the turbot, *Pleuronichthys cornutus* (Temminck et Schlegel). [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 30:613-618.

TOWNSEND, L. D.
1936. Variations in the meristic characters of flounders from the northeastern Pacific. Rep. Int. Fish. Comm. 11, 24 p.

WHITE, W. F.
1977. Taxonomic composition, abundance, distribution, and seasonality of fish eggs and larvae in Newport Bay, California. M.A. Thesis, California State Univ., Fullerton, 107 p.

ASSOCIATIONS OF TUNA WITH FLOTSAM IN THE EASTERN TROPICAL PACIFIC

PAUL R. GREENBLATT[1]

ABSTRACT

The fishing record for flotsam-associated tuna in the eastern tropical Pacific was examined. The rivers of Central America are probably the major source of flotsam. Correlation analysis of the number of sets occurring in an area indicates that unassociated tuna and flotsam-associated tuna are related. The number of sets made on floating objects has increased dramatically since 1971. The percentage of flotsam-associated sets has increased, indicating that flotsam-associated sets are more important to the tuna fishery than in 1963. The catch per set of tuna associated with flotsam has also increased markedly since 1967. Analysis of length-frequency data indicate that, on a single set basis, tuna fork length is more variable in sets associated with flotsam than with unassociated schoolfish sets. Results of the length-frequency analysis support the idea that flotsam aggregates tuna.

The catch of the eastern tropical Pacific tuna fishery consists of mostly yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*. The catch is frequently categorized by the conditions under which the purse seine set is made. Scott (1969) made a major distinction between associated schools and unassociated schools. Associated schools are caught either in "porpoise sets" (sets associated with porpoise) or "floating object sets" (sets associated with logs or other flotsam). Unassociated schools are caught in "night sets" (sets made at night with the aid of bioluminescence) and "schoolfish sets" (schools seen and set upon during the day). Night sets compose a very small proportion of total sets and will not be discussed in this paper. Porpoise sets catch mostly yellowfin tuna. Floating object sets and schoolfish sets catch yellowfin and skipjack tuna, either as pure or mixed species.

Little is known about the attraction of tuna to flotsam. Gooding and Magnuson (1967) and Hunter and Mitchell (1968) observed fish gathering around flotsam. These authors attracted some tuna to their flotsam, but never large schools. Tuna were a minor portion of the observed fish assemblages. Hunter and Mitchell (1968) postulated a connection between schooling behavior and the attraction of fish to flotsam. They concluded that flotsam had the function of providing (p. 27) "... a visual stimulus in an optical void." Gooding and Magnuson (1967) concluded that fish gathered around floating objects at sea primarily because the objects provided shelter from predation. It may be possible that the same factors attracting smaller fish also attract large tuna schools.

This paper examines historical tuna fishery data on the catches of yellowfin and skipjack tuna associated with floating objects in the eastern tropical Pacific from 1963 to 1975. The objectives of the paper are to 1) establish the main sources of flotsam, 2) determine if there is a connection between various set types, 3) see if flotsam-associated sets have become more important to the tuna fishery, 4) determine if the catch rate on flotsam-associated sets has changed, and 5) assess whether flotsam does aggregate tuna schools.

METHODS

Since the catch of tuna associated with flotsam depends on the presence of tuna, flotsam, fishermen, strength of attraction, and suitable fishing conditions, I examined each factor in light of the published literature and available fishery data from the eastern tropical Pacific tuna fishery.

The Inter-American Tropical Tuna Commission (IATTC) collects information from tuna fishermen operating in the eastern tropical Pacific. Information collected in logbooks includes date and location of sets, catch of various species, type of set, and environmental conditions. Although these logbooks remain confidential, it is possible to obtain summaries of the information for certain time-area strata. During the beginning portion of

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; present address: Code A-008, Scripps Institution of Oceanography, University of California, La Jolla, CA 92093.

Manuscript accepted August 1978
FISHERY BULLETIN VOL. 77, NO. 1, 1979

the year, yellowfin tuna fishing is unregulated. After a quota is reached (Table 1), all yellowfin tuna fishing, except for special allowances must be outside the Commission's Yellowfin Regulatory Area (CYRA) (Figure 1). Due to special rules (see Inter-American Tropical Tuna Commission 1967-1975), any detailed reporting of regulated data would compromise the confidentiality of the data; hence, only unregulated catch and number of sets within the CYRA summarized by month and 5° square for 1963-75 were made available to me.

TABLE 1.—Yellowfin quota (thousands of short and metric tons), closure data, and annual total catch (thousands of short and metric tons) for the Commission's Yellowfin Regulatory Area, taken from Calkins (1976).[1] Metric tons are given in parentheses.

Year	Quota	Quota + increment[2]	Closure date	Annual total catch
1966	79.3 (71.9)		Sept. 15	91.1 (82.6)
1967	84.5 (76.6)		June 24	89.6 (81.3)
1968	106.0 (96.1)		June 18	114.6 (103.9)
1969	120.0 (108.8)		Apr. 16	126.5 (114.7)
1970	120.0 (108.8)		Mar. 23	142.6 (129.3)
1971	140.0 (127.0)		Apr. 9	113.9 (103.3)
1972	120.0 (108.8)	140.0 (127.0)	Mar. 5	152.5 (138.3)
1973	130.0 (117.9)	160.0 (145.1)	Mar. 8	177.8 (161.3)
1974	175.0 (158.7)	195.0 (176.9)	Mar. 18	191.3 (173.5)
1975	175.0 (158.7)	195.0 (176.9)	Mar. 13	177.2 (160.7)
1976	175.0 (158.7)	195.0 (176.9)	Mar. 27	205.5 (186.4)

[1]Calkins, T. P. 1976. The 1976 fishing year (through August 30). Background Paper No. 1, 33rd meeting of the Inter-American Tropical Tuna Commission.

[2]The Director of IATTC may increment the established quota, allowing more yellowfin tuna to be caught.

The total number of unregulated sets during the 13 yr was approximately 161,000 of which 8,190 were associated with flotsam. In addition, the IATTC provided the total number of flotsam-associated sets occurring each year (Figure 2). One sees that the major trends in the number of sets are contained in the block of unregulated data.

NOAA's Southwest Fisheries Center (SWFC) periodically sends technicians aboard tuna seiners. These technicians record details about set type, catch, environmental conditions, as well as the fork length (centimeters) of tuna sampled from individual sets. Fork lengths of yellowfin and skipjack tuna were only available for a limited number of sets made in 1973-75. The location of fork length measurements are given in Table 2. Single set catch data were collected by SWFC technicians in 1974-76 (unpubl. data[2]).

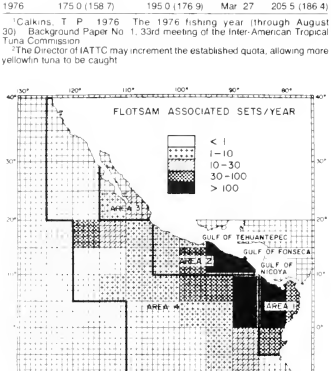


FIGURE 1.—Eastern tropical Pacific fishing area divided into three nearshore areas (Areas 1-3) and one offshore area (Area 4). The heavy line to the west delimits the boundary for the Commission Yellowfin Area (CYRA). The average number of flotsam-associated sets from 1972 to 1975 by 5° squares is shown. Data represent the unregulated fishing period (see text).

[2]Unpubl. data on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

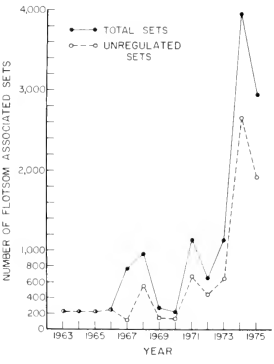


FIGURE 2.—Total number of flotsam-associated sets made in the eastern Pacific and number of unregulated flotsam-associated sets made in the CYRA, 1963-75.

TABLE 2.—Spatial distribution of fork length measurement (centimeters) of yellowfin and skipjack tuna in the Commission's Yellowfin Regulatory Area, 1973-75. CYRA subareas are shown in Figure 1. (Source of data, SWFC.)

CYRA subarea	Number of sets where fork length was measured
1	56
2	12
3	14
4	29

Monthly rainfall in Central America was calculated by averaging the stations reporting to the Environmental Data Service (U.S. Department of Commerce 1963-1975).

In order to achieve the objectives of this paper, the data obtained from IATTC and SWFC were examined and analyzed in several ways. The main sources of flotsam were inferred by examining the average distribution of flotsam-associated sets and consideration of the average surface circulation.

Two methods may be used to determine if different set types are related: correlation of set types occurring in an area and comparison of fork length distributions (length-frequency graphs) stratified by species and set type. Spearman's rank correlation coefficient (Siegel 1956) was calculated to expose possible correlations of numbers of sets. Fork length distributions were weighted by the catch in each set. A high positive correlation between set types occuring in an area would indicate a relationship between set types. Similar looking length-frequency distributions would serve as further evidence that set types are related.

An increase in the percentage of flotsam-associated sets would be evidence that flotsam-associated sets have become more important to the fishery. The CYRA was subdivided into three nearshore areas and one offshore area (Figure 1). Stratifying the number of flotsam-associated sets by area allows the determination of area effects. Hence, the importance of flotsam to the fishing industry may be determined by the percentage of flotsam-associated sets occurring each year and stratifying the number of flotsam-associated sets by area.

Average rainfall was tabulated to determine if any connection existed between river runoff and the number of flotsam-associated sets.

Catch rate is an indicator of the importance of flotsam-associated sets to the tuna fishery. Calculation of the average yearly catch per set (including zero catch sets) for different set types should demonstrate any trends as well as the relative value of making one set type over another.

Calkins (1965) examined tuna length distributions from single sets in the eastern tropical Pacific, finding that single unassociated schoolfish sets caught tuna of a relatively uniform size (i.e., small variance in length). If the fish caught in flotsam-associated sets represent aggregations of solitary tuna, portions of schools, or several schools, then one would expect the variance of tuna length to be greater than for unassociated schools. In order to examine if floating objects act as aggregators, length-frequency data were stratified by species and set type. Mean length and standard deviation were calculated on a single set basis for each category and compared using Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956).

If flotsam does aggregate tuna, one would expect more of the larger flotsam-associated sets than unassociated sets. Differences in catch distribution were observed by plotting histograms of tons of tuna caught per set stratified by year and set type and by calculating catch per successful set for each year and set type. The single set catch data, collected by SWFC technicians, existed for the 1974-76 period.

RESULTS

The availability of logs or other flotsam in an area are determined by the source of the flotsam and the currents in the area. Large rivers flow into the Pacific from southern Mexico (lat. 20°N) and continue down the coast of South America (to lat. 20°S). These rivers are capable of releasing many logs into the Pacific during the rainy season. SWFC and IATTC observers reported large densities of logs near the Gulf of Tehuantepec (lat. 16°N, long. 100°W), the Gulf of Nicoya (lat. 10°N, long. 85°W), and the Gulf of Fonseca (lat. 13°N, long. 87°W).

The average yearly number of flotsam-associated sets in 1972-75 were plotted by 5° squares (Figure 1). In general, most flotsam-associated sets occurred in Areas 1 and 2. Most of the offshore flotsam-associated sets (i.e., Area 4) occurred quite close to Areas 1 and 2. Area 3 did not have large numbers of flotsam-associated sets. If the main source of logs and other flotsam is the rivers of Central America, then it is important to examine the major current patterns in the eastern tropical Pacific to determine if the currents can

explain the observed distribution of flotsam-associated sets.

The average currents in the eastern tropical Pacific, as derived from ship's drift data, were determined by Wyrtki (1965). From January until May, the California Current is strong. Circulation near Area 3 is to the south. Circulation near Areas 1 and 2 is gyral. From May to July, both the Equatorial Countercurrent and the California Current are relatively stong. During this period, most countercurrent water turns north and flows along the coast of Central America. Area 3 has a northern and southern flow, the northern flow along the coast. Area 1 maintains its gyral flow. From August through December, the Equatorial Countercurrent is well developed. Circulation in Area 3 is to the south. Area 2 maintains its northwestern flow along the coast and Area 1 flow maintains a gyral pattern. If logs disperse mainly from the Gulf of Nicoya, the Gulf of Tehuantepec, and the Gulf of Fonseca, then the gyral circulation in Area 1 would tend to maintain logs and other flotsam in the area for a considerable time. The northwest coastal current in Area 2 could transport flotsam through Area 2 and during part of the year into Area 3. Since the North Equatorial and South Equatorial Currents are rather strong, one would not expect floating objects to persist in Area 4 except near the boundaries with Areas 1 and 2. Hence the location of large rivers and the system of currents is reasonably consistent with the geographical distribution of flotsam-associated sets.

In order to compare different set types, Spearman's rank correlation coefficient was calculated. For each 5° square in the CYRA, the total numbers of flotsam-associated sets, porpoise-associated sets, and unassociated schoolfish sets were tabulated for each year. These totals were ranked and the ranks were correlated. Only 5° squares where at least 10 sets occurred were used in calculating correlations. When a minimum of 40 sets was used as the criterion for including a 5° square, the correlations were qualitatively the same as with the 10 sets criterion. The results (Table 3) show that a significant positive correlation exists between number of sets on unassociated schoolfish and flotsam-associated tuna. Porpoise sets were uncorrelated with other set types.

The above results indicate that fish caught associated with flotsam tended to be caught in the same area at the same time as unassociated school fish. Examination of available length-frequency data on a species basis, weighted by the catch in each set (Figure 3), indicated that unassociated schoolfish and flotsam-associated yellowfin and skipjack tuna had very similar length-frequency distributions. The length-frequency information and the correlation analysis support the idea that unassociated tuna and flotsam-associated tuna are related. Flotsam, acting as an attractant, may aggregate tuna that would otherwise be caught in unassociated sets.

TABLE 3.—Spearmans rank correlation between three types of sets by year. Number of sets/5° square. (Source of data: IATTC.)

Year	N	Unassociated schoolfish and porpoise-associated	Unassociated schoolfish and flotsam-associated	Porpoise and flotsam-associated
1963	29	-0.0008	0.5421**	0.2538
1964	27	0.0375	0.1581	0.8138**
1965	25	-0.1597	0.3498*	0.1318
1966	28	-0.1110	0.3513*	0.2914
1967	24	-0.2379	0.4621*	-0.2255
1968	24	-0.1951	0.1886	0.3463*
1969	25	-0.1523	0.5957**	0.2294
1970	27	-0.0088	0.3529*	-0.0173
1971	26	0.0803	0.5819**	0.2398
1972	32	-0.0200	0.5277**	-0.0558
1973	34	0.0523	0.3086*	0.1796
1974	27	0.0168	0.4847**	0.0001
1975	33	0.2444	0.5139**	0.0526

*Significant at $P \leq 0.05$
**Significant at $P \leq 0.01$

The number of flotsam-associated sets has increased dramatically since 1971 (Figure 2). The trend in percentage of flotsam-associated sets (Figure 4) indicates that flotsam-associated sets have increased in importance to the fishery. Stratifying the number of unregulated flotsam-associated sets by area (Figure 5) shows that the trend of more flotsam-associated sets is not an area effect. All areas, except Area 3, have shown a marked increase in number of flotsam-associated sets. Area 3 does not show an increase because logs are only deposited in this region during a limited portion of the year. In January-May, the near surface current in Area 3 is to the south (Wyrtki 1965), cutting off the source of logs that wash down the rivers of Central America. Also, good fishing often occurs in Area 3 during the later months of the year, a period not included in my unregulated data. It appears that the increase in flotsam-associated sets in recent years was not caused by discovery of new areas with abundant flotsam but rather by an increase in fishing effort on flotsam in all areas but Area 3.

Average rainfall in Central America was tabulated (Table 4) to see if there was a correlation between river runoff and the number of flotsam-associated sets. Comparison of number of flotsam-associated sets and rainfall revealed only

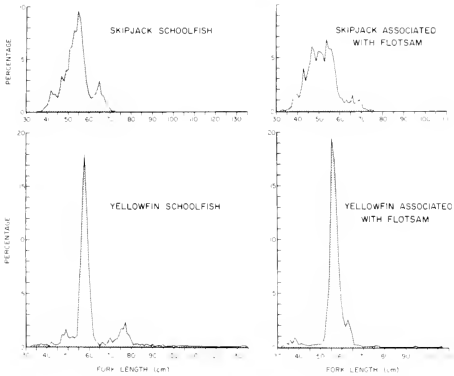


FIGURE 3.—Length-frequency distributions of yellowfin and skipjack tuna caught in unassociated schoolfish and flotsam-associated sets. Data collected 1973-75 in the CYRA (see Table 2).

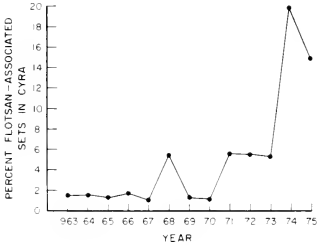


FIGURE 4.—Percentage of total unregulated sets that were associated with flotsam in the CYRA, 1963-75.

TABLE 4.—Average yearly rainfall (centimeters) in Central America in 1963-75. (Source: U.S. Department of Commerce.)

Year	Average yearly rainfall	Year	Average yearly rainfall
1963	139.0	1970	163.8
1964	136.4	1971	145.5
1965	136.9	1972	145.6
1966	158.5	1973	161.4
1967	151.7	1974	172.3
1968	177.3	1975	151.0
1969	177.2		

small similarities, indicating that the supply of suitable flotsam was not greatly influenced by rainfall.

Comparing the average catch per set of different set types indicates the relative importance of each set type to the fishery as well as showing trends in the catch rate (Figure 6). All set types had similar catch rates in 1963-66. Porpoise sets and flotsam-associated sets gave much higher catch per set than unassociated sets in 1971-75. One sees that flotsam-associated sets have been the most valuable set type for the tuna fisherman since 1971.

Fork length data was stratified by set type and species. The mean length, standard deviation, and sample size were calculated on a single set basis (Table 5). The average standard deviation of fork length of yellowfin and skipjack tuna associated with flotsam was larger than the standard deviation found in unassociated sets, though the mean fork length of flotsam-associated sets was smaller. The probability of getting the results shown (Table 5) by chance was calculated using Kruskal-Wallis one-way analysis of variance (Siegel 1956:184) (Table 5). The greater variability of fork length of flotsam-associated tuna supports the hypothesis that flotsam aggregates tuna.

The yellowfin and skipjack tuna catch distribution on flotsam-associated sets was compared with unassociated schoolfish sets. The average catch per successful set was calculated and the data were plotted as histograms of tonnages using an arbitrary interval of 5 tons (Figure 7). The main

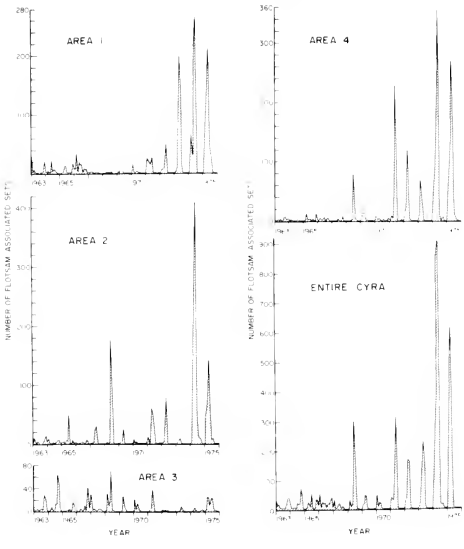


FIGURE 5.—Number of unregulated flotsam-associated sets per month by area, 1963-75

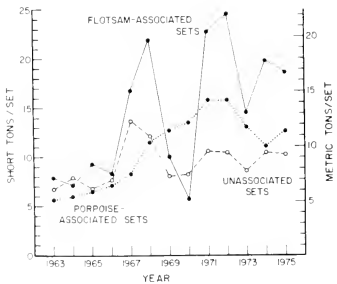


FIGURE 6.—Average yearly catch per set of yellowfin and skipjack tuna in flotsam-associated, unassociated schoolfish, and porpoise-associated sets in the CYRA

differences between the histograms for unassociated schoolfish sets and flotsam-associated sets are a lower proportion of unsuccessful sets and a higher percentage of flotsam-associated sets with catches between 25 and about 60 tons. The higher proportion of large flotsam-associated sets is consistent with the hypothesis that flotsam aggregates tuna.

DISCUSSION

Changes in catch rate (catch per set, Figure 6) of flotsam-associated yellowfin or skipjack tuna may be related to overall abundance of flotsam-associated schools, technological advances such as bigger nets, increased skill and knowledge of the fishermen, changes of the attractability of flotsam, and changes in the residence time of tuna with flotsam. In order to explain the observed increase

TABLE 5.—Variability of fork length (centimeters) in single set data by tuna species and set type, as indicated by average standard devation ($\bar{S}$) and mean ($\bar{x}$) and results of Kruskal-Wallis one-way analysis of variance of standard deviations (Source of data: SWFC.)

Item	Yellowfin tuna	Skipjack tuna
Flotsam-associated sets		
N	35	45
$\bar{S}$	4 96	4 62
$\bar{x}$	55 55	52 49
Unassociated schoolfish		
N	49	43
$\bar{S}$	3 76	3 40
$\bar{x}$	60 94	54 08
Kruskal-Wallis		
H	3 69	33 31
df	1	1
Probability level	$0\ 05 \leq P \leq 0\ 1$	$P < 0\ 001$

in catch rate, it was necessary to examine data that could indicate which factors have most influenced catch rate. Changes in attractability, changes in residence time, technological advances, and increased knowledge of the fisherman could not be rejected or confirmed with existing data. It was possible, with some assumptions, to determine if overall abundance changes or increased skill of the fisherman could explain the increased catch rate.

If the overall abundance of tuna had increased from 1963 to 1975, then one would expect the catch rate to have increased correspondingly. If one accepts the supposition that flotsam-associated fish were from the same population as unassociated schoolfish, then one would expect the catch rate on unassociated schoolfish to have likewise increased. The catch per set on unassociated schoolfish (Figure 6) showed no increase. However, the year-to-year variations in catch per set of flotsam-associated tuna and unassociated tuna (Figure 6) were remarkably similar. The above evidence indicates that changes in overall abundance does not explain the long-term increase of catch per set in flotsam-associated sets. The similarity of the year-to-year variations supports the hypothesized relationship between unassociated schoolfish and flotsam-associated tuna. The year-to-year variation may represent changes of abundance.

The second explanation for the changes in the catch rate of flotsam-associated tuna schools, changes in the skill of the fisherman, can be evaluated by the percentage of successful sets. An increase in the percentage of successful sets on schools associated with flotsam would explain the apparent increase in catch per set. Such an explanation is untenable because the percentage of successful sets would have had to more than double. Greenblatt (1977) calculated the percentage of successful sets associated with flotsam for 1974-76, finding the average percentage of successful sets to be 75%. To account for the change in catch/set, the percentage of successful sets in 1963 would have had to have been about 35%, an unreasonably low figure. Pella and Psaropulos (1975, fig. 2) showed that the percentage of successful sets of unassociated schoolfish sets and flotsam-associated sets (considered as one category) did not increase enough in 1961-71 to account for the observed changes in catch per set. Bayliff and Orange (1967) reported percentages of successful sets stratified by set type for a limited area of the

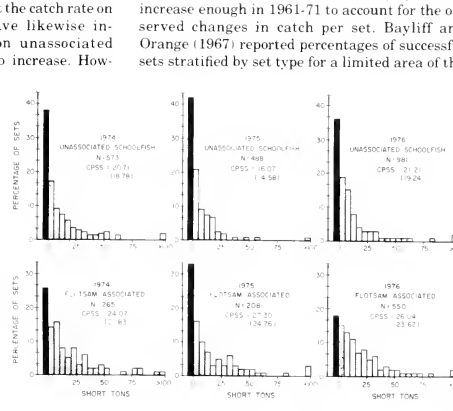


FIGURE 7.—Distribution of catch by 5 short ton intervals for flotsam-associated sets and unassociated schoolfish from 1974 through 1976. Solid boxes indicate percentage of zero catch sets. The average catch per successful set (CPSS) in short and metric tons is given for each category. Metric tons are in parentheses.

CYRA. Although they had small numbers of sets, the percentage of successful flotsam-associated sets from 1962 to 1966 was 67.6%. Changes in percentage of successful sets can not adequately explain the increased catch per set.

No satisfactory explanation for the increase in catch per flotsam-associated set has been found. Overall increases in abundance or increased skill of the fishermen can not explain the increase. The above factors may account for some of the increase. Technological advances may account for the increased catch rate. It is also reasonable to believe that fishermen have learned to catch flotsam-associated tuna more efficiently and the residence time of tuna with flotsam has increased since 1967.

Changes in catch per set on flotsam-associated sets may have been due to technological advances such as bigger nets. If technological advances can explain the increased catch per set on flotsam, then either the catch per set on unassociated schoolfish should have also increased or sets associated with flotsam prior to the technological advances must have caught a low proportion of potential catch. Nets have increased in size, perhaps increasing the probability of catching yellowfin and skipjack tuna which may aggregate around flotsam. It is possible that bigger nets could account for increased catch/set of flotsam-associated sets without likewise affecting catch/set on unassociated schoolfish sets.

Fishermen often will drift with logs for considerable time, waiting for tuna aggregations to reach an optimal size before setting the net. The spread of such behavior throughout the fleet could cause the overall catch per set of flotsam-associated tuna to increase. Adequate data for testing this "increased knowledge" hypothesis was unavailable.

The marked changes occurring in flotsam-associated tuna catch in 1963-75 coincided with a large increase of effort and technology in the porpoise-associated fishery (Green et al. 1971). It is hypothesized that the increased effort and technology in the porpoise-associated fishery may have been related to changes in the catch rate of tuna schools associated with flotsam.

When purse seiners set on porpoise, there is often an incidental kill of the marine mammals. Due to recent technological advances, the porpoise kill has been reduced, but in earlier years of the porpoise-associated fishery (the mid-1960's) porpoise mortality was higher (Southwest Fisheries Center[3]). This incidental kill may have reduced the porpoise population. The porpoise-associated fishery first developed near shore and thus the nearshore porpoise stocks have been affected for a longer time than offshore stocks. One may reasonably speculate that, on a species basis, nearshore porpoise stocks have been affected more by incidental kills than offshore porpoise stocks.

The bond between tuna and porpoise is not understood. It is possible that the mechanisms involved in the association of tuna with porpoise is similar to those responsible for their association with flotsam. Tuna associated with flotsam are, on the average, smaller than tuna associated with porpoise (Calkins 1965, tables 2 and 9; Sharp[4]). Knudsen (1977) gave some evidence that tuna caught in areas where porpoise fishing predominates were generally older and larger than in traditional schoolfish areas. Size overlap, however, did occur (Calkins 1965). Assuming that the number of porpoise schools have declined, the probability of tuna encountering porpoise schools has decreased. The probability of tuna aggregated near flotsam encountering porpoise schools has also decreased. Thus, as a result of decreased encounter rates with porpoise (slower transition from flotsam to porpoise), the size of the aggregations of tuna near flotsam have increased.

In conclusion, the most likely sources of flotsam are the large rivers of Central America. Indirect evidence indicates that tuna caught in unassociated schoolfish sets are from the same population as tuna caught associated with flotsam. It appears that the increase of flotsam-associated sets from 1963 to 1975 was due to an increased interest by fishermen and hence an increased fishing effort on floating objects. The observed increase in catch per set may have been a biological change rather than a change in fishing technology or skill.

ACKNOWLEDGMENTS

I would like to express my thanks to John Hunter who provided guidance in several phases of this study. His comments were extremely help-

[3]Southwest Fisheries Center 1976. Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Tropical Pacific Yellowfin Tuna Fishery. SWFC Adm Rep LJ-76-29, 54 p. Southwest Fisheries Center, La Jolla, CA 92038.

[4]G. Sharp, Inter-American Tropical Tuna Commission, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1977.

ful. Richard McNeely first suggested the possible interaction of porpoise and flotsam-associated tuna. The Inter-American Tropical Tuna Commission provided much of the data. William Flerx and Richard Charter provided insight into the operation of the fishery. Gary Sharp provided useful information about yellowfin tuna. Rainfall data were obtained from Eric Forsbergh. William Lenarz, Douglas Chapman, and Robin Allen reviewed the paper and offered constructive comments.

LITERATURE CITED

BAYLIFF, W. H., AND C. J. ORANGE
1967. Observations on the purse seine fishery for tropical tunas in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Intern. Rep. 4, 79 p.

CALKINS, T. P.
1965. Variation in size of yellowfin tuna (*Thunnus albacares*) within individual purse-seine sets. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 10:461-524.

GOODING, R. M., AND J. J. MAGNUSON.
1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486-497.

GREEN, R. E., W. F. PERRIN, AND B. P. PETRICH.
1971. The American tuna purse seine fishery. *In* H. Kristjonsson (editor), Modern fishing gear of the world, Vol. 3, p. 182-194. Fishing News (Books) Ltd., Lond.

GREENBLATT, P. R.
1977. Factors affecting tuna purse seine fishing effort. ICCAT Rep., Vol. VI (SCRS-1976), No. 1 - Tropical spp., p. 18-31.

HUNTER, J. R., AND C. T. MITCHELL.
1968. Association of fishes with flotsam in the offshore waters of Central America. U.S. Fish Wildl. Serv., Fish. Bull. 66:13-29.

INTER-AMERICAN TROPICAL TUNA COMMISSION.
1967-1976. Annual Report, 1966-1975. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

KNUDSEN, P. F.
1977. Spawning of yellowfin tuna and the discrimination of subpopulations. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 17:117-169.

PELLA, J. J., AND C. T. PSAROPULOS.
1975. Measures of tuna abundance from purse-seine operations in the eastern Pacific Ocean, adjusted for fleet-wide evolution of increased fishing power, 1960-1971. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 16:281-400.

SCOTT, J. M.
1969. Tuna schooling terminology. Calif. Fish Game 55:136-140.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., N.Y., 312 p.

U.S. DEPARTMENT OF COMMERCE.
1963-1975. Monthly climatic data for the world. NOAA, Environ. Data Serv., vol. 16-28, var. pagination.

WYRTKI, K.
1965. Surface currents of the Eastern Tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 9:269-304.

DESCRIPTION OF LARVAE OF THE NORTHERN SHRIMP, *PANDALUS BOREALIS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

EVAN HAYNES[1]

ABSTRACT

Northern shrimp, *Pandalus borealis*, were reared in situ in Kachemak Bay, Alaska, from Stage I (first zoeal) through Stage VIII (second juvenile). Each of the six larval stages and first juvenile stage is described and illustrated, and a brief description is given for the second juvenile stage. Apparently larvae of *P. borealis* in Alaska waters have at least one less stage than larvae of *P. borealis* in either British Columbia, Greenland, or Japan waters. Of the known larvae of the North Pacific Ocean, larvae of *P. borealis* are most similar morphologically to larvae of *P. goniurus* but are separable from them by being slightly larger in size and, in zoeal Stages I-III, by bearing more setae on certain appendages, particularly the antennal scale and certain mouth parts. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*. The criterion of the lack of an outer seta on the maxillule for distinguishing zoeae of *Pandalus* from certain other Caridea is shown to be invalid.

In 1972 the National Marine Fisheries Service began studies on the early life history of pandalid shrimp in Alaska waters with the initial objective of describing in detail laboratory-reared larvae of each pandalid species previously unverified. Two previous reports have described larvae of *Pandalus hypsinotus* Brandt reared in the laboratory (Haynes 1976) and *P. goniurus* Stimpson reared in situ in Kachemak Bay, Alaska (Haynes 1978). This report describes and illustrates each of the six larval stages and the first juvenile stage of northern shrimp, *P. borealis* Krøyer, and compares the stages obtained from rearing in situ with descriptions of pandalid shrimp larvae given by other authors. A brief description of the second juvenile stage is included.

MATERIALS AND METHODS

Rearing techniques were identical in all respects to those described in an earlier report on *P. goniurus* (Haynes 1978). Briefly, the technique consists of obtaining Stage I larvae of known parentage in the laboratory, then rearing the larvae in flasks submerged at sea. Larvae from plankton were also reared in flasks at sea in an identical manner beginning with Stage I. Larvae reared in flasks were compared with larvae from plankton for verification of sequence of stage and larval morphology.

Because the paired appendages of the larvae are symmetrical, only one member (the left) is figured. An exception is the mandibles which are drawn in pairs. Orientation of surface of appendages in the figures is given in the figure legends. The figures of the appendages are in part schematic and represent typical setal counts. Variability in setation or segmentation of paired appendages, such as the difference in number of carpal joints between the left and right second pereopods in the megalopa, is mentioned in the text. Carapace length refers to the straight-line distance from posterior margin of orbit to middorsal posterior margin of carapace. Total body length refers to the distance from tip of rostrum to posterior margin of telson, not including telson spines. Terminology, methods of measuring, techniques of illustration, and nomenclature of gills and appendages follow Haynes (1976). Comparison of larvae from plankton with cast skins from flasks was facilitated by first clearing the larvae in 10% KOH. For clarity, setules on setae are usually omitted but spinulose setae are shown.

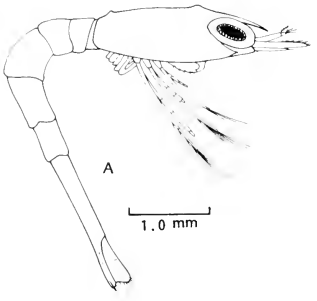
STAGE I ZOEA

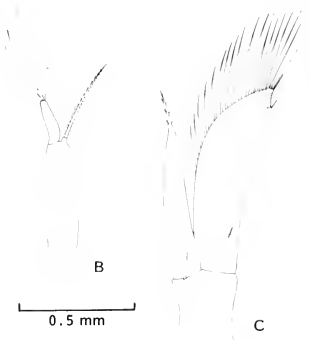
Mean total length of Stage I (Figure 1A) 6.7 mm (range 6.5-7.3 mm; 25 specimens). Live specimens characterized by orange color; conspicuous chromatophores throughout cephalothorax re-

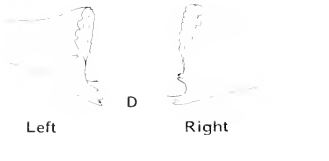
[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821

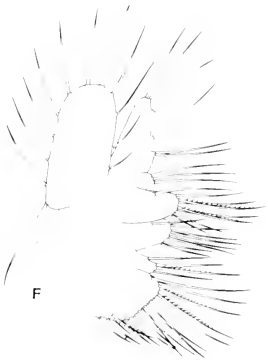
Manuscript accepted July 1978.
FISHERY BULLETIN VOL. 77, NO. 1, 1979

gion, especially in mouth parts; large chromatophore near tip of antennal scale, at base of telson, and at front of eye; smaller but distinct chromatophores on maxillipeds; ventral surface of each abdominal somite tinged orange; faint greenish hue at base of pereopods. Rostrum slender, spiniform, without teeth, about one-third length of carapace, projecting horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller, rounded prominence near posterior edge. These two prominences occur in all zoeal stages. Pterygostomian spines present but usually hidden by sessile eyes. Three or four mi-









nute spinules along ventral margin of carapace immediately posterior to pterygostomian spine (spinules not shown in Figure 1A). These spinules usually occur in all zoeal stages but may vary in number from two to five not only between stages but among individuals within a given stage.

ANTENNULE (Figure 1B).—First antenna, or antennule, consists of simple unsegmented tubular basal portion with heavily plumose seta terminally and distal conical projection with four aesthetascs: one long, one short, and two of intermediate length.

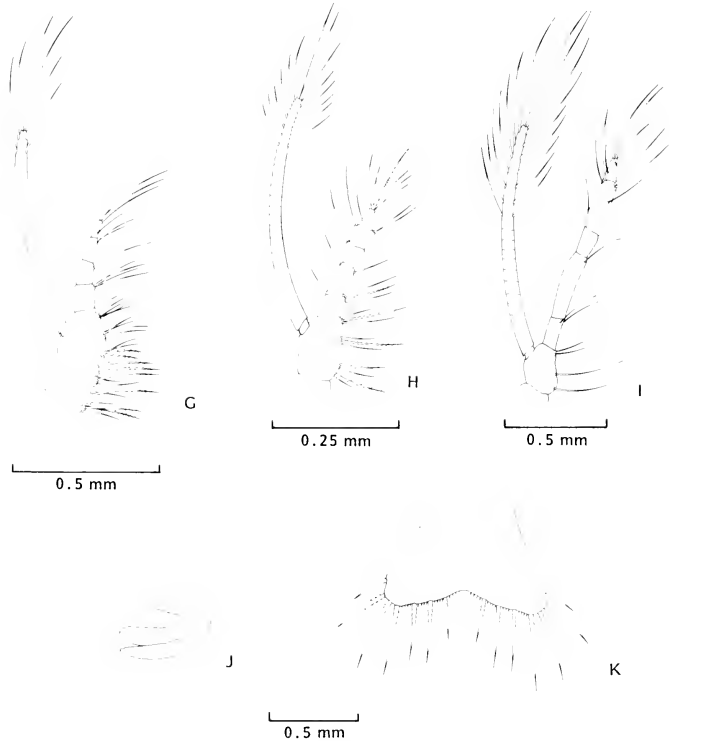


FIGURE 1.—Stage I zoea of *Pandalus borealis*. A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, second pereopod, lateral; K, telson, dorsal.

ANTENNA (Figure 1C).—Second antenna, or antenna, consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, and tipped by spinulose spine. Antennal scale distally divided into six joints (the two proximal joints incomplete) and fringed with 19 heavily plumose setae along terminal and inner margins; small seta occurs on outer margin at base of joints and another proximally near outer margin. Protopodite bears spinous seta at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 1D).—Without palps in this and all succeeding zoeal stages. Incisor process of left mandible bears four teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) whereas right mandible bears two immobile premolar denticles. Truncated molar process of left mandible bears subterminal tooth that occurs throughout all zoeal stages.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and endopodite. Coxopodite (proximal lobe) bears stout seta near base, and eight spinulose spines terminally. Basipodite (median lobe) bears nine spinulose spines on terminal margin and large setose seta proximally. Endopodite originates from lateral margin of basipodite; bears three terminal and two subterminal setae, three of them sparsely plumose and remaining two spinulose.

MAXILLA (Figure 1F).—Second maxilla, or maxilla, bears platelike exopodite (scaphognathite) with 11 long, evenly spaced plumose setae along outer margin and one slightly longer and thicker seta at the slightly expanded proximal end. Endopodite gives indication of four partly fused segments and bears nine large plumose setae. Coxopodite and basipodite bilobed. Coxopodite bears 21 setae, 4 on distal lobe and 17 on proximal lobe. Basipodite bears eight setae on each lobe. Five setae, three on coxopodite (one on distal lobe and two on proximal lobe) and two on distal lobe of basipodite, bear row of little spines along entire length. An additional seta on proximal lobe of coxopodite is especially spinulose.

FIRST MAXILLIPED (Figure 1G).—Most heavily setose of natatory appendages. Protopodite fully segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment, 9 of them spinulose. Endopodite distinctly four-segmented; setation formula 4, 2, 1, 4. Exopodite a longer slender ramus segmented at base; bears two terminal and three or four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite bisegmented; distal segment bears 10 sparsely plumose setae, no setae evident on proximal segment. Endopodite distinctly five-segmented, fourth segment expanded laterally; setation formula 7, 3, 1, 2, 4. A seta on segments 1 and 5 of endopodite and three setae on protopodite especially spinulose. Exopodite with 2 terminal and 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five-segmented; nearly as long as exopodite; setation formula 4, 5, 1, 1, 2. Exopodite with 2 terminal and 14 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3.

PLEOPODS.—Absent.

TELSON (Figure 1K).—Not segmented from sixth abdominal somite; slightly emarginate posteriorly; bears 7 + 7 densely plumose setae. Fourth pair of setae longest, about one-half width of telson. Minute spinules at base of each seta. Larger spinules along terminal margin between bases of four inner pairs and on setae themselves but rarely on seventh pair. Uropods visible and enclosed. No anal spine.

STAGE II ZOEA

Mean total length of Stage II (Figure 2A) 7.5 mm (range 6.7-8.2 mm; 25 specimens). Chromatophore color and pattern essentially identical to Stage I, except chromatophores larger and color more pronounced, especially in mouth parts. Rostrum still without teeth and not curved downward as sometimes in Stage I. Carapace with prominent supraorbital spine and clearly visible antennal and pterygostomian spines. These three

spines persist through all remaining zoeal stages. Epipodite of first maxilliped slightly larger than in Stage I but still not bilobed; pleurobranchiae present as primordial buds.

ANTENNULE (Figure 2B).—Three-segmented; bears large outer and smaller inner flagellum on terminal margin. Flagella not segmented. Inner flagellum conical, bears one long spine terminally. Outer flagellum bears two groups of aesthetascs: one group terminally consisting of eight aesthetascs, two of them larger than remaining six, and a pair of aesthetascs on inner margin. A small budlike projection (not shown in Figure 2B)

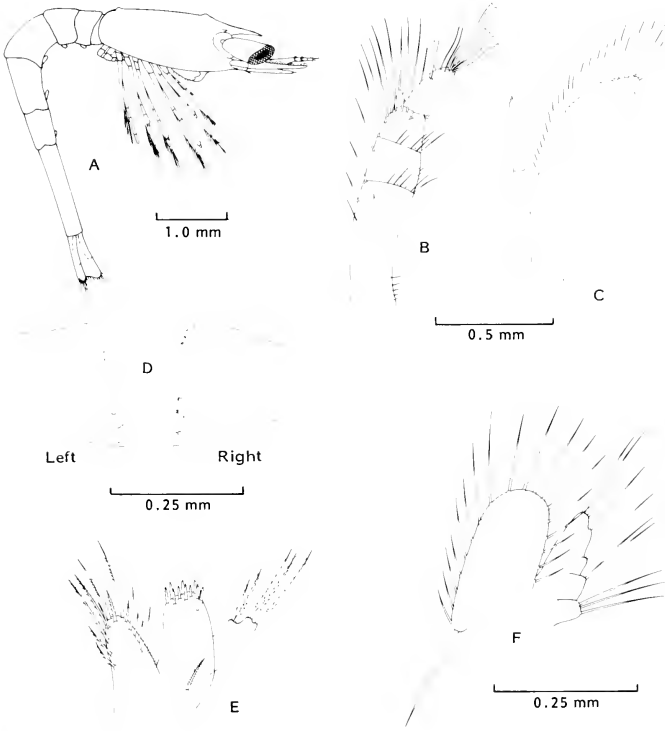


FIGURE 2.—Stage II zoea of *Pandalus borealis*: A, whole animal (right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla (exopodite and endopodite), dorsal.

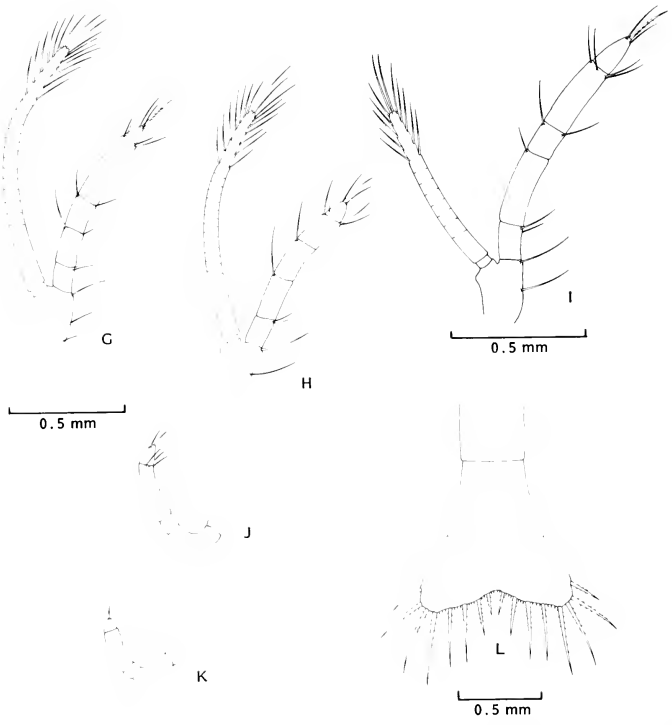


FIGURE 2.—Stage II zoea of *Pandalus borealis*: G, first pereopod, lateral; H, second pereopod, lateral; I, third pereopod, lateral; J, fourth pereopod, lateral; K, fifth pereopod, lateral; L, telson, dorsal.

originates at base of flagella and bears five simple setae. Proximal segment of antennule usually bears five setae laterally near slightly expanded base, three plumose setae laterally and distally, about nine dorsally curving but smaller plumose setae around distal joint, and large spine projecting slightly downward from ventral surface. Second segment bears two plumose setae laterally and about six dorsally curving plumose setae around distal joint. Third segment bears seven plumose setae laterally, about four of them originating ventrally, and three simple setae laterally at base of outer flagellum.

ANTENNA (Figure 2C).—Flagellum two-segmented, still shorter than scale, styliform, and tipped by two small simple setae and short spine. Antennal scale fringed with 25 or 26 long, thin, plumose setae along terminal and inner margins; still has six joints distally but only the three most distal joints complete. Protopodite bears minute spine at base of scale in addition to conspicuous spine at base of flagellum.

MANDIBLES (Figure 2D).—More massive than in Stage I. Incisor processes of both mandibles bear additional tooth. Both mandibles bear additional denticles and molar processes more developed. Lacinia mobilis of left mandible consists of single spinous denticle. Curved lip of truncated end of molar process of right mandible more developed than in Stage I.

MAXILLULE (Figure 2E).—Coxopodite bears 12-15 spines and row of fine hairs proximally; spinules on two of the terminal spines of coxopodite resemble a row of teeth. Basipodite and endopodite essentially unchanged from Stage I, except basipodite bears two additional spinulose spines.

MAXILLA (Figure 2F, exopodite and endopodite).—Exopodite similar in shape to Stage I except more distinctly expanded proximally; bears 17-19 marginal plumose setae in addition to plumose seta at proximal end. Endopodite unchanged from Stage I. Coxopodite bears 3 setae on distal lobe and 17-19 on proximal lobe. Each lobe of basipodite bears additional seta.

MAXILLIPEDS.—Essentially identical to Stage I but bear additional setae as follows. On first maxilliped, protopodite bears 8-10 setae on proximal segment and 19-21 on distal segment; endopodite bears 4, rarely 5, setae on proximal segment; exopodite bears 7 or 8 natatory setae rather than 5 or 6 as in Stage I; no change in epipodite. On second maxilliped, protopodite bears seta on proximal segment and 8-10 setae on distal segment; exopodite bears 14 lateral natatory setae in addition to the 2 terminal setae. On third maxilliped, endopodite bears additional seta terminally on dactylopodite, 2 additional setae on propodite, and additional seta on carpopodite, setation formula 5, 7, 3, 1, 2; exopodite bears 16 lateral natatory setae in addition to 2 terminal setae. No gill buds on second or third maxillipeds.

FIRST PEREOPOD (Figure 2G).—Protopodite bears three setae. Endopodite functionally developed; five-segmented, terminating in simple conical dactylopodite; setation formula 5, 3, 2, 2, 2. Exopodite, longest among pereopods, bears 2 terminal and 14 lateral natatory setae.

SECOND PEREOPOD (Figure 2H).—Protopodite bears two setae. Endopodite similar to first pereopod except shorter; setation formula 4, 3, 1, 1, 2. Exopodite bears 2 terminal and 13 or 14 lateral natatory setae.

THIRD PEREOPOD (Figure 2I).—Protopodite bears two setae. Endopodite one-fourth to one-third longer than exopodite; dactylopodite slightly longer than in first two pereopods; setation formula 3, 4, 2, 1, 2. Exopodite noticeably shorter than exopodites of first and second pereopods and bears 2 terminal and 9 or 10 lateral natatory setae.

FOURTH PEREOPOD (Figure 2J).—Endopodite five-segmented but still poorly developed and directed under body somewhat anteriorly as in Stage I (Figure 2A); dactylopodite and propodite bear two setae and three setae, respectively. No exopodite.

FIFTH PEREOPOD (Figure 2K).—Similar to fourth pereopod but shorter and dactylopodite tipped with single seta. No exopodite.

PLEOPODS (Figure 2A).—Present as distinct buds.

TELSON (Figure 2L).—Similar in shape to Stage I but distinctly jointed from sixth abdominal somite; bears 8 + 8 densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

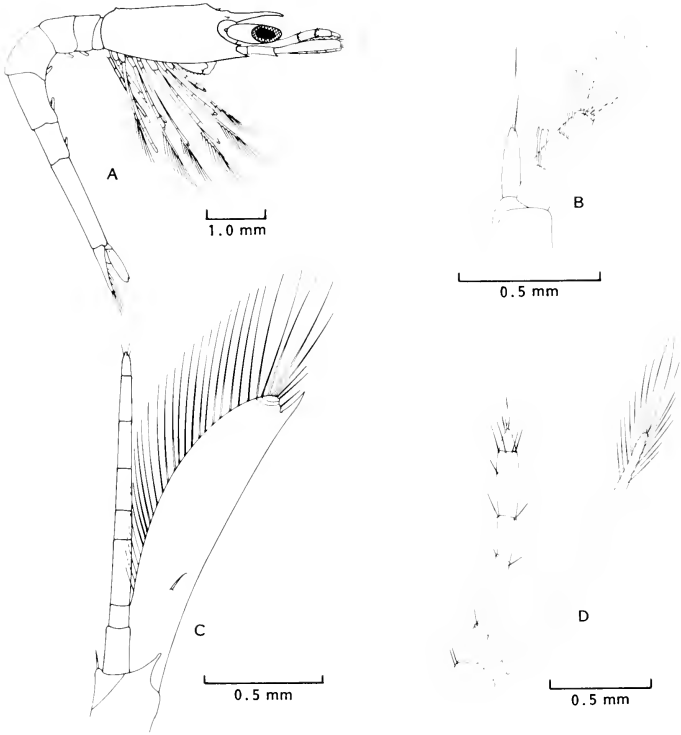
Mean total length of Stage III 9.5 mm (range 9.0-10.0 mm; 10 specimens). From this stage on, zoeae gradually become more orange and color pattern not useful in identifying a given stage. Rostrum (Figure 3A) projects horizontally but curves slightly downward at tip; bears one or two teeth at base. Epipodite of first maxilliped bilobed; pleurobranchiae present as small buds.

ANTENNULE (Figure 3B, inner and outer

flagella).—Flagella not segmented. Inner flagellum about one-half length of outer flagellum, bearing stiff seta at base of terminal spine. Outer flagellum bears four long and two shorter aesthetascs terminally and two groups of three aesthetascs each proximally.

ANTENNA (Figure 3C).—Flagellum eight-segmented, about equal in length to scale, tipped by three short setae and remnant of terminal spine. Antennal scale narrower than in Stage II and fringed with about 30 plumose setae; two complete joints at tip. Spine on protopodite at base of scale considerably larger than in Stage II.

MAXILLIPEDS.—Change in form and setation of maxillipeds from Stage III on is slight and consists primarily of second maxilliped becoming



curved as in adult and its propodite slightly widened, third maxilliped becoming shaped as in adult, and natatory setae on exopodites of second and third maxillipeds increasing in number to usually 20 in Stage V.

FIRST PEREOPOD (Figure 3D).—Has begun to acquire adult shape, particularly in widened propodite and carpopodite segments.

SECOND PEREOPOD (Figure 3E).—Similar to Stage II except distal joint of propodite projects slightly anteriorly.

THIRD, FOURTH (Figure 3F), AND FIFTH PEREOPODS.—Endopodites similar; like first pereopod have begun to acquire adult shape, especially in lengthened dactylopodite and widened propodite. Ischiopodite articulates somewhat laterally with meropodite.

PLEOPODS (Figure 3G, second pleopod).—Bilobed, unsegmented, and without setae.

TELSON (Figure 3H).—Endopodite not fully developed; about one-third length of exopodite and bearing several setae along lateral and posterior margins. Uropods free. Anal spine clearly visible.

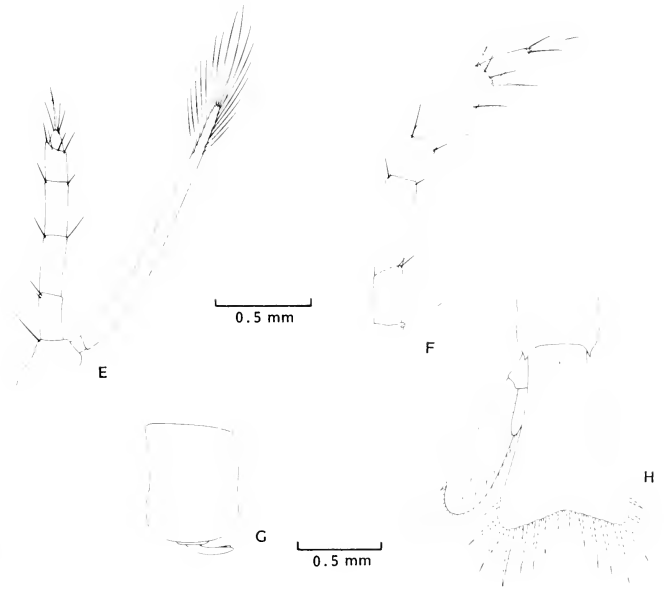


FIGURE 3.—Stage III zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod, lateral; E, second pereopod, lateral; F, fourth pereopod, lateral; G, second abdominal somite and pleopod, right side; H, telson, dorsal.

STAGE IV ZOEA

Mean total length of Stage IV 13.0 mm (range 12.6-13.2 mm; 10 specimens). Rostrum (Figure 4A) bears four to eight but usually six teeth dorsally, no teeth ventrally; tip not bifid. No change in epipodite of first maxilliped or pleurobranchiae except slight increase in size. Epipodite on second maxilliped present as small bud. No mastigobranchiae.

ANTENNULE (Figure 4B, inner and outer

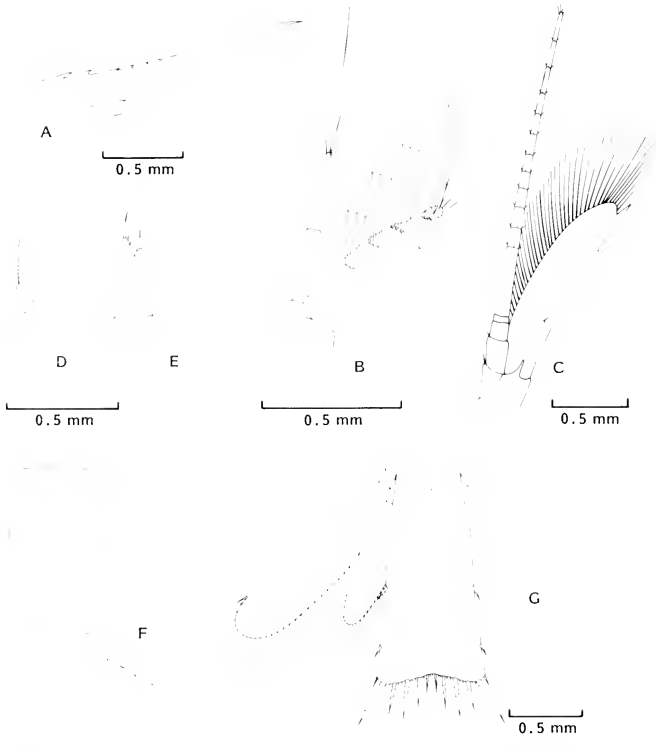


FIGURE 4.—Stage IV zoea of *Pandalus borealis*. A, rostrum, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod (distal segments only), lateral; E, second pereopod (distal segments only), lateral; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

flagella).—Flagella two-segmented. Inner flagellum nearly as long as outer flagellum. Outer flagellum bears four aesthetascs and two spines terminally and three groups of three aesthetascs each on proximal segment.

ANTENNA (Figure 4C).—Flagellum 15-segmented; 1.5-2 times length of scale, extending past tips of plumose setae fringing antennal scale. Antennal scale without joints at tip. Other than increase in size, changes in antennal scale from Stage IV onward are negligible.

FIRST PEREOPOD (Figure 4D).—Distal joint of propodite projected anteriorly and tipped with small spine.

SECOND PEREOPOD (Figure 4E).—Distal joint of propodite projected anteriorly to about one-half length of dactylopodite; projection tipped by two spines, one terminal and other subterminal and much shorter. Dactylopodite bears one terminal spine and two considerably shorter subterminal spines.

PLEOPODS (Figure 4F, second pleopod).—Segmented; length of second pair of pleopods about one-half height of second abdominal somite. Exopodite usually bears one to four small setae terminally and endopodite sometimes bears single seta terminally. Appendices internae not present.

TELSON (Figure 4G).—Endopodite of uropod about two-thirds length of exopodite and fringed with about 20 setae. Lateral margins of telson nearly parallel but slightly divergent posteriorly and bear two spines each. Posterior margin still slightly emarginate; bears 6 + 6 spines, the outermost (sixth) pair usually without spinules.

STAGE V ZOEA

Mean total length of Stage V 16.0 mm (range 15.2-17.1 mm; 10 specimens). Rostrum (Figure 5A) with 9-12 dorsal teeth, bifid tip, and usually 4, but sometimes 5, partially developed ventral teeth. Pleurobranchiae curve somewhat anteriorly and edges minutely lobulate. Mastigobranchiae occur as minute buds on protopodite of third maxilliped and pereopods 1-4.

ANTENNULE (Figure 5B, flagella only).—Inner flagellum four-segmented. Outer flagellum four- or five-segmented; bears six groups of three aesthetascs each. Each segment bears at least one seta but number and location of setae somewhat variable.

ANTENNA (Figure 5C).—Flagellum 2-3 times length of scale.

FIRST PEREOPOD (Figure 5D, distal segments only).—Projection of propodite at least one-half length of dactylopodite; bears two small spines, one terminally and one subterminally. Dactylopodite bears small spine subterminally in addition to terminal spine.

SECOND PEREOPOD (Figure 5E, distal segments only).—Chela well formed. Terminal spine of propodite shorter and stouter than in Stage IV. Dactylopodite bears five spines, the distal two especially stout. Carpopodite usually at least partially segmented.

PLEOPODS (Figure 5F, second pleopod).—Second pair of pleopods about equal in length to height of second abdominal somite; outer flagellum fringed with 11 or 12 plumose setae, inner flagellum with about 8 setae. Appendices internae usually present on pleopods 2-5; tips sometimes bear a few cincinnuli.

TELSON (Figure 5G).—Lateral margins of telson essentially parallel and bear two spines each. Posterior margin straight or slightly emarginate, bearing 6 + 6 spines. Uropods similar in shape to adult; no evidence of transverse hinge of exopodite.

STAGE VI (MEGALOPA)

Mean total length of Stage VI 18.5 mm (range 17.4-20.2 mm, 5 specimens). Rostrum (Figure 6A) shaped as in adult; bears 13-15 dorsal teeth in addition to distinct bifid tip, and 6 or 7 distinct ventral teeth. Usually one or two setae between dorsal teeth. Carapace lacks supraorbital spine. Exopodites on maxillipeds and pereopods 1-3 reduced. Pleurobranchiae and mastigobranchiae shaped as in adult. Inner and outer flagella of antennule eight- to nine-segmented and five-segmented, respectively. Flagellum of antenna about 6 times length of antennal scale. Mandibles still without palps. Chaelae of first and second pereopods shaped as in adult; carpal joints of left

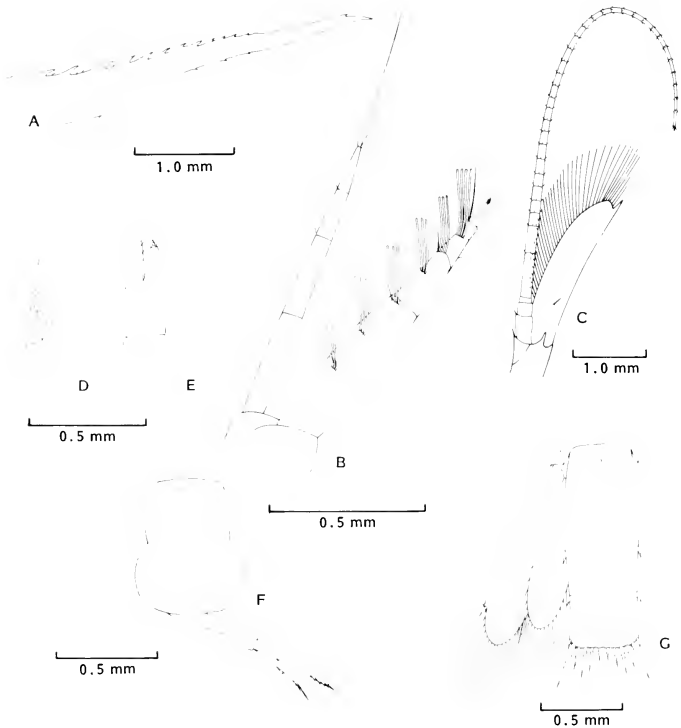


FIGURE 5.—Stage V zoea of *Pandalus borealis*: A, rostrum, right side; B, antennule (flagella only), ventral; C, antenna, ventral; D, first pereopod (distal segments only), dorsal; E, second pereopod (distal segments only), dorsal; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

and right second pereopods 20-25 and 10-13, respectively. Pleopodal setae extend along entire lateral margins of both flagella; tips of appendices internae bear several distinct cincinnuli. Length of second pair of pereopods, excluding setae, 1.5-2 times height of second abdominal segment. Telson (Figure 6B) shows, for first time, shape and spination similar to adult; lateral margins converge posteriorly but widen slightly at junction with posterior margin; typically four spines on each lateral margin but in this stage and Stages VII and VIII one lateral spine often lacking. Posterior margin of telson rounded but not as much as in Stage VII; bears 3 + 3 stout spines and sometimes

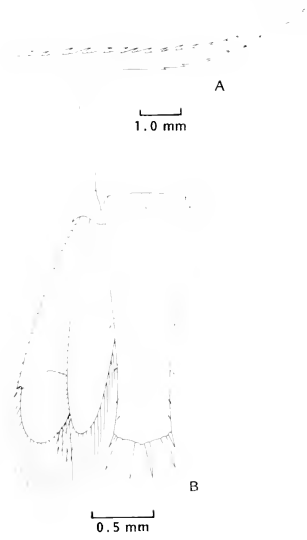


FIGURE 6.—Stage VI (megalopa) of *Pandalus borealis*. A, rostrum, right side; B, telson, dorsal.

remnants of a spine or two from Stage V. Transverse hinge of exopodite of uropod complete.

STAGES VII AND VIII (JUVENILES)

Mean total length of Stage VII (first juvenile) 18.4 mm (range 15.1-21.0 mm; 5 specimens). Usually two setae between most rostral teeth. Carapace without supraorbital spine. Arthrobranchiae on third maxilliped and pereopods 1-4 present as minute buds. Mandibular palp present for first time; three-segmented. Inner and outer flagella of antennule each 11- to 13-segmented. Exopodites on maxillipeds and pereopods 1-3 remnant. Third abdominal somite sometimes bears minute spine on middorsal posterior margin. Carpal joints of left and right second pereopods 28-30 and 14-17, respectively. Lateral margins of telson (Figure 7) typically bear 5 + 5 spines; posterior margin rounded as in adult.

Mean total length of Stage VIII (second juvenile) 21.6 mm (range 19.0-23.6 mm; 8 specimens). Morphological differences between Stages VII and VIII slight. Most notable features of Stage VIII: at least three or four setae between most rostral spines; complete lack of exopodites on third maxilliped and pereopods 1-3; inner and outer flagella of antennule each 15- to 16-segmented; lateral margins of telson typically bear 6 + 6 spines.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The first description of larvae ascribed to *Pandalus borealis* was given by Sars (1900), based on specimens collected from plankton. Berkeley (1931) showed that Sars' larvae could not be *P. borealis*; almost simultaneously Lebour (1930) showed that they were *Caridion gordoni* (Bate). Sars' "post-larval" specimen, however, is considered by both Lebour and Berkeley to be correctly identified as *P. borealis*. As far as can be compared, my Stage VI (megalopa) and Sars' "post-larval" specimen are essentially identical except for the

FIGURE 7.—Stage VII (first juvenile) of *Pandalus borealis*. telson, dorsal

rostral tip, which in my larva is bifid but in Sars' is styliform, and the chela of the first pereopod, which is completely developed in my larva but not in Sars'.

Stephensen (1912) described zoeal Stages I to V from plankton that he provisionally identified as *"P. propinquus* (?)" and Stage III zoeae (1916) as *"Spirontocaris*-larva No. 4." Berkeley (1931) noted the close similarity of the *"P. propinquus* (?)" specimens to zoeae of *P. borealis* from British Columbia waters. Stephensen (1935) later decided that both *"P. propinquus* (?)" and *"Spirontocaris*-larva No. 4" were actually zoeae of *P. borealis*. He also compared his zoeae with fragments of a specimen identified by Krøyer as *Dymas typus* and decided Krøyer's specimen was a Stage IV zoea of *P. borealis*.

Comparing the description and figures of Stephensen's (1912) zoeae and mine in general for each stage, my zoeae are slightly more advanced than Stephensen's. In my Stage I zoeae the antennal scale bears 19 plumose setae; the basipodite and coxopodite of the maxillule bear 9 + 1 and 9 spines, respectively; the endopodite of the first maxilliped is segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 6, 14, and 16 natatory setae, respectively. In Stephensen's Stage I zoeae the antennal scale bears only eight or nine plumose setae; the basipodite and coxopodite of the maxillule bear five and six spines, respectively; the endopodite of the first maxilliped is not segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 4, 10, and 10 natatory setae, respectively. In Stage II, the relative difference in number of setae and spines between my zoeae and Stephensen's remains essentially the same, except in my zoeae the exopodites of pereopods 1, 2, and 3 bear 16, 16, and 12 setae, respectively, whereas in Stephensen's zoeae they each bear 18 setae. In Stage III, the rostrum of my zoeae bears only a single tooth and the antennal flagellum is eight-jointed, but in Stephensen's zoeae the rostrum bears as many as three teeth and the antennal flagellum is not jointed. In Stage IV, the rostrum of my zoeae bears six or seven teeth, the antennal flagellum is 15-segmented, and the telson bears eight pairs of spines whereas in Stephensen's zoeae the rostrum bears only four teeth, the antennal flagellum is still unsegmented, and the telson bears only seven pairs of spines. In Stage V, the most obvious difference is that the pleopods are segmented in my zoeae but not in Stephensen's.

In his 1916 report, Stephensen described an additional larva which he considered the sixth stage of *P. propinquus* G. O. Sars; later (1935) he decided it was *P. borealis*. According to Stephensen, this stage closely resembles his Stage V zoeae, differing primarily in the left second pereopod being considerably longer than the right, and, for both second pereopods, the joint at the distal end of the carpopodite being complete. In my larvae, morphological change from Stage V to Stage VI is sufficiently pronounced that I consider the sixth stage to be the megalopa. If Stephensen was correct in assuming his specimen to be a sixth stage zoea, then *P. borealis* in Greenland waters has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

In her classic study of pandalid larvae from British Columbia waters, Berkeley (1931) described and figured *P. borealis* Stage I zoeae reared in the laboratory and Stages II-VI collected from plankton. Her larvae follow a pattern of development similar to my larvae but each stage is less well developed. For instance, she described the antennal flagellum in her Stage I zoeae as tipped by a simple seta whereas in my zoeae it is tipped by a spinulose spine, and she neither figured nor described the spinous seta which my zoeae bear on the protopodite at the base of the flagellum. Also, the exopodite of the maxilla of her Stage I zoeae bears 8-10 long simple setae and has no trace of a proximal expansion whereas in my zoeae the exopodite of the maxilla bears 11 long plumose setae as well as one longer, thicker seta at the proximal end which is slightly expanded. In Stage II, the outer flagellum of the antennule of Berkeley's zoeae is figured as bearing only three aesthetascs distally whereas my zoeae bear eight. The proximal expansion of the exopodite of the maxilla is "just appearing" in Berkeley's Stage II but in mine it is distinctly expanded. Moreover, she described the telson as being still indistinctly segmented from the sixth abdominal somite but in my zoeae it is always distinctly segmented at Stage II. Berkeley's Stage III zoeae are essentially identical to mine as far as can be determined from her description. Her Stage IV zoeae have four small teeth at the base of the rostrum, the pleopods are without joints, and there is no epipodite on the second maxilliped. In my Stage IV zoeae, the rostrum usually has six teeth, the pleopods are jointed, and an epipodite occurs on the second maxilliped. In Stage V, the rostral tip of Berkeley's zoeae is still styliform. There is no evidence

from either her description or figure of ventral teeth on the rostrum, and the pleopods have not yet developed appendices internae. In my Stage V zoeae the rostral tip always bears at least a protuberance indicative of the bifid tooth, and pleopods 2-5 bear at least partially developed appendices internae. In contrast to my Stage VI, the megalopa, Berkeley's Stage VI is still typically zoeal: there is still no mention of ventral rostral teeth, the carapace still bears a supraorbital spine, the carpopodites of the second pereopods are not segmented, and the telson bears three pairs of lateral spines (not including the sixth terminal pair) and terminal setal pairs 2-4 have begun to degenerate.

Berkeley (1931) also mentioned a *P. borealis* larva she obtained from plankton that, according to her, corresponds to the sixth stage of *P. danae* Stimpson and is similar to that described by Sars (1900) as the "post-larval" stage of *P. borealis*. Berkeley's sixth stage and Sars' "post-larval" stage are typically nonzoeal as indicated by the lack of supraorbital spines, segmentation of the carpopodites of the second pereopods, degeneration of the pereopodal and third maxilliped exopodites, and the typically adult shape and spination of the telson. Because this stage would be at least the seventh stage, it appears that *P. borealis* in British Columbia waters, as well as Greenland waters (Stephensen 1916), has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

The preceding comparisons show that Berkeley's zoeae were less well developed at each given stage than mine and an additional stage or two was probably necessary for her zoeae to reach the megalopa stage. An apparent contradiction to this delayed development is the lack of segmentation of the antennal scale in the early stages of Berkeley's zoeae. As shown by Haynes (1976), however, Berkeley was mistaken in this regard and her specimens undoubtedly possessed a segmented scale in the early stages.

The only other description of larvae of *P. borealis* known to me is that of Kurata (1964) who, like Berkeley (1931), obtained Stage I zoeae in the laboratory from known parentage but Stages II-VII from plankton. Kurata's zoeae are essentially identical to mine through Stage V, except the rostrum of Kurata's Stage V zoeae is identical to the rostrum of my Stage IV zoeae. Kurata's Stage VI corresponds to my Stage V, but his Stage VII possesses characteristics intermediate between my Stages V and VI. For instance, in Kurata's Stage VII the exopodites on pereopods 1-3 and the third maxilliped have not begun to degenerate nor are the carpopodites segmented whereas in my Stage VI (megalopa) the exopodites on pereopods 1-3 and the third maxilliped are reduced and the carpopodites of the left and right second pereopods are segmented. Also, the lateral spination and shape of the telson of Kurata's Stage VII are typical of postzoeae but posteriorly the telson bears 6 + 6 spines, a typically zoeal characteristic. By studying Stage VII individuals just prior to molting, Kurata found that Stage VIII individuals possessed a distinct mandibular palp and degeneration of posterior telson spines 2-4. He concluded that Stage VII was the last zoeal stage and Stage VIII the first postzoea, or megalopa.

According to Lebour (1930), the lack of an outer seta on the maxillule in zoeae of *Pandalus* is one criterion for distinguishing this genus from certain other Caridea. Pike and Williamson (1964), however, found the seta consistently present in early stages of British species of *Pandalus*. Occurrence of the seta in Stage I zoeae has been reported by Gurney (1942) for *Pandalus montagui* Leach and *P. stenolepis* Rathbun; by Kurata (1955, 1964) for *P. borealis* and *P. kessleri* Czerniavski; and Modin and Cox (1967) for *P. jordani* Rathbun. I have consistently found the seta in the early stages of *P. hypsinotus*, *P. goniurus*, and *P. borealis*. Lebour's suggestion that the lack of the seta is a distinguishing criterion for zoeae of *Pandalus* should, therefore, be disregarded.

In addition to *P. borealis*, larvae have been described, at least in part, for nine other species of pandalids from the North Pacific Ocean: *P. goniurus*, *P. jordani*, *P. platyceros* Brandt, *P. danae*, *P. kessleri*, *P. hypsinotus*, *P. stenolepis*, *Pandalopsis dispar* Rathbun, and *P. coccinata* Urita. Of these nine species, larvae of *Pandalus stenolepis*, *P. jordani*, and *P. goniurus* are most like larvae of *P. borealis*, being characterized by exopodites on pereopods 1-3 rather than only on pereopods 1 and 2 and by poorly developed pereopods in Stage I. Zoeae of *P. stenolepis* were described by Needler (1938). Based on her descriptions, zoeae of *P. stenolepis* are readily distinguished from zoeae of *P. borealis* by 1) the shape and spination of the rostrum, which in Stage I *P. stenolepis* is about as long as the carapace and projects upward rather than downward as in *P. borealis*, and 2) the fringed posterior edge of the abdominal somites and the serrated margins of

the carapace, both of which persist to Stage V in *P. stenolepis* but never occur in *P. borealis*.

Larvae of *P. jordani* have been described from specimens reared in the laboratory. Compared with development of similar species, Modin and Cox (1967) and Lee (1969) obtained more stages (11-13 and at least 8, respectively) than expected for larvae of *P. jordani* from plankton. Because of the possibility of these extra stages, only Stage I zoeae of *P. borealis* and *P. jordani* can be compared. Upon hatching, zoeae of *P. borealis* are slightly more developed than zoeae of *P. jordani*. For instance, in Stage I *P. jordani*, the exopodites of maxillipeds 1, 2, and 3 bear 4, 9-11, and 11 or 12 natatory setae, respectively; the left mandible bears no lacinia mobilis; the basipodite of the maxillule bears six spines terminally; and the scaphognathite of the maxilla bears seven to nine setae along its outer margin. In Stage I *P. borealis*, maxillipeds 1, 2, and 3 bear 5 or 6, 13 or 14, and 16 natatory setae, respectively; the left mandible bears a single lacinia mobilis; the basipodite of the maxillule bears 9 spines terminally; and the scaphognathite of the maxilla bears 12 setae along its outer margin. Beyond Stage I, the most distinguishing difference between zoeae of *P. jordani* and *P. borealis* seems to be the development of the rostral tip which in zoeae of *P. jordani* remains acuminate but in zoeae of *P. borealis* becomes bifid in later stages.

In an earlier report (Haynes 1978), I described larvae of *P. goniurus* reared in the same manner as larvae of *P. borealis* described here. Larvae of both species are morphologically similar, especially in early stages, and often occur together in plankton. To facilitate identification of larvae of these two species, the most readily observable morphological differences are listed by stage in Table 1. Larvae of *P. goniurus* are characteristically smaller than those of *P. borealis* and in

TABLE 1.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska.

Stage and characteristic	*P. borealis*	*P. goniurus*
Stage I zoea		
Mean total length (mm)	6.7 (range 6.5-7.3, 25 specimens)	4.0 (range 3.7-4.2, 10 specimens)
No. of plumose setae fringing antennal scale	19	9
No. of spines terminally on basipodite of maxillule	9	5
No. of plumose setae on scaphognathite (in addation to single proximal seta)	11	4
No. of natatory setae on exopodites		
Maxillipeds 1, 2, 3,	5-6, 13-14, 16	4, 8, 12
Stage II zoea		
Mean total length (mm)	7.5 (range 6.7-8.2, 25 specimens)	5.9 (range 4.5-5.3, 10 specimens)
No. of plumose setae fringing antennal scale	About 25	About 19
No. of natatory setae on exopodites		
Maxillipeds 1, 2, 3,	7, 16, 18	6, 12, 14
Pereopods 1, 2, 3,	16, 16, 12	12, 8, 8
Stage III zoea		
Mean total length (mm)	9.5 (range 9.0-10.0, 10 specimens)	6.2 (range 6.0-6.6, 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	About 30 setae	About 20 setae
Stage IV zoea		
Mean total length (mm)	13.0 (range 12.6-13.2, 10 specimens)	7.7 (range 6.8-8.3, 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	About $1\frac{1}{2}\times$ scale, extending past tips of plumose setae	Longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	Projected anteriorly about $\frac{1}{2}$ length of dactylopodite	Projected anteriorly only slightly
Pleopods	Segmented, pleopod 2 about $\frac{1}{2}$ height of abdominal somite	Unsegmented, pleopod 2 about $\frac{1}{4}$ height of abdominal somite
Stage V zoea		
Mean total length (mm)	16.0 (range 15.2-17.1, 10 specimens)	10.3 (range 8.2-11.3, 10 specimens)
Rostrum	9-12 dorsal teeth, tip bifid, 4-5 partially developed ventral teeth	5-6 dorsal teeth, tip not bifid (but may show slight protuberance), no ventral teeth
Chela of pereopod 2	Fully formed	Not fully formed, propodite extension about $\frac{1}{3}\times$ length of dactylopodite
Pleopods	With appendices internae, fringed with plumose setae; pleopod 2 as long or longer than height of abdominal somite	Without appendices internae, 2-4 simple setae terminally, pleopod 2 about $\frac{2}{3}\times$ height of abdominal somite
Stage VI (megalopa)		
Mean total length (mm)	18.5 (range 17.4-20.2, 5 specimens)	13.8 (range 11.1-15.8, 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Stages I-III the number of setae on certain appendages, particularly the antennal scale and certain mouthparts, is fewer than for zoeae of *P. borealis*. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*.

LITERATURE CITED

BERKELEY, A. A.
1931 The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. 6(6): 79-163.

GURNEY, R.
1942 Larvae of decapod Crustacea. Ray Soc. (Lond.) Publ. 129, 306 p.

HAYNES, E.
1976 Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory. Fish. Bull., U.S. 74: 323-342.
1978 Description of larvae of the humpy shrimp, *Pandalus goniurus*, reared in situ in Kachemak Bay, Alaska. Fish. Bull., U.S. 76: 235-248.

KURATA, H.
1955 The post-embryonic development of the prawn, *Pandalus kessleri*. Bull. Hokkaido Reg. Fish. Res. Lab. 12: 1-15.
1964 Larvae of decapod Crustacea of Hokkaido. 3. Pandalidae. Bull. Hokkaido Reg. Fish. Res. Lab. 28: 23-34. (Transl., Fish. Res. Board Can., 1966, Transl. 693.)

LEBOUR, M. V.
1930 The larval stages of *Caridion*, with a description of a new species, *C. steveni*. Proc. Zool. Soc. Lond. 1930: 181-194.

LEE, Y. J.
1969 Larval development of pink shrimp, *Pandalus jordani* Rathbun, reared in laboratory. M.S. Thesis, Univ. Washington, Seattle. 62 p.

MODIN, J. C., AND K. W. COX
1967 Post-embryonic development of laboratory-reared ocean shrimp, *Pandalus jordani* Rathbun. Crustaceana 13: 197-219.

NEEDLER, A. B.
1938 The larval development of *Pandalus stenolepis*. J. Fish. Res. Board Can. 4: 88-95.

PIKE, R. B., AND D. I. WILLIAMSON
1964 The larvae of some species of Pandalidae (Decapoda). Crustaceana 6: 265-284.

SARS, G. O.
1900 Account of the postembryonal development of *Pandalus borealis* Kröyer with remarks on the development of other pandali, and description of the adult *Pandalus borealis*. Rep. Norw. Fish. Mar. Invest. 1: 1-45.

STEPHENSEN, K.
1912 Report on the Malacostraca collected by the "Tjalfe"-Expedition, under the direction of cand. mag. Ad. S. Jensen, especially at W. Greenland. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 64: 57-134.
1916 Zoogeographical investigation of certain fjords in southern Greenland, with special reference to Crustacea, Pycnogonida and Echinodermata including a list of Alcyonaria and Pisces. Medd. Gronl. 53: 230-378.
1935 Crustacea Decapoda. The Godthaab Expedition 1928. Medd. Gronl. 80: 1-94.

RELATIONSHIPS OF THE BLUE SHARK, *PRIONACE GLAUCA*, AND ITS PREY SPECIES NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

TIMOTHY C. TRICAS[2]

ABSTRACT

Small fishes and cephalopods associated with both pelagic and inshore habitats composed the major prey for the blue shark, *Prionace glauca*, near Santa Catalina Island, Calif. The northern anchovy, *Engraulis mordax*, was the predominant prey for sharks in the immediate study area while at least 13 species of pelagic cephalopods constituted major prey for sharks in more distant oceanic waters. Inshore species taken by sharks included pipefish, *Syngnathus californiensis*; jack mackerel, *Trachurus symmetricus*; and blacksmith, *Chromis punctipinnis*. In addition, sharks moved inshore to feed on winter spawning schools of market squid, *Loligo opalescens*. Digestive rate studies and telemetric monitoring of activity patterns indicate that sharks forage in waters near the surface from around midnight through dawn. Diel activities of prey species were examined and show that most prey dispersed in the upper water column at night and refuged during the day either by schooling (anchovies and jack mackerel) or by retreating to deeper waters (pelagic cephalopods). Field observations of shark feeding behavior indicate that predatory modes vary in response to prey behavior.

The blue shark, *Prionace glauca* (Carcharhinidae) (Figure 1), is a pelagic carnivore cosmopolitan in tropical and warm temperate seas. Because of its pelagic habits, the majority of ecological studies on this species have been predicated on data from sharks captured by sport and commercial fisheries. As a result data has been largely qualitative, and the shark's role as a predator in the epipelagic habitat has remained unclear.

The importance of small fish as prey items for blue sharks has been described by Couch (1862), Lo Bianco (1909), Bigelow and Schroeder (1948), Strasburg (1958), LeBrasseur (1964), Bane (1968), Stevens (1973), and others. These prey generally are schooling species common in productive coastal waters. Cephalopods were also reported as major prey but little information is available on specific identifications (see Stevens 1973; Clarke and Stevens 1974).

Although blue sharks have been observed feeding on dead or wounded cetaceans (Bigelow and Schroeder 1948; Cousteau and Cousteau 1970) there is little indication that they habitually prey on live, healthy marine mammals. The occurrence of mammalian tissue in the diet of blue sharks is rare (Strasburg 1958; Stevens 1973), and such feeding is most likely directed to dead mammals or those in poor health. Air/sea disasters have resulted in attacks on humans by blue sharks (see Schultz and Malin 1963; Fitch[3]) but these cases usually involved injured persons or corpses.

Standard tagging programs (Weeks 1974; Casey 1976; Stevens 1976) and telemetric trackings (Sciarrotta and Nelson 1977) have provided some information on large-scale movements of blue sharks but relatively little is known of their orientation mechanisms and predatory behavior.

Despite the profusion of descriptive reports, there still exists a great need for quantitative data on ecological relationships between the blue shark and its prey species. With these ideas in mind, I undertook this study within a limited geographic area to 1) provide a quantitative assessment of the diet of blue sharks near Catalina Island, 2) establish temporal and/or geographical shifts in food habits, and 3) describe behavioral interactions between the blue shark and its prey species.

METHODS

The study area was located north of the Isthmus, Santa Catalina Island, Calif. (Figure 2). Beds of

[1]Based on a portion of a thesis submitted in partial fulfillment of the requirements for the M.A. degree in the Department of Biology, California State University, Long Beach, Calif. Contribution no. 27 from the Catalina Marine Science Center, University of Southern California.

[2]Department of Biology, California State University, Long Beach, Calif.; present address: Department of Zoology, University of Hawaii at Manoa, Honolulu, HI 96822.

[3]J. E. Fitch, California Department of Fish and Game, Operations Research Branch, 350 Golden Shore, Long Beach, CA 90802, pers. commun. May 1976.

Manuscript accepted July 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

FIGURE 1.—Female blue shark near the ocean surface.

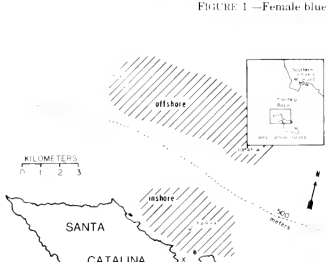


FIGURE 2.—Study area at Catalina Island, Calif. Hatching indicates sampling regions. Sharks feeding among squid schools were observed at ×.

giant kelp, *Macrocystis pyrifera*, composed the major habitat along the island shore. A submarine shelf, averaging 150 m deep, extends approximately 2 km seaward then slopes to depths near 900 m and forms the floor of the San Pedro Basin. "Inshore" sampling stations were located above the shelf within 3 km of the island, and "offshore" stations centered approximately 6 km north of the Isthmus, over deeper basin waters.

Sharks were collected monthly between March 1975 and March 1976. Samples were taken during morning and afternoon hours at both inshore and offshore areas with an attempt to maintain a consistent area-time sampling schedule. Sharks were attracted to a drifting 7-m work boat by baiting with slashed Pacific mackerel, *Scomber japonicus*, suspended in a wire basket 5 m beneath the surface. Once attracted, sharks were captured by hook and hand line using mackerel or market squid, *Loligo opalescens*, as bait. Sharks were landed as quickly as possible to minimize regurgitation and then measured, sexed, and inspected for mating scars and general health. Contents of esophagi and stomachs were filtered through 1-mm mesh netting and preserved. Recognizable prey items and their digestive states were recorded on site. Intestinal tracts were occasionally examined but contributed little information on the diet because of the small pylorus which restricted passage of identifiable prey fragments.

Except for the market squid, cephalopods in the diet were represented exclusively by beaks. Beaks were paired into sets of upper and lower halves, and identified when possible according to Clarke (1962) and Pinkas et al. (1971). Specific identifications were verified by comparisons with beaks from collections of local species. Whole volumes of squid were estimated from beak-size body-weight regressions for the major cephalopod families given by Clarke (1962). For calculations, the density of cephalopod flesh was assumed to be 1 g cm^3. A regression for the family Ocythoidae (not given by Clarke) was generated by plotting beak measurements and body weights from local specimens on Clarke's Octopodidae and Argonautidae regressions and constructing a parallel relationship curve. Beak-size body-weight regressions for *Vampyroteuthis infernalis* were obtained from specimens of local collections. Unidentified cephalopods were omitted from the quantification as they represented only a minor portion of the diet (four small, infrequent species in eight stomachs).

In order to approximate normal shark feeding times, digestive rates for captive sharks were determined and then compared with field data on the

digestive states of anchovies recovered from wild sharks. Three healthy, active sharks were acclimated for 24 h in large seawater holding tanks (14°-16°C) at Marineland of the Pacific, and then fed marked anchovies and market squid. Stomach contents were examined at 6, 12, and 24 h after feeding and the digestion rates recorded.

Short-term movements of sharks were monitored in the fall and winter seasons by telemetric instrumentation similar to those of Ferrel et al. (1974) and Nelson (1974). Transmitters were applied externally to free-swimming sharks with stainless-steel darts. Effective transmission range was approximately 2 km under good conditions but depended largely upon ambient noise from waves, wind, and biological sources. Some transmitters included a depth sensor for a record of vertical movements. Signals were tracked using a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. These trackings supplement the spring through fall trackings of Sciarrotta and Nelson (1977).

The feeding behavior of blue sharks among spawning squid was studied in January 1976. Just before sunset, squid schools were detected near the bottom (30-40 m deep) using a recording Fathometer[4] and the work boat anchored directly above. A 1,500-W light was then suspended over the water. Squid typically converged beneath the light and formed a large surface school at which sharks usually appeared and began to feed.

Orientation and feeding responses of sharks to moving prey were documented during baiting sessions at offshore stations. In these tests, a dead anchovy, attached to a light fishing line was cast beyond the bait-attracted sharks and then retrieved back towards the boat. All field observations of shark and prey activities were made from the boat, using scuba and/or by snorkeling.

RESULTS

Sharks were captured during all months of the 1-yr study. Of the 81 sharks sampled, 94% had recognizable food items in their stomachs. The northern anchovy, *Engraulis mordax*, was the predominant prey item for sharks in the study area while other small fishes occurred at much lower frequencies (Figure 3).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Although sharks fed on a wide variety of cephalopods, an analysis of relative importance (Table 1) showed *L. opalescens* and squid of the genus *Histioteuthis* as the most common and substantial cephalopod prey. Monthly analysis revealed important shifts between these prey items

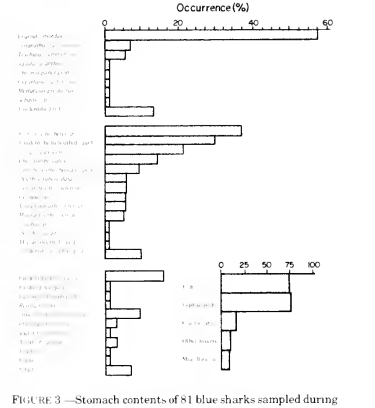


FIGURE 3.—Stomach contents of 81 blue sharks sampled during the year. Occurrence = percent of the 81 individuals containing that prey species. Inset gives a summary by broader food categories.

TABLE 1.—Annual relative importance of identified cephalopod prey in the diet of blue sharks near Santa Catalina Island, Calif. Importance was estimated as an index of relative importance (*IRI*) in accord with Pinkas et al. (1971) $IRI = (N + V)F$, where N (numerical percent) is the percent of individuals of that species among all individual cephalopods recovered; V (volumetric percent) is the percent volume represented by that species of all cephalopods recovered, and F (frequency) is the percent of individual shark stomachs containing that prey species.

Rank	Species	*F*	*N*	*V*	*IRI*
1	*Loligo opalescens*	21.0	70.6	31.9	2,152.5
2	*Histioteuthis heteropsis*	37.0	11.4	10.4	806.6
3	*Histioteuthis* sp	23.5	5.0	3	124.6
4	*Chiroteuthis calyx*	14.8	5.3	1.4	99.2
5	Thysanoteuthid squid	1.2	.2	43.3	52.2
6	*Onychoteuthis borealijaponicus*	8.6	2.4	3.6	51.6
7	*Vampyroteuthis infernalis*	4.9	.8	2.2	14.7
8	*Octopoteuthis deletron*	6.2	1.0	.8	11.2
9	*Dosidicus gigas*	1.2	.2	5.1	6.4
10	*Ocythoe tuberculata*	4.9	.8	.4	5.9
11	*Mastigoteuthis pyrodes*	3.7	.6	.3	3.3
12	*Octopus* sp	4.9	1.4	.2	7.8
13	*Leachia* sp	1.2	.2	.004	.3

(Table 2). The high index for *L. opalescens* in January 1976 reflected the squid's extensive winter spawning assemblages in the study area, and similarly is the reason for its high annual rank (Table 1). Histioteuthid squid were probably the most significant cephalopod prey for sharks in more oceanic waters away from inshore spawning aggregations of *L. opalescens*. The low average number of anchovies and histioteuthid squid per stomach and the relatively small coefficients of dispersion for these two prey indicate that sharks obtained them somewhat regularly over a wide area (Table 3). Conversely, the large coefficient for market squid during its spawning season concurs with observations that this prey was taken from large schools during its spawning runs at inshore areas.

Digestive rate tests for healthy, captive sharks were in order with digestive states of prey recovered from wild sharks. Anchovies removed from captive sharks at 6 h after feeding were easily identified, and showed only preliminary digestion of fins and margins of the opercula. Likewise, whole squid were easily recognized and had only slight signs of external surface decomposition. At 12 h after feeding, digestion of anchovies was characterized by decomposed abdominal walls, moderate scale loss, and some skin deterioration. Digestion of squid was still negligible. At 24 h, anchovies were well digested with only vertebrae, otoliths, and small sections of muscle present. Squid heads were separated from the body and lenses had detached from the optic cups, but beaks were still implanted within the buccal mass. In general, digestive rates were at least twice as fast for anchovies than for squid.

Times of normal feeding activity were estimated by comparing the digestive rate data obtained from captive sharks with recognizable anchovies recovered from wild sharks. Anchovies that were freshly ingested predominated in sharks captured in early morning hours (Figure 4) and corresponded to a duration of approximately 0-8 h after ingestion. Moderately digested anchovies were prevalent in sharks sampled in the afternoon and represent anchovies held about 9-20 h after consumption.

TABLE 3.—Dispersion of the three major prey species in blue shark stomachs off Santa Catalina Island, Calif. Means for market squid were computed for squid spawning season (Mar. 1975, Dec.-Jan. 1976) and nonspawning season (Apr.-Nov. 1975, Feb. 1976). Coefficients of dispersion (ratio of variance to mean) indicate grouping of prey among stomachs. A coefficient of 1 describes a random distribution. Larger coefficients describe increasingly contagious (clumped) distributions of prey among shark stomachs (Sokal and Rohlf 1969).

Prey item	No. of sharks sampled	Mean no. prey per stomach	Coefficient of dispersion
Anchovies	81	1.06	1.92
Histioteuthid squid	81	1.52	2.68
Market squid			
Spawning season	29	11.52	162.57
Nonspawning season	52	0.423	6.81

Tooth marks on anchovies recovered from wild sharks indicate that prey were almost exclusively captured from behind. When present, tooth marks were usually located on the posterior lateral one-third of the anchovy, and in many cases impressions penetrated only the skin and not the myotome.

The movements of four sharks were monitored using ultrasonic telemetry in the winter (October-February) and supplement the spring, summer, and fall trackings of a previous study in the same area (Sciarrotta and Nelson 1977). Sharks ranged over wide areas (e.g., approximately 50 km^2 in 18 h; Tracking 2) and did not exhibit movements oriented towards the island shore. Vertical movements, except for the initial plunge immediately following tag application, were confined to the upper 15-m depth range.

TABLE 2.—Monthly index of relative importance (*IRI*) of identified cephalopod prey in stomachs of blue sharks near Santa Catalina Island, Calif. See caption of Table 1 for calculation of *IRI*.

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Loligo opalescens	1 596	—	—	392	21	378	1 597	9 571	—	1 098	11 564	—
Histioteuthis heteropsis	780	17 369	3 917	6 454	166	9 406	2 298	254	—	1 376	370	—
Histioteuthis sp.	21	440	1 596	—	234	275	1 800	102	1 625	388	—	4 000
Chiroteuthis calyx	—	429	—	—	67	1 318	783	1 259	6 395	1 174	—	—
Thysanoteuthis rhombus	—	—	—	—	—	—	—	—	—	1 561	—	—
Onychoteuthis borealijaponicus	68	—	—		169	—	—	—	—	1 188	23	—
Vampyroteuthis infernalis	—	—	—		130	—	521	—	—	136	—	—
Octopoteuthis deletron	40	—	1 373	—	19	—	—	—	—	55	—	—
Ostrichus gigas	—	—	—	—	216	—	—	—	—	—	—	—
Ocythoe tuberculata	14	—	—	—	23	—	138	—	—	47	—	—
Mastigoteuthis pyrodes	—	—	—	—	—	—	—	—	1 825	189	—	—
Octopus sp.	—	—	—	—	142	—	—	102	—	50	—	—
Leachia sp.	—	—	—	—	14	—	—	—	—	—	—	—

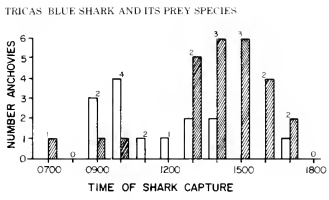


FIGURE 4.—Frequency of digestive states of anchovies in relation to time recovered from wild blue shark stomachs. Freshly ingested (light bars): anchovy body, scales, skin, and fins intact, represent anchovies about 0-8 h after ingestion. Moderate digestion (hatched bars): anchovy with head detached, open body cavity, and exposed myotome; represents anchovies about 9-20 h after ingestion. Advanced digestion (identification of anchovy possible only by vertebrae or otoliths) not included in distribution because of broad time span represented by this state (about 20 h or longer). Numbers indicate sharks sampled that contained anchovies in freshly ingested or moderately digested states. Water temperatures in the field ranged from 13° to 19°C.

Free-swimming sharks responded to moving prey (bait on slowly retrieved light fishing line) with a consistent posterior orientation, as illustrated in my field notes: "As I retrieved the bait towards the boat, a 1.5-m male shark sighted the anchovy and then swam in a wide arc so as to approach the bait from behind. He then made a rapid posterior-oriented dash up to the anchovy, bit the bait once at mid body, and swallowed it whole." Replicate tests using Pacific mackerel elicited similar posterior attacks; in these cases, the shark rolled partially on its side to take the larger fish prey. Tooth marks on bait in these test situations were similar to those on anchovies recovered from stomachs of wild sharks.

Sharks also showed several distinct patterns of predatory behavior while feeding on schools of spawning squid. Each feeding pattern appeared to be correlated with the size and level of activity of each shark as well as the physical configuration and alertness of the squid within the school. Surface and underwater observations of sharks feeding on night-light attracted squid revealed four feeding responses:

1) SLOW HEAD SWAYING: This feeding behavior was most common among larger sharks moving either through the center of moderately dense squid schools, or at the periphery of large, more diffuse aggregations. Sharks swam among the squid at a relatively slow speed, with pronounced lateral head movements and corresponding broad tail sweeps. Squid were generally captured in the corners of the mouth and swallowed whole. In this behavior, sharks did not show rapid head shaking (as often occurs when sharks bite on relatively large prey) although lateral head jerks to position prey for swallowing were common. Sharks moved in a relatively straight path, and created minimal disturbance to the school.

2) TURNING: Turning behavior was most frequent among sharks feeding at the surface when squid were in an alert state or not in tight schools. As the shark approached the school, the squid (which swam backwards and could view the predator's approach) began to turn in tight arcs away from the shark's path. The shark would respond by turning in an accelerated pursuit, but was most often eluded by the squid. Sharks that were successful quickly whipped their heads to one side and captured squid in the corner of their mouths.

3) CHARGING: This behavior can best be described as a straight accelerated rush through a dense school of squid. Charging was most prevalent among the more active sharks that had just arrived at a squid congregation. Typically, the shark showed no orientation to specific individuals, and indiscriminately engulfed large numbers of prey.

4) TAIL STANDING: Sharks also fed on the lower portions of squid schools. As previously described, squid would often be concentrated directly beneath the light source so as to form a dense school. In this feeding behavior, the shark first circled the lower portion of the school and then moved up to the squid and assumed a near vertical attitude, using broad tail sweeps to maintain position. Then the shark lunged its head into the bottom of the school and engulfed many individual squid. The longest duration of a tail-standing posture was 20 s in which approximately 30 squid were consumed by one individual. This behavior was observed only when squid schools were most dense and was not as common as other feeding modes.

DISCUSSION

Blue sharks fed on a variety of small fishes and cephalopods associated with both pelagic and inshore habitats. Northern anchovies were the major prey for sharks in this investigation, and off Newport Beach, Calif. (Bane 1968), while small schooling fishes composed a major portion of blue

shark diets in other coastal areas of the world (Bigelow and Schroeder 1948; LeBrasseur 1964; Stevens 1973). Major concentrations of anchovies in the California Current system were centered in the semiprotected waters of the Southern California Bight (Mais 1974) which lies between Point Conception and Point Descanso, Mexico (approximately from lat. 32.0°N to 34.5°N, area of about 50,000 km²). The main portion of the southern California anchovy population was reported by Mais to be distributed within 37 km of the mainland over deep water (228.6-731.5 m) which includes the study area at Catalina.

The most prevalent schooling behavior for anchovies in deep open waters (bottom depth >183 m) was the formation of small (4-15 m thick), near-surface daytime schools (0-54.9 m deep) that dispersed at night into a thin surface scattering layer (Mais 1974). Field observations from the present study indicate a similar behavior for anchovies near Catalina. In offshore waters during the day, anchovies occurred in large, dense, polarized schools near the surface. In the early evening, schools dispersed horizontally into less dense feeding assemblages with individuals spaced approximately 0.5 m apart. Later at night (0100-0400 h) more dispersed groups and solitary individuals were observed on several occasions, indicating a more complete nocturnal dissolution.

In spite of the abundance of this prey no sharks examined near Catalina had stomachs distended with anchovies; usually only one or two had been taken per day. Data from the digestion studies indicate that most predation on anchovies occurred in predawn hours which correlates with the increased nocturnal activity of telemetered sharks reported by Sciarrotta and Nelson (1977). It seems probable then, that the few anchovies taken by each shark was at least partially due to the nocturnal dispersion of schools in offshore waters, whereby assemblage densities were reduced and anchovies taken individually.

The localized variability of anchovy abundance and schooling behavior that existed between areas and seasons presented different feeding opportunities for sharks. For example, blue sharks captured during the day off Newport Beach, Calif., and in commercial anchovy fishing grounds near Los Angeles Harbor (author unpubl. data) contained many more anchovies (approximately 10-20 individual) than did sharks sampled in the Catalina study area. The two former areas feature nearshore submarine escarpments where the size and concentrations of anchovy schools were among the greatest anywhere in southern California (Mais 1974).

The present status of the blue shark-anchovy association may be the aftermath of a previously more complex predator-prey web. Southern California commercial fisheries have severely depleted *Scomber japonicus* and Pacific sardine, *Sardinops sagax*, populations (MacCall et al. 1976), both natural prey for blue sharks (author unpubl. data). Although such declines in major forage species may have resulted in increased predation on anchovies, the southern California population is apparently in little danger of overexploitation by commercial fisheries or pelagic fish predators (Pinkas et al. 1971; Mais 1974; MacCall et al. 1976).

Fishes associated with inshore habitats were also taken by sharks. Jack mackerel, *Trachurus symmetricus*, are widely distributed throughout the Gulf of Alaska (Miller and Lea 1972), and inhabit both inshore and pelagic habitats (Feder et al. 1974). In southern California waters, adults of this species generally aggregate near the bottom or under kelp forests at rocky banks and shallow coastal areas during daylight and venture into deeper waters at night. Only rarely do jack mackerel form sizeable surface schools in the open sea (Mais 1974). Similarly, smaller jack mackerel (e.g., near 25 cm TL), common at inshore areas of Catalina, swam along the outer edges of kelp beds during the day in closely spaced schools and sometimes aggregated within the kelp forest proper. At night jack mackerel occurred in open waters (away from kelp) often interspersed with *Scomber japonicus*. Larger pelagic individuals might represent a schooling prey source for blue sharks in open waters, but stomach content data indicate this was not the case near Catalina. Neave and Hanavan (1960) described concurrent expansion of blue shark and jack mackerel ranges in the Gulf of Alaska during the summer, although no data was presented on possible predator-prey interactions.

Pipefish were the second most frequent fish prey for sharks in this study and a principal prey for blue sharks off Newport Beach (Bane 1968), but because of their small biomass must be regarded as a prey species of minor importance. Free-swimming pipefish were observed at the surface in open water (far from surfgrass or kelp beds) at night, among flotsam kelp during daylight, and during daytime scuba dives in kelp forest and

surfgrass, *Phyllospadix torreyi*, habitats along the shore of the island. The occurrence of pipefish at the surface in the San Pedro Channel at night and the fact that sharks containing freshly ingested pipefish were captured 2-5 km from the island imply that this prey was most likely taken in waters away from inshore kelp and surfgrass habitats.

Freshly ingested blacksmith, *Chromis punctipinnis*, were recovered from a shark captured near Ship Rock at noon. At Catalina, this planktivorous damselfish formed midwater feeding aggregations at the outer edges of the kelp forest during the day, and at times ranged seaward up to 100 m from the nearest kelp. At dusk, blacksmith retreated to the protection of rocks and crevices (see Quast 1968; Hobson 1976). Blue sharks frequented waters near exposed kelp stands at Ship Rock and have been reported chasing and feeding on blacksmith during the day (Sciarrotta and Nelson 1977, Given[5]).

With the exception of *Mastigoteuthis pyrodes*, *Vampyroteuthis infernalis*, and nonspawning *Loligo opalescens*, all of the cephalopod prey species (or their congeners for which data are available) occur near the surface at night through vertical ascent from greater depths or by normal epipelagic distribution (Roper and Young 1975; Tricas 1977). *Mastigoteuthis pyrodes* (mesopelagic) and *V. infernalis* (bathypelagic) occasionally migrate to the lower limits of the epipelagic zone at night (Roper and Young 1975).

In their study of blue shark movements near Catalina, Sciarrotta and Nelson (1977) described evening-twilight shoreward movements of sharks from late March through early June and suggested the change in movement patterns as a response to seasonal increases of inshore spawning squid and decreases in availability of pelagic fishes offshore. Such movements, however, may not be strictly food related. For example, daily inshore-offshore migrations of sharks (late March through early June) would not be synchronous with the cold-water winter peak (December through February) of inshore squid spawning activity near the Isthmus. Also, some sharks observed during this study fed among spawning squid schools throughout the day and therefore did not exhibit the diel inshore-offshore movement pattern. Furthermore, sharks fed upon anchovies in offshore waters throughout the year and there is no indication that the availability of anchovies or jack mackerel to blue sharks significantly changed over the course of this study.

Detection of prey by sharks is often dependent on the reception of abnormal or unusual stimuli such as low-frequency vibrations of struggling or fleeing fishes (Nelson and Gruber 1963; Nelson and Johnson 1972). In addition, olfaction plays a well-documented role in location of injured, stressed, or bleeding prey (Tester 1963; Hobson 1963). Ultimately, however, vision (Gilbert 1963) and possibly electroreception (Kalmijn 1971) are the principal senses used immediately prior to attack. For blue sharks in a normal nocturnal feeding mode, it is probable that search images are formed for a general size rather than for a particular species. Pipefish, for example, were relatively small in biomass, but represented a length characteristic of other prey species. Similarly, most cephalopods in the diet fell within the common prey size range (e.g., 5-25 cm TL). Bioluminescent trails of darting anchovies and other small fish and squid were frequently seen while snorkeling at night in offshore waters and likewise would be readily visible to sharks. Also, the majority of cephalopod species taken by sharks possessed photophores. Bioluminescence associated with prey movements and light organs may represent significant predatory cues for sharks at night.

ACKNOWLEDGMENTS

Thanks to D. R. Nelson for his assistance and to R. Given and R. Zimmer of the Catalina Marine Science Center, F. G. Hochberg, Santa Barbara Museum of Natural History, and L. Pinkas, California Department of Fish and Game, provided helpful suggestions and access to their cephalopod collections. J. Goldsmith, Marineland of the Pacific, provided sharks and facilities for the digestion rate studies. Thanks to C. Shoemaker for her help in the field, J. McKibben for his technical assistance, and H. Izuta Tricas for her help in preparation of the manuscript. E. S. Hobson and J. C. Quast constructively criticized the manuscript. Special thanks to F. Banting and C. Best for their contribution that made this work possible. Financial support was granted by the Office of Naval Research through contract N00014-75-C-0204, under project NR-104-062, for the program of shark research of which this study is a part.

[5]R. Given, Catalina Marine Science Center, P.O. Box 398, Avalon, CA 90704, pers. commun. July 1977.

LITERATURE CITED

BANE, G W
1968 The great blue shark Calif Curr. 1(1):3-4

BIGELOW, H B, AND W C SCHROEDER
1948. Sharks. *In* J Tee-Van, C M Breder, S F Hildebrand, A E Parr, and W C Schroeder (editors), Fishes of the western North Atlantic, Part one, p. 59-546. Mem Sears Found Mar Res , Yale Univ. 1.

CASEY, J G
1976 Migrations and abundance of sharks along the Atlantic coast. *In* W Seaman, Jr (editor), Sharks and man—a perspective, p 13-14. Fla. Sea Grant Program, Rep. 10

CLARKE, M R
1962. The identification of cephalod "beaks" and the relationship between beak size and total body weight. Bull Br. Mus (Nat Hist), Zool 8:419-480

CLARKE, M R , AND J D STEVENS.
1974 Cephalods, blue sharks and migration J Mar Biol. Assoc U K 54:949-957

COUCH, J
1862 A history of the fishes of the British Islands Vol 1, p 26-36, 41-44 Groombridge and Sons, Lond

COUSTEAU, J Y , AND P COUSTEAU
1970 The shark splendid savage of the sea Doubleday and Co , Garden City, N Y , 277 p.

FEDER, H M , C H TURNER, AND C LIMBAUGH
1974 Observations on fishes associated with kelp beds in southern California Calif Dep Fish Game, Fish Bull 160, 144 p

FERREL, D W , D R NELSON, T C SCIARROTTA, E A STANDORA, AND H C CARTER
1974 A multichannel ultrasonic biotelemetry system for monitoring marine animal behavior at sea ISA (Instrum Soc Am) Trans 13:120-131

GILBERT, P W
1963 The visual apparatus of sharks *In* P W Gilbert (editor), Sharks and survival, p 283-326 D C Heath and Co , Boston

HOBSON, E S
1963 Feeding behavior in three species of sharks Pac Sci 17:171-194

HOBSON, E S , AND J R CHESS
1976 Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California Fish Bull , U S 74:567-598

KALMIJN, A J
1971 The electric sense of sharks and rays J Exp Biol 55:371-383

LEBRASSEUR, R J
1964 Stomach contents of blue shark (*Prionace glauca* L) taken in the Gulf of Alaska J Fish Res Board Can 21:861-862

LO BIANCO, S
1909 Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del golfo di Napoli Mitt Zool Stn Neapel 19:666-667

MACCALL, A D , G D SFAKTER, AND J-P TROADEC
1976 Southern California recreational and commercial marine fisheries Mar Fish Rev 38(1):1-32

MAIS, K F
1974 Pelagic fish surveys in the California current Calif. Dep. Fish Game, Fish Bull 162, 79 p

MILLER, D J., AND R N LEA
1972. Guide to the coastal marine fishes of California Calif Dep Fish Game, Fish Bull. 157, 235 p

NEAVE, F., AND M G. HANAVAN.
1960 Seasonal distribution of some epipelagic fishes in the Gulf of Alaska region J Fish Res. Board Can 17:221-233.

NELSON, D R
1974 Ultrasonic telemetry of shark behavior Nav Res Rev. 27(12):1-21.

NELSON, D R , AND S H GRUBER
1963 Sharks: Attraction by low-frequency sounds Science (Wash), D C):142-975-977.

NELSON, D R , AND R H JOHNSON
1972 Acou-tic attraction of Pacific reef sharks Effect of pulse intermittency and variability Comp Biochem. Physiol 42A:85-96

PINKAS, L , M S OLIPHANT, AND I L K IVERSON
1971 Food habits of albacore, bluefin tuna, and bonito in California waters Calif Dep Fish Game, Fish Bull 152, 105 p

QUAST, J C
1968 Observations on the food of the kelp-bed fishes *In* W J North and C L Hubbs (editors), Utilization of kelp-bed resources in southern California, p 109-142 Calif Dep Fish Game, Fish Bull 139

ROPER, C F E , AND R E YOUNG
1975 Vertical distribution of pelagic cephalopods Smithson. Contrib Zool 209, 51 p

SCHULTZ, L P , AND M H MALIN
1963 A list of shark attacks for the world *In* P W Gilbert (editor), Sharks and survival, p 509-567 D C Heath and Co , Boston

SCIARROTTA, T C , AND D R NELSON
1977 Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California Fish Bull , U S 75:519-528

SOKAL, R R , AND F J ROHLF
1969 Biometry W H Freeman and Co , San Franc , 776 p

STEVENS, J D
1973 Stomach contents of the blue shark (*Prionace glauca* L) off south-west England J Mar Biol Assoc U K 53:357-361
1976. First results of shark tagging in the North-east Atlantic, 1972-1975 J. Mar Biol Assoc U K 56:929-937

STRASBURG, D W
1958 Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean U S Fish Wildl Serv , Fish. Bull 58:335-361

TESTER, A L
1963. The role of olfaction in shark predation Pac Sci 17:145-170

TRICAS, T C
1977 Food habits, movements, and seasonal abundance of the blue shark, *Prionace glauca* (Carcharhinidae), in southern California water M S Thesis, California State Univ , Long Beach, 79 p

WEEKS, A
1974 Shark! NOAA 4(1):8-13

LIFE HISTORY AND VERTICAL MIGRATION OF THE PELAGIC SHRIMP *SERGESTES SIMILIS* OFF THE SOUTHERN CALIFORNIA COAST

MAKOTO OMORI[1] AND DAVID GLUCK[2]

ABSTRACT

Sergestes similis in the southern California eddy was observed with respect to reproduction, daily and ontogenetic vertical migrations, growth, and longevity. The period of highest spawning activity occurs between late December and early April, but small pulses of spawning are occasionally observed in late spring and summer. The release of eggs takes place close to shore above the continental slope, and then the eggs sink to 200 m or deeper. Nauplius larvae ascend and protozoeal and zoeal larvae stay mostly above 100 m. The daily vertical migration becomes evident after the second protozoeal stage. Adults are abundant between 50 and 200 m at night and 250 and 600 m in the daytime.

The spawning activity of *S. similis* becomes highest during the period when the vertical thickness of the optimum temperature zone (10°-15° C) is the greatest. The authors speculate that the local population off the southern California coast may be joined by the subarctic population. It is possible that multiple spawnings occur from females of the southern California population.

The lifespan of *S. similis* is 2.0-2.5 years for females and about 1.5 years for males. Sexual maturity is reached at about 1 year in both sexes. Females reproduce in two successive spawning seasons, and males seem to accomplish multiple fertilizations. Growth trends are similar to those reported for *S. similis* off Oregon. Growth rates are described using growth curves fitted by the von Bertalanffy and logistic equations.

Sergestes similis Hansen is the most abundant, oceanic, pelagic shrimp in the North Pacific Drift, lat. 40°-50° N. This subarctic to transitional species occurs mainly in waters whose temperature ranges between 3° and 12°. Its distribution extends from Japan to the coast of North America as far south as lat. 27°N (Pearcy and Forss 1969; Omori et al. 1972).

In the cooler part of the California Current, *S. similis* composes a substantial fraction of all microneckton. The adults perform extensive vertical migrations, living between 250 and 600 m in the daytime and ascending to 50-200 m depths at night. According to Barham (1963) and Clarke,[3] *S. similis* is consistently associated with the lower component of a sonic scattering layer off southern California.

Sergestes similis sheds eggs in the sea. From eggs hatch the first of four naupliar stages (N1-N4), which go on to develop three protozoeal stages (PZ1-PZ3), and two zoeal stages (Z1, Z2) before entering postlarval stages (PL) (Omori 1979).

Sergestes similis plays an important role in the dynamics of northern Pacific oceanic ecosystems. As an adult, it feeds mainly on copepods and euphausiids and is, in turn, preyed upon by squids, mesopelagic fishes, rockfishes, albacore, basking shark, and baleen whales (Pereyra et al. 1969; Judkins and Fleminger 1972; Omori et al. 1972; Mutoh and Omori 1978). In certain areas there is a strong possibility that the enormous standing stock can be exploited by commercial fisheries (Omori 1974).

In spite of the great importance of this species, little is known about its life history, especially its reproduction, development, and growth. Although the distribution and daily vertical migration of adult *S. similis* off the coasts of California and Oregon have been studied (Barham 1963; Clarke, see footnote 3; Pearcy and Forss 1966; Davies and Barham 1969; Pearcy et al. 1977), no work has been done on the biology of larval and early postlarval stages. Details of the spawning season and lifespan of the species have not yet been confirmed. Barham (1957) stated that *S. similis* in Monterey Bay, Calif., reached maturity at age 1 yr and dis-

[1]Institute of Marine Resources, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, Calif.; Ocean Research Institute, University of Tokyo, Nakano, Tokyo, Japan, present address: Division of Marine Sciences, UNESCO, Place de Fontenoy, 75700 Paris, France.

[2]Institute of Marine Resources, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, Calif.; present address: Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

[3]Clarke, W. D. 1966. Bathyphotometric studies of the light regime of organisms of the deep scattering layers. U.S. AEC Res. Dev. Rep. UC48, Biol. Med., TID-4500, 47 p.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

appeared after spawning. He found that the two size-groups, which spawned in December-January and June-July, respectively, showed the same developmental history but 6 mo out of phase with each other. On the other hand, *S. similis* off the Oregon coast spawned during most of the year but predominantly during the winter and spring, with the individuals living for about 1 yr (Pearcy and Forss 1969). Genthe (1969) determined that the lifespan for the southern California population is 2 yr and that the maximum breeding activity occurs in the early summer and fall. The disagreement in these conclusions is mainly due to two factors: first, the difficulty of sampling a nonrandomly distributed population which moves both horizontally and vertically with time and spatial location; and second, the lack of knowledge about the developmental biology of the larval stages of *S. similis*. Knowledge of the development and growth of larvae and juveniles of *S. similis* has been severely restricted by the difficulties of maintaining this oceanic species under laboratory conditions. Recently, however, Omori (1979) has successfully reared this species from the egg to the eighth postlarval stage. This success prompted us to examine the life history of *S. similis* off southern California and to provide further biological information about its population dynamics.

The present study deals with the reproduction, growth, longevity, and both daily and ontogenetic vertical migrations of *S. similis*. The study area is the southern California eddy, which is bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. The east-west extent of the eddy is about 250 km. This region is the southernmost in which *S. similis* is abundant. The sluggish, cyclonic circulation of this eddy, defining a singular water mass, permits substantial autonomy for the resident population. Complex topography, including a scattering of islands, basins, and canyons in the area, appears to provide substantial swarming grounds for *S. similis*. Because the majority of the population resides in an area such as the southern California eddy, which Brinton (1976) has described as "hydrographically restricted," data on the life history of *S. similis* may be measured more easily than in other oceanic areas.

MATERIALS AND METHODS

In the present study, data on occurrence of the larvae and early postlarvae were determined from examination of California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples.

Samples were obtained from selected stations in CalCOFI cruise 6401 (January-February 1964). Stratified plankton sampling was carried out along three parallel transects: Line 60, Line 90, and Line 100 (Figure 1). The samples were collected by oblique tow to various depths of water with a standard CalCOFI net of 1-m diameter and 0.55-mm mesh openings (Ahlstrom 1948). The mesh size of the cod end and the 40-cm section in front of it was 0.25 mm. Opening-closing net series were obtained to depths of approximately 100 m at three stations and 450 m at one other station on Line 60, and to depths of 400-600 m at all stations on Line 90. Sampling was carried out at whatever time of day the ship arrived on station. Both day and night series, to approximately 600 m depth, were obtained at all station on Line 100. In the present study the samples obtained from the usual habitat of *S. similis*, i.e., above 400 m depth, were examined (Table 1). At each station, usually two to six nets were towed in each of two or three series of tows. The opening and closing of the nets were messenger-activated, using a Leavitt-type device, and a flowmeter was mounted within the mouth of each net. A net filtered an average volume of about 600 m^3/tow. A trace of depth vs. time was made during the course of a tow by a recorder attached near the bottom net. For a detailed description of the sampling procedure and the analysis of depth recorder traces, see Brinton (1967).

The spawning season of *S. similis* was determined by examining CalCOFI standard oblique haul samples obtained at Stn. 90.37 from January 1951 to December 1954. Station 90.37, lat. 33°11'N, long. 118°37'W, was selected because it was located near the center of *S. similis* larval distribution in CalCOFI 6401. Sampling was not conducted in October and December 1952, May, September, and November 1953, and June and September 1954, but sampling from a nearby station, 90.35, was done in May 1953. Details of this sampling method are described by Ahlstrom (1948) and Fleminger (1964). The net was towed obliquely between the surface and a depth of about 140 m while the ship proceeded at a speed of about 2 kn. As explained later, this sampling depth covered the entire vertical distribution of protozoeal and zoeal stages of *S. similis*. Because free eggs and nauplii of *S. similis* are <0.5 mm, they were not retained by the CalCOFI net. Specimens of protozoeal stages were retained by the fine meshes

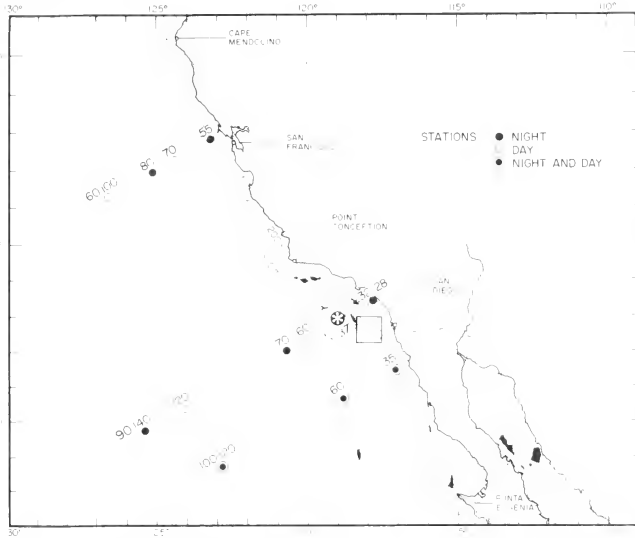


FIGURE 1.—Sampling stations for *Sergestes similis* off southern California. Circles indicate stations sampled by stratified opening/closing oblique net hauls with CalCOFI net (CalCOFI 6401, January-February 1964). Line 60 (Stn. 60 55, 60 70, 60 80, and 60 100) extending southwestward from Pt. Reyes, Calif.; Line 90 (Stn. 90 28, 90 32, 90 37, 90 60, 90 70, 90 120, and 90 140) extending southwestward from Dana Pt., Calif.; and Line 100 (Stn. 100 35, 100 60, and 100 120) extending southwestward from Punta Banda, Baja California. Number 37 (flowered circle) marks Stn. 90 37 at which monthly CalCOFI standard oblique haul samples were obtained. The square indicates the area of IKMT trawls.

TABLE 1.—Summary of data from stratified plankton sampling off southern California with standard CalCOFI net (CalCOFI cruise 6401, January-February 1964).

Station	Period	Depths covered by series of tows	Number of stratified samples	Date	Towing times including 2-3 series of tows	Light condition
60 55	Night	0-108	3	31 Jan	2316-0056	Dark
60 70	Day	0-450	10	1 Feb	1241-1455	Clear
60 80	Night	0-72	4	1 Feb	2024-2044	Dark
60 100	Day	0-108	6	2 Feb	0829-1003	Clear
90 28	Night	0-80	4	6 Feb	0342-0407	Clear, ½ moon
90 32	Day	0-140	8	6 Feb	0854-1052	Clear
90 60	Day	0-373	8	7 Feb	1053-1346	Clear
90 70	Night	0-100	5	7 Feb	2044-2149	Dark
90 120	Day	0-490	8	9 Feb	1345-1640	60-90% clouds
90 140	Night	0-132	6	9 Feb	2330-2356	Dark
100 35	Night	0-236	7	16 Feb	2242-0106	Dark
	Day	0-400	9	17 Feb	0715-0903	Clear
100 60	Night	0-260	8	16 Feb	0041-0300	Dark
	Day	0-355	9	16 Feb	0930-1140	95% clouds
100 120	Night	0-185	6	14 Feb	0203-0538	Dark
	Day	0-500	8	14 Feb	1051-1302	60% clouds

of the posterior part of the net and were thus counted as being indicative of their general occurrence.

Juvenile and adult *S. similis* were collected by a 6-ft (1.8-m) Isaacs-Kidd Midwater Trawl (IKMT), having mesh width of 2 mm, on the continental slope of the San Diego Trough, Calif., at five occasions in 1976 and 1977. Sampling was done at night and daytime by releasing the cable at 50m/min until the net reached a desired depth and then retrieving. Ship speed was 4 kn while the net was sinking, and 2 kn during the retrieval. Usually the biomass of shrimp was large when the net was towed at the depths of 50-200 m at night and 250-600 m in the daytime. To fill in gaps where sampling was sparse and to provide more information on reproduction and growth of *S. similis*, six IKMT collections from the SIO (Scripps Institution of Oceanography) Invertebrate Collection were examined. These samples were all collected by 10-ft IKMT with mesh width of 5 mm between lat. 32°28'N and 33°15'N and long. 117°29'W and 118°38'W (Table 2).

TABLE 2.—Summary of data from sergestid sampling with Isaacs-Kidd Midwater Trawl off southern California. Six-foot IKMT with 2-mm mesh size; 10-ft trawl with 5-mm mesh size

Date	Local time	Location Lat	Location Long	Estimated depth of haul (m)	IKMT (ft)
26 Jan 1977	1915-1935	32°44'N	117°30'W	0-200	6
3 Mar 1977	1810-1836	32°43'N	117°29'W	0-250	6
12 Apr 1972	2206-2345	33°15'N	118°38'W	0-500	10
21 Apr 1977	0332-0414	32°47'N	117°29'W	0-300	6
21 June 1957	1601-1937	32°37'N	118°13'W	0-1490	10
27 July 197[illegible]	1725-2320	32°28'N	117°56'W	0-800	10
19 Aug. 1976	1800-1830	32°[illegible]'N	117°29'W	0-300	6
24 Aug. 1954	2400-0400	33°[illegible]0'N	117°35'W	0-549	10
28 Oct 1972	1800-1900	32°[illegible]5'N	117°30'W	0-500	10
29 Oct 1976	2000-2100	32°[illegible]0'N	118°20'W	0-350	6
8 Nov. 1975	1600-[illegible]	32°36'N	117°20'W	0-500	10

An aliquot of [illegible] to [illegible] each CalCOFI sample was examined, and the number of individuals of each developmental stage from the first protozoeal stage to the second zoeal stage was counted. Postlarvae having a body length (BL) < 5.0 mm (stages I-VI) were classified together as early postlarvae. In order to increase accuracy, if the initial aliquot contained only two or fewer individuals of any particular stage, a second aliquot of equal size was examined for specimens of that stage. All counts were then standardized for 1,000 m^3 of water filtered by the net. An estimate of the total number of individuals of each stage beneath 1 m^2 of sea surface was made using the equation,

$$n = \frac{N}{1000} \times d$$

where n is number of individuals per square meter, N is the number of individuals/1,000 m^3, and d is the depth of the stratum sampled. Data on physical and chemical environments were obtained from "Oceanic observations of the Pacific" 1951-53 (Scripps Institution of Oceanography 1963, 1965a, b) and "CalCOFI cruise 6401 data report" (Scripps Institution of Oceanography[4]).

In January and March 1977, a small number of healthy females carrying well-developed eggs in their ovaries were removed from the IKMT collection to be used for spawning and rearing experiments. They were transferred immediately after sampling to chilled filtered seawater in large containers and were brought back to the laboratory. The spawning of eggs was observed individually. The sinking speed of the eggs over a 70-cm distance was measured at 10° and 14°C in a constant temperature room using a graduated glass cylinder of 70-mm diameter. Seawater used for the experiment was obtained at the station where ovigerous females were collected. It was filtered through Millipore[5] filters HA (0.45 μm). Salinity was 33.72‰.

The remaining specimens in the IKMT collections were preserved in 5% Formalin-seawater. Most specimens of *S. similis* having carapace lengths (CL) > 5.0 mm were sorted, counted, and sexed. The carapace length from the tip of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.5 mm.

Change through time in the carapace length-frequency histograms of *S. similis* was graphically analyzed using probability paper (Harding 1949; Cassie 1954). In order to compare the growth trends of the *S. similis* population off southern California with trends in other waters, previous data on the size-frequency distribution of *S. similis* reported by Genthe (1969), Pearcy and Forss (1969), Omori et al. (1972), and Mutoh and Omori (1978) were reanalyzed to obtain average or modal carapace lengths[6] for the populations at

[4]Scripps Institution of Oceanography. 1965. Physical and chemical data CalCOFI cruise 6401, 10 January-4 March 1964. SIO Ref. 65-7, 76 p.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6]BL-CL regression of *Sergestes similis* (< 5.5 mm CL) are as follows

different sampling dates and locations. The von Bertalanffy and logistic equations were used to fit these growth data.

RESULTS

Daily and Ontogenetic Vertical Migrations of Larvae and Early Postlarvae

Coastal upwelling is generally weak in southern California during the winter (Bakun 1973). This is consistent with the data on environmental properties at the sampling stations (Figure 2). The thermocline remained at about 75 m at all stations on Line 60 with the mixed layer temperature ranging from 11.5°C inshore to 14.0°C offshore. Salinity was usually < 33.30‰ in water above 75-m depth. On Line 90, except for the two outermost stations, the thermocline was at 30-50 m and the temperature within the mixed layer was >13.5°C. Salinity was >33.20‰ at all depths. On Line 100 the thermocline was at about 50 m at Stn. 100.35 and 100.60. Temperature within the mixed layer was about 15°C, and salinity was >33.50‰. The position of the oxycline coincided with that of the thermocline at nearly all stations. Generally, the oxygen level at depths below the mixed layer increased going seaward.

The main population of *S. similis* larvae was always between the surface and 100-m levels, and they occurred in greater abundance at stations on the continental slope (Figure 3). The population density was highest at Stn. 90.32 (101 individuals m^3). The larvae did not occur at Stn. 90.120, 90.140, and 100.120. In these southern offshore stations the temperature above 100 m was >16°C. The temperature-salinity curves characterized the water mass as eastern North Pacific Central water, where *S. similis* has never been found. In this water mass, the "ortmanni type" larvae (the *Sergestes corniculum* group, see Yaldwyn 1957 and Omori 1974) were commonly distributed.

The vertical distributions of larvae and early postlarvae from eight stations where they were abundant shows that the larvae were scattered from 20 to 100 m during the daytime (Figures 4, 5). On Line 90, the distribution pattern did not coincide well between the stations closest to shore (Stn. 90.28 and 90.32) and the offshore stations (Stn. 90.60 and 90.70). At Stn. 90.60 in the daytime, the larvae were widely distributed throughout the 0-110 m layer, but larvae occurred only between 44 and 88 m at Stn. 90.32 during the day. The greatest population density observed was within the 66-88 m layer at Stn. 90.32 (about 3,500 individuals 1,000 m^3). Nighttime larval distribution was between 20 and 90 m at Stn. 90.70, but again, it was below 40 m at the closest inshore station. A similar inshore and offshore assemblage was observed along Line 100, although the vertical distribution of the larvae was expanded more widely. At Stn. 100.35 the larvae were most abundant between 50 and 100 m in the daytime and 0 and 80 m layer at night. On the other hand, at Stn. 100.60 the main population in the daytime occurred between 20 and 120 m, while at night the distribution ranged from the surface to 140 m with considerable numbers in the 0-40 m layer. At both stations, there was a clear daily vertical migration of the main population of zoeal and postlarval stages.

With the present sampling method, there was some doubt whether the same population was measured by day and night tows. However, as indicated in Figures 4 and 5, the estimates of abundance beneath 1 m^2 of sea surface did not differ appreciably between day and night at the two closest stations on Lines 60 and 90 and between day and night tows at the same station on Line 100. It can be said, at the least, that the avoidance of nets by larvae in the daytime was no greater than at night.

When abundance vs. depth is combined and averaged for each larval stage at each station, the extent of daily vertical migration becomes clear. The first protozoeal stage shows at least a restricted daily vertical migration (Figure 6). The larvae gradually increase their range of vertical distribution with growth while gradually inhabiting deeper water. Thus, the main population of early postlarva (40-45 m at night and 70-75 m in the daytime) shows a deeper distribution than earlier larval stages.

Eggs of *S. similis* (about 0.3 mm in diameter) were slightly heavier than the density of the experimental water; the difference in sinking rates was not significant at the 5% level between 10° and 14°C under laboratory conditions (Table 3).

BL = 3.15 + 2.85 CL for females,
BL = 2.55 + 3.11 CL for males (Omori et al. 1972)
The regression for juveniles with carapace length 5.5 mm or less is
BL = 3.08 CL

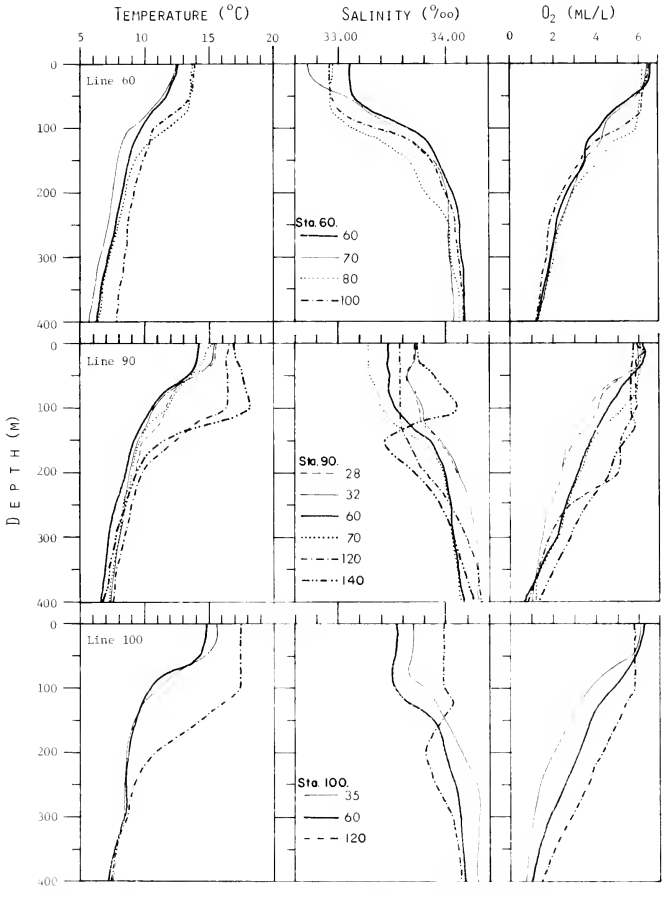


FIGURE 2.—Vertical profiles of temperature, salinity, and oxygen on CalCOFI Lines 60, 90, and 100, January-February 1964, off southern California

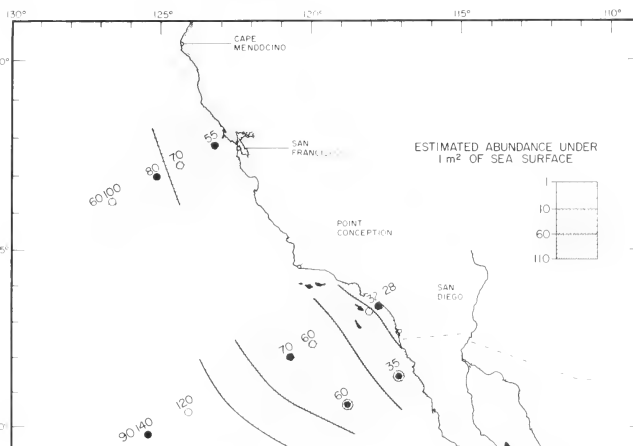


FIGURE 3.—Distribution and abundance of *Sergestes similis* larvae from January to February 1964. Estimated abundance is expressed as number of individuals beneath 1 m² of sea surface in depths between 0 and 100 m.

TABLE 3.—Experimental data on sinking velocity of eggs of *Sergestes similis* in water of salinity 33.72‰. Difference in sinking rates is not significant at the 5% level.

Temperature (°C)	Replicates	Sinking velocity (m·h)		
		Average	SD	Range
10	9	1.45	0.44	0.91-2.19
14	9	1.81	0.52	1.04-2.99

Spawning Season

The highest spawning of *S. similis* took place from late December to early April. Protozoea larvae occurred most abundantly between January and April at Stn. 90.37 (Figure 7), but were not found in samples collected in November and December. During 1951-54, a number of PZ2 and PZ3 appeared each year between January and July, but the occurrence of PZ1 was restricted to January-April, except for August 1952 and July 1954. Although one-third of the autumn months were not represented by samples, these months were scattered enough to make the data significant. Seasonal abundance of zoeal stages duplicated that of PZ1. Early postlarvae were found in plankton from February to early July. Considerable numbers of PZ1 and PZ2 (< 1.3 mm BL) apparently passed through the mesh of the CalCOFI net, as their measured population densities were almost always lower than those measured for PZ3.

The optimum temperature range for larval development is 10°-15°C (Omori 1979), and the highest temperature at which adult *S. similis* occur is 13°C. Thus, the best temperature for the larvae is close to the upper temperature limit of the adult's habitat. Furthermore, comparison of the reproductive activity of *S. similis* with physical and

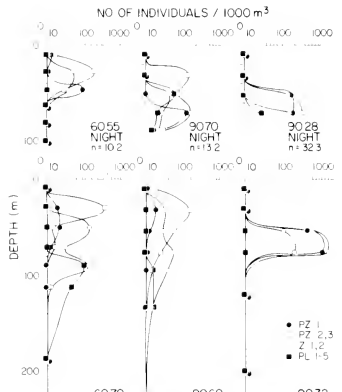


FIGURE 4.—Vertical distribution of larvae and postlarvae of *Sergestes similis* on CalCOFI Lines 60 and 90 off southern California. PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

chemical environmental data indicates that there is a relationship between temperature and spawning season (Figure 7). Spawning activity was highest during the period when the vertical stratum of optimum temperatures for larvae was thickest. It decreased before colder water was brought in by coastal upwelling which was normally most intense from May to August (see Bakun 1973). A seasonal minimum, or cessation, of spawning occurred during the summer and autumn when the upper layer was covered by unfavorably warm temperatures (>15°C).

Growth

Because of the smaller mesh size, the 6-ft IKMT retained a larger proportion of small shrimp than did the 10-ft IKMT (Figure 8). While specimens of 4 mm CL occurred in the smaller net, few < 7 mm were retained in the larger net.

Well-defined progressions of size-frequency modes gave indications of average growth rates for certain cohorts, although we sometimes encountered difficulties in interpreting these trends due to inadequate sampling, and possibly to extended spawning of the species. One 1975 cohort (12.0-14.5 mm CL) and two conspicuous 1976 cohorts (5.0-11.0 mm CL) were seen in females collected in August 1976 (Figure 8A). The former cohort was not found in the following two samplings. The large-sized 1976 cohort (mean modal length, 8.4 mm CL in August) reached 9.9 mm CL in October, 10.5 mm CL in January, and 11.8 mm CL in March 1977. Growth of the small-sized cohort was traceable until April 1977, when the shrimp attained an average carapace length of 10.4 mm. Recruitment of postlarvae < 6.0 mm CL (1977 cohort) was intense in April. The histogram for March showed only a single mode of males, and it is not possible to

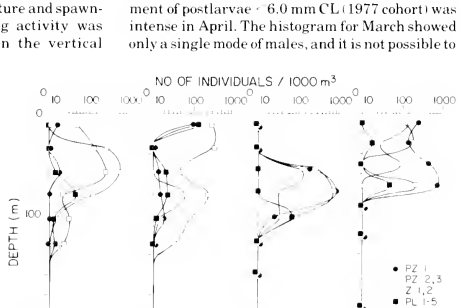


FIGURE 5.—Vertical distribution of larvae and postlarvae of *Sergestes similis* at CalCOFI Stn 100 35 and 100 60 off southern California. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

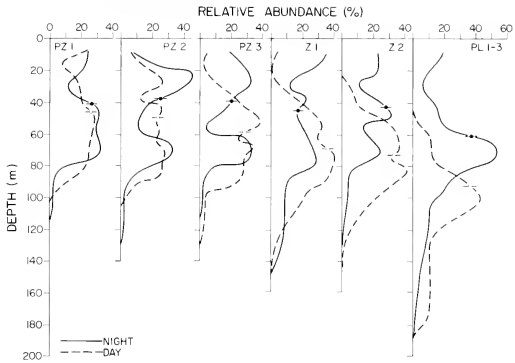


FIGURE 6.—Vertical distribution of larvae and postlarvae of *Sergestes similis* off southern California. Abundance vs. depth at all sampling stations was combined and averaged. Horizontal line indicates the depth at which the cumulative catch represented 50% of the total catch. PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages.

say whether this 1976 cohort represents the large-sized group or not. In the 10-ft IKMT samplings the most conspicuous female cohort of 10.5-13.0 mm CL in April reached 13.5-15.5 mm CL in October (Figure 8B). The males grew from an average 10.8 to 11.7 mm CL between April and August. In many cases, the size structure of the population showed the presence of only one or two obvious size groups, but in three cases (April 21, June 21, and July 29) the histograms of females indicated three size groups. Development of the smallest cohort of 0 age-group was traceable until August in both females and males, but in October and November, two cohorts of 0 age were apparent.

Some estimates of growth were attempted using changes in the average or modal lengths in various months. In order to show the growth trend more definitely, the results of all previous length measurements of *S. similis* from various waters were reanalyzed and the average or modal lengths for each size group were plotted together with the present data (Figure 9). Except for the points derived from the offshore population in the subarctic North Pacific, where the environment is quite different from that of southern California, the majority of cohorts had average or modal lengths which fell within the growth curves of three year classes fitted by eye.

These data indicate the following: 1) as expected from spawning season data, in most cases the modal progressions are evident starting in winter or early spring, 2) growth trends of *S. similis* off southern California appear similar to the population off Oregon (Pearcy and Forss 1969), and 3) growth rates do not vary greatly among many different populations, although there is evidence that a few modal groups grew about twice as rapidly as the ordinary one.

The ratio of females to males in all collections was 1.3:1 (553:422). Sex ratio in a cohort was not skewed greatly towards females until the modal length of the female population reached about 13 mm CL. At that point, the males of the cohort rapidly disappeared from the collection, accounting for the observed imbalance in sex ratio (69:2).

DISCUSSION

Ontogenetic Migration

Omori (1979) found experimentally that: 1) ovigerous females of *S. similis* shed their eggs at night, 2) the eggs took 105 h to hatch into nauplii

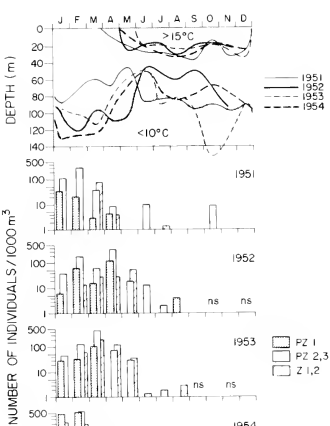


FIGURE 7.—Isotherms of 10°C and 15°C and occurrence of larvae of *Sergestes similis* at CalCOFI Stn. 90.37, 1951-54, off southern California at 0-140 m. Shadow indicates zones where temperatures exceed the average 10°-15°C range of 1950-55. No sampling indicated by ns. PZ, protozoeal stages; Z, zoeal stages.

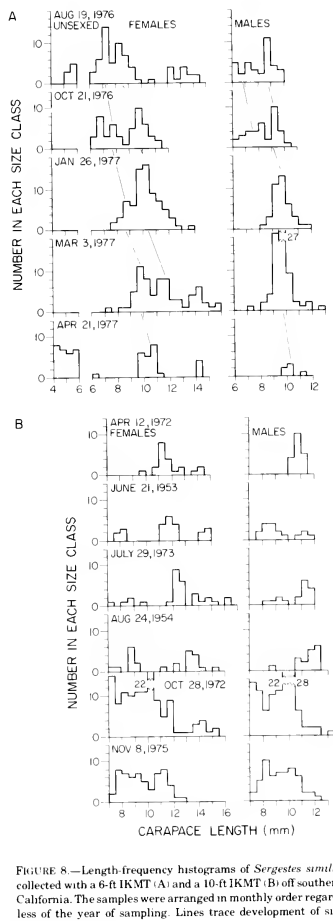


FIGURE 8.—Length-frequency histograms of *Sergestes similis* collected with a 6-ft IKMT (A) and a 10-ft IKMT (B) off southern California. The samples were arranged in monthly order regardless of the year of sampling. Lines trace development of significant cohorts.

at 10°C, and 3) mortality increased greatly in temperatures beyond 10°-15°C. We do not know the depth where spawning and hatching of *S. similis* take place in the natural habitat. However, the laboratory observations, coupled with biological information on the other species of sergestids and euphausiids (Omori et al.[7]), indicate that the eggs of *S. similis* are shed in shallow water at night when ovigerous females rise upwards. Adult *S. similis* seldom occur above the 50-m level at night where the temperature is usually >13°C off southern California. Assuming that

[7]Omori, M., M. Mutoh, and M. Kaetsu. 1974. Prediction of *Sergia lucens* fishery in 1974/75 season. [In Jpn.] Unpubl. manuscr., 5 p., distributed at the annual meeting of the "Sakura-ebi" Fishing Unions, Shizuoka Prefecture, Japan.

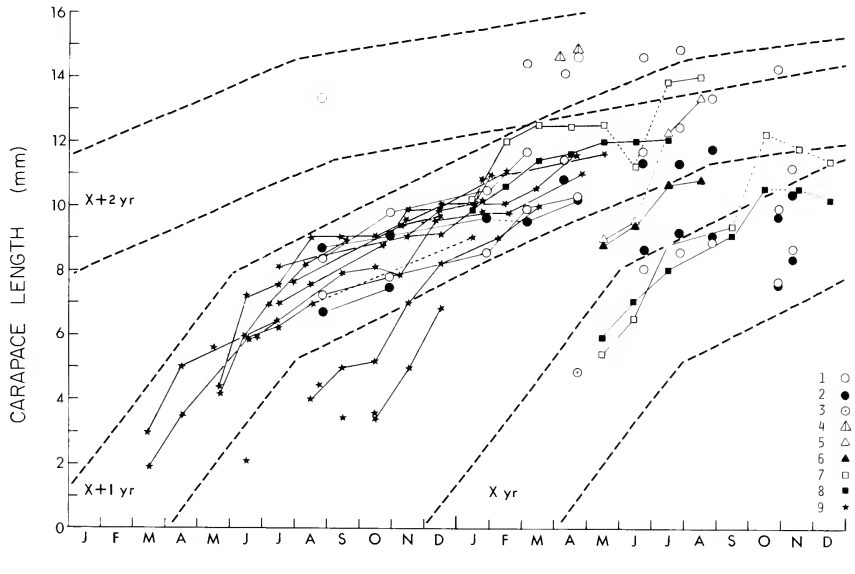


FIGURE 9.—Growth trends in different waters of *Sergestes similis*, derived from average modal length of different cohorts. Solid and dashed lines trace development of cohorts. Solid lines trace sequences considered clear, dashed trace those less clear. Data sources: 1, present study, female; 2, the same, male; 3, the same, unsexed juvenile; 4, off Japan, female (Mutoh and Omori 1978); 5, subarctic North Pacific, female (Omori et al. 1972); 6, the same, male; 7, off southern California, female (Genthe 1969); 8, the same, male; 9, off Oregon, sexes combined (Pearcy and Forss 1969).

spawning takes place around 50 m and using data on both the sinking velocity of the eggs and the development time of eggs at 10°C, we can estimate that the eggs sink to about 220-m depth before hatching. The ambient temperatures which eggs may encounter during their descent are 7°-13°C. It is probable that some eggs are laid deeper than 50 m. However, like the population off the Oregon coast (Pearcy and Forss 1969), *S. similis* is seldom distributed over the continental shelf off southern California. Therefore the majority of eggs would not sink to the bottom but remain within the water column.

A comparison of vertical distribution patterns at all stations confirms the following hypotheses: 1) the occurrence of larvae is restricted to water <140 m where the temperature range is 9°-16°C, 2) the larvae often appear in the 0-20 m level at night but rarely in the daytime, and 3) the larval distribution is more restricted inshore than offshore to a limited vertical range. The descent of eggs and ascent of naupliar larvae are well documented in the oceanic euphausiid *Euphausia superba* and *Meganyctiphanes norvegica* (Mauchline and Fisher 1969). Presumably the nauplii of *S. similis* rise from 200 m or deeper to layers where the temperature is usually >10°C. In this manner, the nauplius, which is probably highly vulnerable to predation, develops in the less hazardous layers which are deeper than the following larval stages. Protozoeal and zoeal larvae stay mostly in the shallower environment which is relatively rich in food (phytoplankton and microzooplankton). They perform daily vertical migration starting PZ1, and their downward migration at daytime becomes more marked with each stage. This hypothesis is further supported by the positive phototaxis in N3 to PZ1 larvae and negative phototaxis after PZ2 observed in the laboratory (Omori 1979).

According to Omori (1974), the larvae of pelagic shrimps can be classified into several types on the basis of their ontogenetic migration. The first group is composed of the species living in the epipelagic and upper mesopelagic zones. Their larvae perform migration within the euphotic zone. *Sergestes similis* belongs to this group, having a similar pattern to that described for *Sergia lucens* (Omori 1974), but the negatively buoyant eggs of *Sergestes similis* differ from *Sergia lucens* eggs which have density similar to seawater.

Adult *Sergestes similis* were abundant inshore off Oregon during the winter, but they tended to shift to an offshore distribution during the summer (Pearcy and Forss 1969). This inverse relationship between nearshore and offshore stations indicates a horizontal ontogenetic migration of this species by active swimming with the help of subsurface currents. The movement by a species to nearshore regions for spawning is a characteristic behavior among several sergestid shrimps (Omori 1974).

Relationship Between Spawning Season and Environment

Larvae of *S. similis*, in particular PZ1, were more abundant inshore than offshore, which indicates that the spawning of *S. similis* is taking place mainly close to shore above the continental slope off southern California (but not as far inshore as the continental shelf). The assumption by Pearcy and Forss (1969) that *S. similis* in the Oregon population spawns during most of the year with a seasonal minimum occurring during the summer was partially true in the southern California population as there were small pulses of spawning in summer and autumn. However, the southern California adult population appears to be recruited largely from the local population spawned from late December to early April.

One may argue that the decrease of larvae in the study area in summer and autumn was caused merely by the seasonal change off the southern California gyre. It would be interesting to compare our data with samples from stations outside of the northward flowing path of the gyre. However, we do not think that such an extreme absence of larvae in summer and autumn is taking place with the year-round spawning of *S. similis*. At least some larvae should have successfully remained in the study area to yield noticeable recruitment during those months. Incidentally, females having fully developed ovaries (Omori 1979) were seldom found in the IMKT collection from summer and autumn. Genthe (1969) assumed that maximum reproductive activity of *S. similis* from the Santa Barbara Channel was in summer and autumn, but his assertion that juveniles collected in August of 5.0-6.5 mm CL are 11 or 12 mo old is misleading. Shrimp of this size are more likely to be of the 6-7 mo class.

Omori et al. (see footnote 7) studied the relationship between environments and reproductive behavior of another sergestid, *Sergia lucens*, in Suruga Bay, Japan, and found that the com-

mencement of spawning and the survivorship of larvae are closely related to the ambient temperature rather than the quantity of food available. This study showed that: 1) *S. lucens* started spawning in June, immediately after the temperature exceeded 18°C at 20-50 m, and the number of larvae increased with increasing vertical thickness of the optimum temperature zone for the growth of larvae (18°-25°C), 2) the population size of *S. lucens* was determined by the abundance of larvae during the first half of the breeding season, June-August, and 3) the abundance of larvae was often related to the fluctuation in vertical width of the optimum temperature zone. During midsummer the warming of surface waters above to 25°C and the shoaling of cold water <18°C restricted the optimum temperature zone, and consequently the mortality of protozoeal larvae increased.

As with *S. lucens*, a rise in temperature may trigger the commencement of spawning of the *Sergestes similis* population in the northern subarctic waters where surface temperature is <10°C during most of the year. However, this seems not to be the case for the southern California population where favorable temperatures were available year-round in some stations between 50 and 100 m. Yet, the spawning began abruptly when the temperature around 100-m depth began to rise. Abundance of larvae was greatest during the period when the vertical thickness of the optimum temperature zone was the greatest, and spawning activity almost ceased both when the ambient temperature was lowered by coastal upwelling and when warm surface water subsequently appeared. Thus, the spawning season of *S. similis* is not always positively correlated with the upwelling which causes environmental enrichment and subsequent increase of plankton biomass in the southern California eddy. The correlation of spawning to coastal upwelling in *Euphausia pacifica*, another very abundant species of the California Current zooplankton assemblage, is the most striking difference affecting the spawning seasons of that organism and *S. similis*. Similar to *S. similis*, the southern California population of *E. pacifica* seems to be adapted for larval development between 12° and 16°C, but its spawning is highest when coastal upwelling is strongest in May-June (Brinton 1976). Although true mechanisms remain unexplained, we theorize that the distinctive spawning season of *S. similis* in southern California is based mainly on the adaptation of this species to the vertical thickness of optimum temperature. The vertical thickness of the optimum temperature zone was also correlated with the abundance and survival of larvae of *S. similis*. The cumulative depths of the optimum temperature ranges for *S. similis* from January to March were 220, 318, 311, and 380 m from 1951 to 1954 whereas the average numbers of protozoeal larvae occurring from January to April were 129, 218, 224, and 543 individuals/1,000 m^3, respectively. In 1951, zoeal larvae were found in the lowest numbers when the cumulative depth was the smallest.

One possible interpretation of the irregular small pulse of spawning of *S. similis* in seasons other than winter and early spring is that shrimp which reproduce during these periods are carried from northern offshore waters, i.e.,subarctic North Pacific, to the study area. If temperatures of 9°-10°C in the habitat of *S. similis* really trigger the commencement of spawning, those living in subarctic waters would start spawning later than July in most areas. The yearly mean velocity of the eastward component of the North Pacific Drift is about 3 cm/s at the surface in the areas lat. 45°N west of long. 150°W. On the other hand, a strong south-flowing current, which flows at the velocity of 5-10 cm/s but occasionally >20-30 cm/s is observed throughout the year both at the surface and at 200-m depth off the west coast of the United States (Wyllie 1966; Stidd[8]). If part of the population of *S. similis* near lat. 47°N, long. 140°W, e.g., where tremendous numbers are eaten by baleen whales (Omori et al. 1972), is carried southeastward by the currents, the shrimp can easily reach the southern California coast within 2 yr at a mean speed of 5 cm/s of flow. The spawning occurs in the summer off California due to continuous recruitment of such northern populations. An electrophoretic study of *S. similis* population may help to answer this question, although, due to diverse trophic regimes, genetic variability of the southern California population may be too large to distinguish it from the subarctic population (see Valentine and Ayala 1976).

Another possible interpretation is that the phenomenon is caused by the adaptation of the local population to mid latitude irregularities in oceanographic and trophic conditions. It has been observed for several penaeids, sergestids, and euphausiids in temperate and tropical regions

[8]Stidd, C. K. 1974. Ship drift components: means and standard deviations. SIO Ref. 74-33, 57 p.

that the ovary may contain ova at different developmental stages and that not all ova are necessarily released at once (King 1948; Mauchline 1968; Roger 1973; Omori 1974). We observed that *S. similis* off southern California always retained considerable numbers of immature ova after spawning. Because the volume of a pair of mature ovaries from this shrimp represents about 10% of the body volume, we can estimate from the volume of each egg that one female has at least 1,500 but probably closer to 2,000-2,500 eggs. Nevertheless, the number of eggs released by a female in the laboratory was always <1,140 (Omori 1979). Thus, as has been pointed out for *Euphausia pacifica* off southern California (Brinton 1976), it appears possible that under optimal environmental conditions small ova of *S. similis* may develop later and produce a second spawning. If a female, which produced the first clutch in late December, released the second clutch 3-4 mo later, two modal size-groups might be seen sometimes in the same age-group. It is probable that unfavorable environmental conditions would prevent the spent ovary from maturing again until the following year. Further evidence of this phenomenon is provided by the increase in the number of spent females and the decrease in the number of fully grown ova in ovaries of *S. similis* off southern California and Oregon during the summer (Genthe 1969; Pearcy and Forss 1969). The length-frequency histograms in October 1972, November 1975, and from August 1976 to March 1977 (Figure 8) indicate either the occurrence of multiple spawnings for *S. similis* or individuals from farther north being mixed into the southern California population.

Growth, Sexual Maturity, and Longevity

If *S. similis* population is composed of 0 age-group shrimp only and all attain sexual maturity after about 1 yr, the size structure of the population sampled shows the presence of only one or two size groups. However, the obvious occurrence of three size groups of females during certain periods of the year in this study indicates that the females of *S. similis* live 2 yr or more. Large females, 13-16 mm CL, carrying developed ovaries are sometimes collected, indicating that *S. similis* can reproduce at least twice during its lifetime. The absence of male individuals >14 mm CL resulted in a strong imbalance of sex ratio, indicating that the males die out at an age of <20 mo. Genthe (1969) showed evidence of sex reversal (protandrous hermaphroditism) from male to female in *S. similis*. Similar phenomena have been observed in other sergestids of the genus *Acetes* (Omori 1975). A detailed study is needed to determine the meaning of these findings, although at the present time we believe that the variance may be explained by abnormalities, since the frequency of occurrence is small. The bias in sex ratio favoring females above a certain size indicates the possibility of multiple fertilizations by males. Thus some females of the 2 age-group may mate with males of the 1 age-group.

We obtained an average growth trend of *S. similis* throughout its life by shifting the average or modal lengths of populations off the California and Oregon coasts horizontally in accordance with the month of their sampling. The growth of *S. similis* >6 mm CL was best fitted by the von Bertalanffy equation (Figure 10):

$$l_t = 14.7(1 - e^{-0.00378t}) \text{ for females, and}$$
$$l_t = 12.0(1 - e^{-0.00481t}) \text{ for males,}$$

where l_t is the carapace length in millimeters at t days. Because of the large mesh sizes of the IKMT nets, however, any average or modal length calculated from these samples over considerable size ranges on either side of 7 mm CL is probably greater than the length of the natural population. Therefore, the initial modal length of the 3-mo old population was fit by eye and connected with those growth curves of larval and early postlarval stages at 10° and 14°C which were obtained under laboratory conditions. It took 52 days for *S. similis* to reach the first postlarval stage at 14°C (Omori 1979). Under these conditions the logistic equation (Figure 10B) seemed to give the better fit to the growth curves:

$$l_t = \frac{14.7}{1 - e^{-0.00920(t-234.5)}} \quad \text{for females,}$$

$$l_t = \frac{12.0}{1 - e^{-0.01254(t-188.4)}} \quad \text{for males.}$$

Growth is very rapid during the postlarval stages. The juveniles at 4-8 mo old grow, at 0.91 mm CL/mo, during the period from April to August (logistic equation). The biomass of total zooplankton, as well as young *Calanus* and *Euphausia*, which are considered to be the most important food for juvenile and adult *S. similis*,

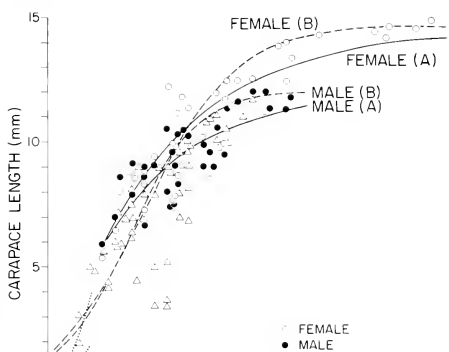


FIGURE 10.—Average growth of *Sergestes similis* off the California and Oregon coasts. Solid lines (A) are growth curves fit by the von Bertalanffy equation and (B) are those fit by the logistic equation. Dashed lines are growth curve of early developmental stages of 10° and 14°C determined in the laboratory (Omori 1979).

usually peaks in the April-July period in southern California waters (Mullin and Brooks 1970; Brinton 1976). Shrimp which encounter the best feeding conditions probably grow rapidly with low mortality rates and form distinctive modal groups such as those traced in Figure 9. The growth rate gradually decreases after 10-mo old, and the females add only 5 mm CL in 20 more months before dying. The difference in growth rates between the sexes becomes apparent after the shrimp attain a length of about 8 mm CL. The males grow slower than the females, but attain sexual maturity ½-1 mo earlier than females because the females become mature at 10.5-11.0 mm CL, whereas the males mature at 9.5-10.0 mm CL (see Genthe 1969; Omori 1979). Since five data points for females on the upper right-hand side of Figure 10 are on the asymptote, it is highly speculative whether these shrimps represent that age-group, or possibly an age-group spawned 5-6 mo later; in which case they would be placed on a different curve. It is apparent, however, that the longevity of the females of *S. similis* is more than 2 yr and that they spawn in two successive spawning seasons during their lives. These observations agree well with those of Matthews and Pinnoi (1973) on *Sergestes arcticus* Kröyer, which is the most closely related species to *S. similis* (Judkins 1972), in Kursfjordan, western Norway.

ACKNOWLEDGMENTS

We acknowledge the helpful reviews by M. M. Mullin and J. G. Morin. Thanks also to the staff and graduate students of the Food Chain Research Group of the Institute of Marine Resources for their assistance in sampling at sea. Omori is indebted to the Institute of Marine Resources and the Marine Life Research Group of Scripps Institution of Oceanography for the financial support and hosting of his visit.

LITERATURE CITED

AHLSTROM, E. H.
1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 54, 76 p.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARHAM, E. G.
1957. The ecology of sonic scattering layers in the Monterey Bay area, California. Hopkins Mar. Stn., Stanford Univ. Tech. Rep. 1, 182 p.

1963. The deep-scattering layer as observed from the bathyscaph "Trieste". Proc. 16th Int. Congr. Zool. 4:298-300.

BRINTON, E.
1967 Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.
1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull., U.S. 74:733-762.

CASSIE, R. M.
1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. J. Mar. Freshwater Res. 5:513-522.

DAVIES, I. E., AND E. G. BARHAM
1969. The Tucker opening-closing micronekton net and its performance in a study of the deep scattering layer. Mar. Biol. (Berl.) 2:127-131.

FLEMINGER, A.
1964. Distributional atlas of calanoid copepods in the California Current region, Part. I. Calif. Coop. Oceanic Fish. Invest., Atlas 2, 313 p.

GENTHE, H. C., JR.
1969. The reproductive biology of *Sergestes similis* (Decapoda, Natantia). Mar. Biol. (Berl.) 2:203-217.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

JUDKINS, D. C.
1972. A revision of the decapod crustacean genus *Sergestes* (Natantia, Penaeidea) *sensu latu*, with emphasis on the systematics and geographical distribution of *Neosergestes*, new genus. Ph.D. Thesis, Univ. California, San Diego, 274 p.

JUDKINS, D. C., AND A. FLEMINGER.
1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70:217-223.

KING, J. E.
1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). Biol. Bull. (Woods Hole) 94:244-262.

MATTHEWS, J. B. L., AND S. PINNOI
1973. Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. The species of *Pasiphaea* and *Sergestes* (Crustacea Decapoda) recorded in 1968 and 1969. Sarsia 52:123-144.

MAUCHLINE, J.
1968. The development of the eggs in the ovaries of euphausiids and estimation of fecundity. Crustaceana (Leiden) 14:155-163.

MAUCHLINE, J., AND L. R. FISHER.
1969. The biology of euphausiids. Adv. Mar. Biol. 7, 454 p.

MULLIN, M. M., AND E. R. BROOKS.
1970. The ecology of the plankton off La Jolla, California, in the period April through September, 1967. VII. Production of the planktonic copepod, *Calanus helgolandicus*. Bull. Scripps Inst. Oceanogr. Univ. Calif. 17:89-103.

MUTOH, M., AND M. OMORI.
1978. Two records of patchy occurrences of the oceanic shrimp *Sergestes similis* Hansen off the east coast of Honshu, Japan [In Jpn.] J. Oceanogr. Soc. Jpn. 34:36-38.

OMORI, M.
1974. The biology of pelagic shrimps in the ocean. Adv. Mar. Biol. 12:233-324.
1975. The systematics, biogeography, and fishery of epipelagic shrimps of the genus *Acetes* (Crustacea, Decapoda, Sergestidae). Bull. Ocean Res. Inst., Univ. Tokyo 7, 91 p.
1979. Growth, mortality, and feeding of larval and early postlarval stages of the oceanic shrimp, *Sergestes similis* Hansen. Limnol. Oceanogr. 24:273-288.

OMORI, M., A. KAWAMURA, AND Y. AIZAWA.
1972. *Sergestes similis* Hansen, its distribution and importance as food of fin and sei whales in the North Pacific Ocean. *In* A. Y. Takenouti et al. (editors), Biological oceanography of the northern North Pacific Ocean, p. 373-391. Idemitsu Shoten, Tokyo.

PEARCY, W. G., AND C. A. FORSS.
1966. Depth distribution of oceanic shrimps (Decapoda; Natantia) off Oregon. J. Fish. Res. Board Can. 23:1135-1143.
1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. Limnol. Oceanogr. 14:755-765.

PEREYRA, W. T., W. G. PEARCY, AND F. E. CARVEY, JR.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.

ROGER, C.
1973. Biological investigations of some important species of Euphausiacea (Crustacea) from the equatorial and south tropical Pacific. *In* R. Fraser (editor), Oceanography of the South Pacific 1972, p. 449-456. New Zealand National Commission for UNESCO, Wellington.

SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA.
1963. Oceanic observation of the Pacific. 1951. Univ. Calif. Press, Berkeley and Los Ang., 598 p.
1965a. Oceanic observations of the Pacific. 1952. Univ. Calif. Press, Berkeley and Los Ang., 617 p.
1965b. Oceanic observations of the Pacific. 1953. Univ. Calif. Press, Berkeley and Los Ang., 576 p.

VALENTINE, J. W., AND F. J. AYALA.
1976. Genetic variability in krill. Proc. Natl. Acad. Sci. USA 73:658-660.

WYLLIE, J. G.
1966. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest., Atlas 4, 288 p.

YALDWYN, J. C.
1957. Deep-water Crustacea of the genus *Sergestes* (Decapoda, Natantia) from Cook Strait, New Zealand. Zool. Publ. Victoria Univ. Wellington 22:1-27.

THE OCEANIC MIGRATION OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, ALONG THE ATLANTIC COAST

RICHARD J. NEVES[1] AND LINDA DEPRES[2]

ABSTRACT

The migratory route of American shad, *Alosa sapidissima*, in the Atlantic Ocean was studied using 14 yr of catch data collected during bottom trawl surveys by the U.S. National Marine Fisheries Service (and its predecessor) and cooperating foreign countries. All shad catches occurred at bottom temperatures from 3° to 15°C, with the most frequent catches between 7° and 13°C. Water temperatures between initial and peak entry of shad into home estuaries along the Atlantic coast are within the same thermal regime (3°-15°C). During the summer, all shad catches occurred north of lat. 40°N in two primary areas: Gulf of Maine and an area south of Nantucket Shoals. Previous studies on food habits and differences in time of capture during National Marine Fisheries Service surveys indicated that shad were vertical migrators, probably following the diel movements of large zooplankters in the water column. Shad were generally absent from the Gulf of Maine by late autumn, and concentrations were found between lat. 39°and 41°N during the winter. Based on previous tagging studies, National Marine Fisheries Service surveys, and coastal temperature data, most prespawning adults enter coastal waters along the Middle Atlantic Bight from lat. 36° to 40°N and then proceed north or south to natal rivers. Coastal surveys for river herring by North Carolina's anadromous fishery research program and commercial shad catches reported to the International Commission for the Northwest Atlantic Fisheries by member nations concur with our proposed bottom temperature (3°-15°C)-migratory route hypothesis for shad.

The American shad, *Alosa sapidissima*, is an anadromous fish ranging from the St. Johns River, Fla., to the St. Lawrence River, Canada (Walburg and Nichols 1967). Meristic and tagging studies indicate that discrete spawning populations of shad exist in river systems along the Atlantic coast (Hollis 1948; Hill 1959; Nichols 1960, 1966; Carscadden and Leggett 1975a). Juveniles leave freshwater in autumn and generally remain in the ocean for 3-5 yr before returning to their natal rivers to spawn. Spawning runs occur in a south to north temporal progression, beginning as early as December in Florida and as late as June in Canada (Walburg 1960). Virtually all shad south of Cape Hatteras, N.C., die after spawning, whereas the percentage of repeat spawners in rivers north of North Carolina increases with latitude (Leggett 1969; Chittenden 1975).

A considerable amount of literature exists on this species because of its commercial and recreational importance inshore, but little research has been done on the oceanic phase of its life history. Talbot and Sykes (1958) provided the first evidence of an annual oceanic migration based on 19 yr of tagging studies by the U.S. Fish and Wildlife Service. Tag returns indicated that shad from U.S. rivers congregated with those from Canadian rivers (Vladykov 1950, 1956) in the Gulf of Maine during summer and autumn and moved south to possibly overwinter off the Middle and South Atlantic States (Talbot and Sykes 1958; Walburg 1960; Walburg and Nichols 1967; Cheek 1968). In the spring, shad moved north or south toward natal rivers to spawn.

Temperature monitoring in rivers with major shad runs, and laboratory experiments, have provided convincing evidence that the timing of diadromous movements corresponds with specific water temperatures (Walburg and Nichols 1967; Chittenden 1969, 1972; Williams and Bruger 1972; Leggett and Whitney 1972; Leggett 1973). Leggett and Whitney (1972) also postulated that the oceanic distribution of shad was temperature-controlled; tag returns plotted on surface isotherm charts fell within the 13°-18°C isotherms. However, all of the tag returns used to establish this "migrational corridor" at sea were collected inshore during the spring coastal migration toward

[1]Massachusetts Cooperative Fishery Research Unit, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, Mass.; present address: Virginia Cooperative Fishery Research Unit, Virginia Polytechnic Institute & State University, Blacksburg, VA 24061.

[2]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543

Manuscript accepted August 1978.
FISHERY BULLETIN VOL. 77, NO. 1, 1979

home rivers. The correlation between offshore distribution and surface temperatures was therefore based on extrapolation.

The U.S. shad fishery is essentially an inshore operation and commercial catch records have limited value in evaluating the distribution of shad at sea. Previous tagging studies have relied on other commercial fisheries for offshore tag returns, but these fisheries concentrate effort at a time or place where principal species aggregate. Tag returns from shad taken as bycatch may therefore contain a geographical bias and reflect only the distribution of fishing effort. This paper examines offshore collections of shad from 14 yr of bottom trawl surveys by United States and foreign research vessels and interprets available literature on the coastal occurrence of shad. An alternative temperature-based hypothesis is presented to explain the offshore migratory cycle of shad.

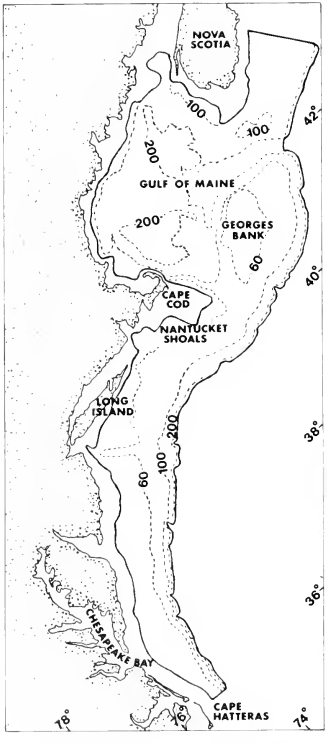


FIGURE 1.—National Marine Fisheries Service bottom trawl survey area between 27 and 366 m, Cape Hatteras, N.C., to Nova Scotia, western North Atlantic

METHODS

The U.S. National Marine Fisheries Service (NMFS) and its predecessor have conducted autumn bottom trawl surveys since 1963 using the RV *Albatross IV* and the RV *Delaware II*. The survey area extends from Nova Scotia to Cape Hatteras, out to 366 m (200 fm) (Figure 1) and is stratified into geographical zones based on depth and area. Coastal sampling stations are outside the 27-m (15-fm) depth contour. Middle Atlantic stations between New Jersey and Cape Hatteras were added during autumn 1967. A stratified random sampling design is used in the surveys; trawl stations are allocated to strata in proportion to stratum area and randomly assigned within strata (Grosslein 1969). A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner is towed at each station for 30 min at an average speed of 3.5 kn. Autumn surveys were conducted 24 h/day during 1963-76, between 3 September and 16 December.

Spring bottom trawl surveys have been conducted by NMFS since 1968 over the same geographical area (Figure 1). The No. 36 Yankee trawl was used from 1968 to 1972 and a larger No. 41 Yankee trawl from 1973 to 1976. Trawling procedures were the same as during autumn surveys and occurred between 4 March and 16 May. A detailed description of NMFS bottom trawl surveys and survey procedures is provided by Fleschер[3] and Grosslein.[4]

In addition to U.S. cruises, periodic autumn trawl surveys were conducted cooperatively with

[3]Flescher, D. 1976. Research vessel cruises, 1963-1975. National Marine Fisheries Service Woods Hole, Massachusetts. NMFS, Woods Hole, Mass., Lab. Ref. No. 76-14, 30 p.

[4]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

the U.S.S.R., Poland, and France from 1969 to 1976, mainly between Georges Bank and Cape Hatteras. Spring trawl surveys, intended primarily as juvenile herring surveys, have been made since 1973 by vessels from U.S.S.R., Poland, German Democratic Republic, and Federal Republic of Germany between Nova Scotia and Cape Hatteras. Most of the foreign surveys followed NMFS sampling procedures, sampled all or selected strata within respective survey areas, but used various types of bottom trawls. All spring and autumn surveys and additional cruises during summer and winter are summarized in Table 1. Survey station and catch data pertinent to this study included: date, location, time, depth, bottom and surface temperatures, and number, length frequencies, and weight of shad caught.

We plotted catch locations from all surveys (Table 1) by 10′ rectangles of latitude and longitude on depth contour maps according to month or season. Locations of shad collections during spring (March-May) and autumn (September-November) were plotted by month. Summer (June-August) and winter (December-February) surveys were grouped by season because of less sampling effort and lower catch frequency. Commercial shad catches by month reported to the International Commission for the Northwest Atlantic Fisheries (ICNAF) by member nations from 1970 to 1975 were provided by Hodder[5] and used to define major shad catches within each ICNAF division and their correlation with distribution patterns based on survey data. Surface and bottom temperatures (nearest 1°C) were plotted for each trawl tow that collected shad; foreign catches with missing temperature data were omitted from this analysis. Additional oceanographic data on temperature (Walford and Wicklund 1968; Colton and Stoddard 1972; Churgin and Halminski 1974; U.S. Coast Guard Oceanographic Unit[6]) and oceanic currents (Bumpus and Lauzier 1965; Stommel 1965; Bumpus 1973) were reviewed for seasonal patterns along the Atlantic coast.

RESULTS

Bottom trawls at 10,435 stations during the 77 surveys collected 4,770 subadult and adult shad at 527 stations throughout the survey area. United States and foreign research vessels accounted for 315 and 212 of the successful collecting stations, respectively. Shad ranged in size from 8 to 50 cm fork length (FL). Surface and bottom temperatures were recorded at 448 of these stations and used to plot catch frequency at 1°C intervals. Shad were collected at survey stations with surface temperatures between 2° and 23°C, and frequent catches occurred throughout most of this temperature range (Figure 2). Bottom temperatures at successful collecting stations ranged from 3° to 15°C, but primarily between 5° and 13°C (Figure 3). Most stations with bottom temperatures <3°C occurred in the Gulf of Maine during late winter and early spring; stations with bottom temperatures >15°C were mainly off the mid-Atlantic coast during late summer and early autumn. This apparent relationship between shad occurrence and bottom temperatures was examined further by comparing the catches of shad with total sampling effort at each temperature (Table 2). Bottom temperatures during surveys ranged from 1° to 23°C, but shad were captured only between 3° and 15°C. Shad catches occurred more frequently at

TABLE 1.—Summary of bottom trawl surveys conducted by United States and foreign research vessels between Cape Hatteras, N.C., and Nova Scotia, 1963-76

Season	Country	No. of surveys	No. of stations	Inclusive dates
Spring	United States	15	2,514	4 Mar-16 May
	Foreign	10	597	26 Feb-29 May
Summer	United States	4	810	7 July-28 Aug
	Foreign	6	618	9 Aug-3 Sept
Autumn	United States	21	3,657	3 Sept-16 Dec
	Foreign	18	1,676	3 Sept-11 Dec
Winter	United States	3	563	16 Jan-8 Apr
Totals		77	10,435	

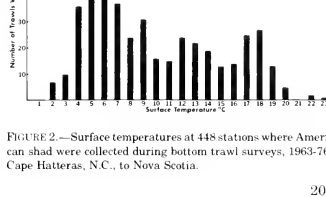


FIGURE 2.—Surface temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

[5]V. M. Hodder, ICNAF Office, Dartmouth, N. S., Canada B2Y 3Y9, pers. commun. July 1977.

[6]U.S. Coast Guard Oceanographic Unit. 1970, 1975. Monthly temperature charts, January to December 1970, January to December 1975, available U.S. Coast Guard Oceanographic Unit, Bldg. 159-E Navy Yard Annex, Washington, DC 20590.

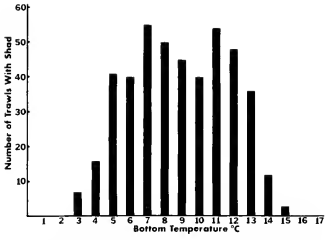


FIGURE 3.—Bottom temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 2.—Total sampling effort, number of shad catches, and percent catch frequency of shad at each bottom temperature during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia

Bottom temperature (°C)	Total no. of trawls	Trawls with shad	
		No.	%
1	16	0	0
2	104	0	0
3	270	7	2.59
4	567	16	2.82
5	987	41	4.15
6	864	40	4.15
7	1,047	55	5.25
8	997	50	5.02
9	909	45	4.95
10	750	40	5.33
11	741	54	7.29
12	739	48	6.50
13	626	37	5.91
14	333	12	3.60
15	164	3	1.83
16	71	0	0
17	56	0	0
18	41	0	0
19	30	0	0
20	29	0	0
21	34	0	0
22	19	0	0
23	5	0	0

temperatures between 7° and 13°C, with the greatest capture frequency at 11°C (Table 2).

Ocean depths at stations with shad ranged from 20 to 340 m, but most of these stations (65%) were <100 m deep (Figure 4). Of the 527 successful collecting stations, 269 (51%) occurred at depths between 50 and 100 m. Since trawling effort during U.S. spring and fall surveys was proportional to the area of each depth interval (Table 3), the number of shad catches within these depth strata was amenable to chi-square analysis. A comparison between shad catches at each depth interval and catches at all other depths combined indicated

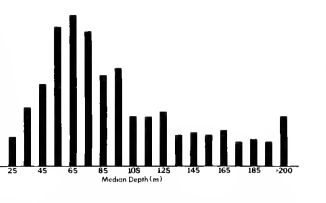


FIGURE 4.—Frequency of American shad catches with depth at 527 survey stations, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 3.—Depth intervals within the survey area and associated shad catches during U.S. bottom trawl surveys, 1967-76, Cape Hatteras, N.C., to Nova Scotia.

Depth interval (m)	Survey area		Number of trawls with shad		
	km²	%	Observed	Expected	χ^2
27-55	47,412	25.4	45	58	3.89*
56-110	55,009	29.5	109	68	35.10**
111-185	53,789	28.9	53	67	4.13*
186-366	30,181	16.2	23	37	6.32*
Totals	186,391	100.0	230	230	

*$P < 0.05$
**$P < 0.01$

that the greater capture frequency in the 56-110 m interval was highly significant ($P<0.01$); shad catches at all other depths were significantly fewer ($P<0.05$) than expected (Table 3).

Spring surveys were conducted mainly in March and April, accounting in part for the more frequent collections during these 2 mo (Figure 5). In March, shad were distributed along the Middle Atlantic Bight. Most fish between Long Island, N.Y., and Cape Cod, Mass., were taken in 60-200 m of water, many along the outer continental shelf (Figure 5). Few shad occurred in <60 m of water north of lat. 40°N, whereas most catches south of Long Island were at depths <60 m.

During the summer, shad were not captured south of lat. 40°N (Figure 6). Forty-six collections in July and August were made in two general areas: the Gulf of Maine and southeast of Cape Cod, near Nantucket Shoals. Mean depth at these stations was 95 m, but ranged from 35 to 214 m. Catches were distributed along the coastal margin of the Gulf of Maine and the southern half of Georges Bank; most trawling stations in the deeper, central Gulf did not collect shad.

October received the greatest trawling effort during autumn surveys. Shad were again distrib-

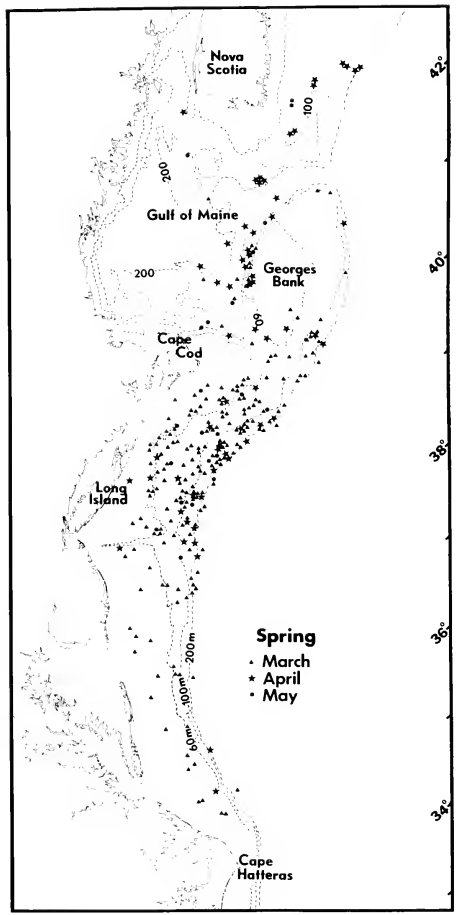


FIGURE 5.—Location of all American shad catches during spring bottom trawl surveys, 1968-76, Cape Hatteras, N.C., to Nova Scotia.

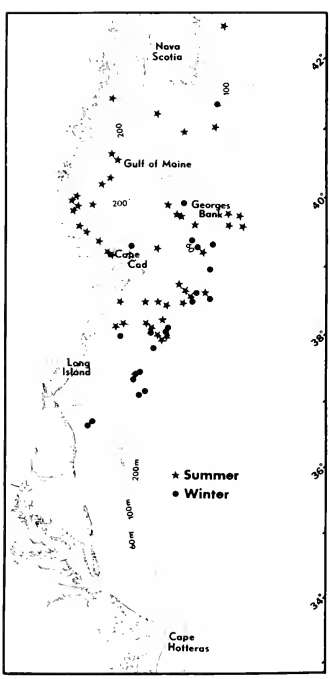


FIGURE 6.—Location of all American shad catches during summer and winter bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia

uted along the Gulf of Maine and Georges Bank perimeter, as well as south of Nantucket Shoals (Figure 7). Most of these captures were along the continental shelf at depths of >60 m. Monthly catches indicated a southward movement out of the Gulf of Maine in late autumn, although some shad remained there into November. During 10 yr of autumn bottom trawl surveys along the Middle Atlantic States, shad were never collected offshore south of lat. 39°N.

The relatively low number of successful trawling stations during the winter may be inadequate to define the southern limit of the wintering area (Figure 6). Winter catches occurred at 22 stations from southern Long Island (lat. 39°N) to the southern edge of Georges Bank (lat. 41°N) and reflected the same general area where shad began congregating in autumn (Figure 7). Except for two shallow-water stations, winter collections of shad were made at a mean depth of 108 m.

DISTRIBUTION OF INTERNATIONAL CATCHES

The season for major shad catches in ICNAF divisions (Figure 8) agreed closely with distribution according to bottom trawl surveys. Largest annual catches were reported by the United States in Subarea 6 (1,517-2,812 t). United States catches between 1970 and 1976 occurred primarily in Division 6B and ranged from 112 to 1,272 t in March and April. Most of this spring catch was taken by the inshore commercial fishery. The only other catch of comparable size was made in Division 5Ze by the Federal Republic of Germany during September 1973 and totaled 302 t. Catches in Subarea 5 occurred mainly in autumn; however, winter catches were reported in Division 5Zw and 6A between New Jersey and Cape Cod. Canadian catches in Subarea 4 were greatest in May, with decreasing catches throughout the summer.

DISCUSSION

The sampling design of NMFS bottom trawl surveys covers a large area in a relatively short period of time and provides good data on fish distribution and concurrent environmental conditions. Even though these surveys were initially designed to sample primarily demersal species, results do reflect major changes in the abundance of pelagic species as well (Schumacher and Anthony[7]; Anderson[8]). Bottom trawls used during U.S. surveys are less effective on *Alosa* spp. than

[7]Schumacher, A., and V. C. Anthony. 1972. Georges Bank (ICNAF Division 5Z and Subarea 6) herring assessment. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 24, Serial No. 2715, 36 p.

[8]Anderson, E. D. 1973. Assessment of Atlantic mackerel in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 14, Serial No. 2916, 37 p.

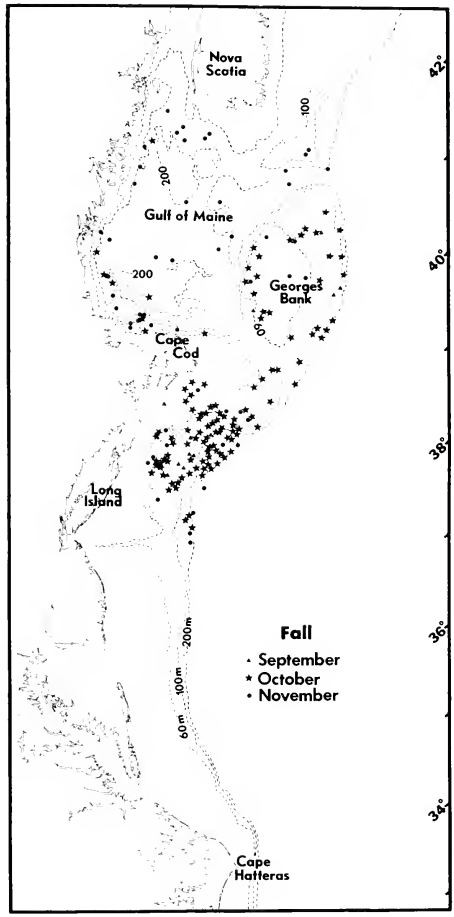


FIGURE 7.—Location of all American shad catches during autumn bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia

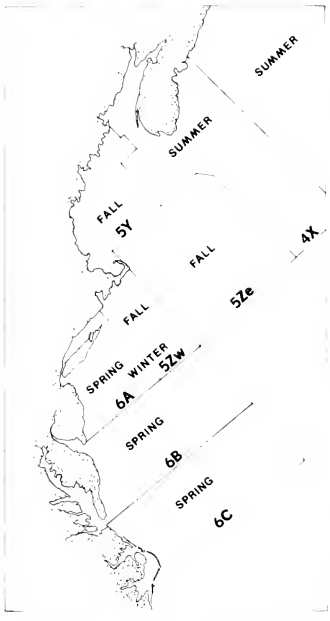


FIGURE 8.—Seasonal distribution of major American shad catches in the International Commission for the Northwest Atlantic Fisheries divisions, 1970-75, Cape Hatteras, N.C., to Nova Scotia.

foreign midwater trawls or the wing trawl (Holland[9]), but bottom trawl survey data provide the most complete, available records on offshore occurrence.

Based on the data presented, survey-related observations to be discussed, and literature to be reviewed, we propose the following migratory cycle for American shad. Offshore movements are limited to areas and depths with near-bottom temperatures between 3° and 15°C. Shad occur most frequently in offshore areas of intermediate depths (approximately 50-100 m). Adults that survive spawning together with subadults migrate to the Gulf of Maine or to an area south of Nantucket Shoals and remain there through the summer and early autumn. During this period of active feeding, shad are vertical migrators and follow the diel movements of zooplankton in the water column. Most shad move out of the Gulf of Maine in autumn with declining water temperatures and congregate offshore, between southern Long Island and Nantucket shoals (lat. 39°-41°N) during the winter. Adults enter coastal waters in a broad front toward the Middle Atlantic coast, as far south as North Carolina during the winter and spring. Shad populations returning to South Atlantic rivers migrate south adjacent to the coast and within the 15°C isotherm to reach home rivers by winter and early spring. North Atlantic populations proceed north up the coast in the spring with the warming of coastal waters above 3°C.

Offshore Distribution

The wide range of surface temperatures at stations where shad were caught does not support the extrapolation of the inshore temperatures-shad migration regime proposed by Leggett and Whitney (1972) to explain offshore movements. The influence of temperature on fish behavior and physiology is most pronounced during the spawning season (Laevastu and Hela 1970), particularly for anadromous fishes. Tag returns within the 13°-18°C isotherms (Leggett and Whitney 1972) may have reflected inshore physiological changes in prespawning adults, leading to higher optimal temperatures approaching those for spawning. Our results indicate that near-bottom temperatures between 3° and 15°C provide a better basis for predicting shad movements in offshore waters.

Offshore catches during NMFS surveys revealed that shad are not limited to the Gulf of Maine in summer months as reported by Talbot and Sykes (1958). Shad were also collected in an area south of Nantucket Shoals during summer and autumn surveys. Although shad from most river systems have been collected in the Gulf of Maine during the summer (Talbot and Sykes 1958), it is not known whether all populations migrate together at sea. Distribution during the spring is widespread and not indicative of a syn-

[9]Holland, B. F., Jr. 1975. Anadromous fisheries research program, northern coastal area. Section II. N.C. Proj. AFCS 11-1 Job 6, 43 p.

chronous species migration as suggested by Leggett (1977). Coastal tagging studies during the spring reveal an aggregation of many spawning stocks that often detour into estuaries along the coast (Sykes and Talbot 1958; Talbot and Sykes 1958; Chittenden 1974; Leggett 1977; White et al.[10]). However, the length of time each population has been inshore is unknown. Until stock identification at sea is feasible, the regional composition and extent of offshore mixing cannot be documented.

The location of winter collections (lat. 39°-41°N) coincides with two previously published capture records (Talbot and Sykes 1958; Walburg and Nichols 1967), but the extent of overwintering in deep water off the continental shelf is unknown. Shad collections in the northern Gulf of Maine during November and December were made at depths >100 m and do not conform (based on previous studies) with the expected migration south in late autumn. These and other shad captured in deep water near Nova Scotia during March (Vladykov 1936) are outside the apparent wintering area, south of Nantucket Shoals. The possibility that some shad overwinter or become thermally isolated in deepwater areas off Nova Scotia (Vladykov 1936; Hodder 1966) needs further investigation.

Circulation patterns along the Atlantic coast do not account for the seasonal distribution of shad according to survey data or their coastal migration routes based on tagging studies (Talbot and Sykes 1958; Leggett 1977). Bottom drift toward shore and coastal drift south in the Middle Atlantic Bight during winter (Bumpus 1973) would aid migrants moving south, but seasonal shifts in directional flow along the east coast and their effect on shad movements are liable to subjective interpretation. Spawning populations moving north and south concurrently could be helped or hindered by circulation patterns in the mid-Atlantic area. We believe that seasonal shifts in isotherms, as influenced by circulation patterns, are of greater importance in defining the migratory route of shad.

Vertical Distribution

Presently there is little information on the depths preferred by shad at sea. We inferred distribution in the water column from three separate sources: food habits, diel differences in catchability, and effectiveness of various trawls in capturing shad. Adult shad are zooplankton feeders and consume primarily large copepods, mysids, and euphausiids (Bigelow and Schroeder 1953; Hildebrand 1963; Leim and Scott 1966). The consumption of food organisms such as mysids and zoobenthos indicates that part of a shad's life is spent near the ocean bottom (Leim 1924; Walburg and Nichols 1967). In general, stomach analyses reveal that shad feed at all depths but particularly where concentrations of zooplankton occur.

Trawling stations where shad were collected during U.S. surveys (24 h/day) were partitioned by capture time (Eastern Standard Time) into day (0600-1800 h) and night (1800-0600 h). Chi-square analysis on time of capture revealed that daytime catches occurred significantly more often ($P<0.01$) than night collections (Table 4). Of the night catches, 25% occurred within 1 h of the daytime interval. Shad were apparently closer to the bottom during daylight hours and thus more susceptible to bottom trawling gear. Further corroboration of this daytime occurrence nearer to the bottom is evidenced by the frequency of shad catches in foreign bottom trawls. During daylight hours in March 1974-76, foreign research vessels used herring trawls to sample 280 stations from Long Island to Georges Bank and recorded shad at 71 (25%) of these stations. Contemporary surveys by the United States in the same area with the No. 41 Yankee trawl sampled 207 daytime stations and collected shad at 22 (11%) of them. Maximum headrope distance off the bottom for the U.S. trawl was 5 m. The larger foreign trawls had a higher opening (6 m) which increased their effectiveness on off-bottom species, although extra-trawl factors such as vessel size, speed, and gear rigging certainly contributed to the greater overall fishing power of these trawls (Grosslein 1969, 1971).

We deduce from the above observations that shad are vertical migrators like other schooling planktivores such as herring, *Clupea harengus*, and mackerel, *Scomber scombrus* (Blaxter 1975;

TABLE 4.—Chi-square test comparing the number of day and night catches of shad during U.S. bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

Time	Observed	Expected	χ^2
Day (0600-1800 h)	217	157.5	
Night (1800-0600 h)	98	157.5	45.0**
Totals	315	315.0	

**P 0.01

[10]White, R. L., J. T. Lane, and P. E. Hamer. 1969. Population and migration study of major anadromous fish. N.J. Div. Fish Game Misc. Rep. No. 3M, 21 p.

Isakov[11]; Rikhter[12]), following the diel movements of zooplankton in the water column. This reliance on zooplankton for food may be an additional factor influencing shad distribution during the year. Zooplankton distribution in the Gulf of Maine during summer and autumn is closely tied to local and regional hydrography (Redfield 1941; Sherman 1966; Cohen[13]); concentrations generally occur along areas of current convergence and divergence (Zinkevich 1967) and at depths <100 m (Bigelow 1926; Whiteley 1948). During winter, the waters around Georges Bank are nearly devoid of zooplankton, whereas sizeable neritic populations occur from Nantucket Shoals to southern Long Island (Clarke 1940; Grice and Hart 1962; Zinkevich 1967). Sette (1950) concluded that water temperature had a limiting rather than causal influence on the seasonal movements of mackerel, and Redfield (1941) noted a parallelism between mackerel distribution and areas of zooplankton abundance. Similarly, Zinkevich (1967) related herring movements to water temperature and seasonal shifts in zooplankton concentrations. Catches of shad during bottom trawl surveys along Georges Bank, Gulf of Maine perimeter, and south of Nantucket Shoals may therefore be related to zooplankton abundance in these areas, but direct evidence is lacking.

Coastal Migration

Tagging studies and the location of NMFS and ICNAF catches during the spring indicate that most shad populations move toward the mid-Atlantic coast from offshore waters, between lat. 36° and 40°N in the winter and early spring. The time and location of tag returns by the mid-Atlantic shad fishery demonstrate that shad from most populations occur in this region during the spring (Talbot 1954; Talbot and Sykes 1958; Leggett 1977; White et al. see footnote 10). Shad tagged near southern Long Island in early spring were recaptured on spawning runs as far south as North Carolina (Talbot and Sykes 1958). Tagging of shad in North Atlantic rivers during the spawning period produced recaptures as far south as the North Carolina coast in subsequent years (Talbot 1954; Vladykov 1956; Talbot and Sykes 1958; Leggett 1977). These tag returns provide an approximate geographical range of entry into coastal waters by returning oceanic migrants (lat. 36°-40°N).

Assuming that the 3° and 15°C isotherms define the northern and southern limits respectively of shad movements at sea, prespawning adults returning to coastal waters from the ocean would face a thermal barrier south of Cape Hatteras. Offshore bottom temperatures along the South Atlantic coast remain above 17.5°C during the year, whereas bottom temperatures on the continental shelf north of Cape Hatteras and inshore temperatures for the South Atlantic coast drop below 15°C by December (Figure 9). The proximity of the Gulf Stream to North Carolina creates a narrow coastal corridor at Cape Hatteras, providing the only migratory route to southern rivers if shad returning to these home rivers are to remain within their marine temperature regime. Migration toward shore north of Cape Hatteras and then south along the coast appear to be essential prerequisites for successful homing to South Atlantic rivers. In contrast, shad returning to North Atlantic rivers during the spring are not obliged to follow a coastal route because offshore temperatures in the Middle Atlantic Bight are well within the shad's range of oceanic occurrence (Figure 9). However, tag returns from adults tagged on spawning runs into North Atlantic rivers indicate that many (most?) adults do enter coastal waters in the lower mid-Atlantic region and migrate north along the coast to reach home rivers as repeat spawners the following spring (Talbot 1954; Leggett 1977). Results of Atlantic coast tagging are consistent with our upper temperature limit (15°C) for shad migration at sea; all prespawning, oceanic migrants enter inshore waters as far south as North Carolina. The significance of the Cape Hatteras region to other aspects of northern versus southern shad biology was discussed by White and Chittenden (1977).

Based on our proposed migratory route, large shad catches in ICNAF Division 6B during the spring would consist of shad entering home rivers and populations moving toward and along the coast. Catches in Chesapeake Bay and the sounds of North Carolina from late November to early December (Hildebrand and Schroeder 1928; Talbot and Sykes 1958; Walburg and Nichols 1967)

[11]Isakov, V. I. 1976. The peculiarities of diurnal vertical migrations of mackerel in the northwestern Atlantic. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 111, Serial No. 3934, 3 p.

[12]Rikhter, V. A. 1976. Proposal on trawling surveys for estimation of pelagic fish stocks in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 116, Serial No. 3939, 3 p.

[13]Cohen, E. B. 1975. An overview of the plankton communities of the Gulf of Maine. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 106, Serial No. 3599, 16 p.

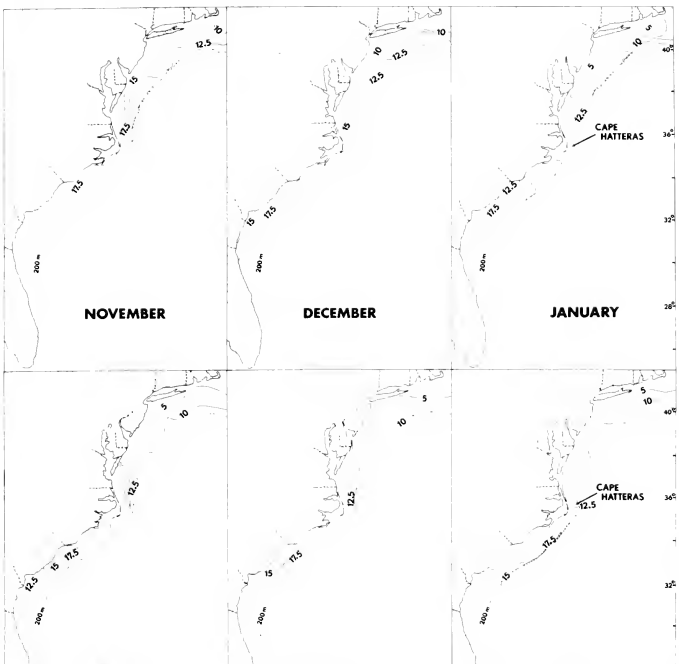


FIGURE 9.—Mean monthly bottom temperatures during winter and spring along the eastern U.S. coast, Cape Cod, Mass., to Florida (From Walford and Wicklund 1968.)

would be shad returning to natal rivers farther south. Inshore temperatures are unstratified along the Atlantic coast during the winter (Parr 1933). Since freshwater discharge generally occurs along the surface from estuaries, water temperatures would not preclude near-surface movements of shad to detect essential olfactory and rheotaxic cues for successful homing (Dodson and Leggett 1974).

Estuarine temperatures from initial to peak arrival of shad at home rivers along the Atlantic coast are between 3° and 15°C (Talbot 1954; Massmann and Pacheco 1957; Walburg and Nichols 1967; Leggett 1972; Leggett and Whitney

1972; Chittenden 1976; Sholar[14]). Within this temperature regime, southern populations begin reaching home estuaries at the higher temperatures, while northern populations do so at the lower temperatures. Peak numbers of shad enter the St. Johns River, Fla., in mid-January when water temperatures are at an annual low of 15°C; the peak in juvenile emigration occurs simultaneously (Leggett and Whitney 1972; Williams and Bruger 1972). Shad first enter the Connecticut River in late March-early April when water temperatures are approximately 4°C and peak in abundance at 13°C (Leggett and Whitney 1972). In general, most shad populations north of Cape Hatteras begin entering rivers at approximately 4°C, and the peak in upstream migration occurs at temperatures between 10° and 15°C (Leggett and Whitney 1972).

The lower thermal tolerance of juvenile shad in freshwater was near 2.2°C in a short-term laboratory study (Chittenden 1972) and roughly 3°-4°C in small outdoor ponds (Blair[15]). This lower thermal limit agrees closely with the lowest temperature at which subadult shad were collected during NMFS offshore surveys (3°C). Chittenden (1972) also reported that juveniles ceased feeding when water temperatures dropped below 4.4°C. However, we collected 17 juvenile and subadult shad (9-32 cm FL) during a NMFS coastal survey in January 1978, at stations with bottom temperatures between 2.8° and 4.3°C. All but one stomach were filled with mysids and copepods, indicating active feeding at these temperatures in saltwater.

Further evidence to support our bottom temperature regime for predicting the coastal movements of shad is provided by North Carolina's anadromous fishery research program. Their annual surveys on river herring since 1971 show that shad occur off the North Carolina coast from January to April, at bottom temperatures between 6° and 12°C and at depths <26 m (Johnson et al.[16]). Shad catches decline substantially when water temperatures exceed 12°C, coinciding with entry into estuaries or possibly, northward migration. This temperature range concurs with offshore bottom temperatures having the most frequent shad catches during NMFS bottom trawl surveys (7°-13°C). The shallow depths traveled by coastal migrants during the winter and spring would account for their unavailability to offshore sampling.

Critical data on the oceanic phase of most anadromous fishes are lacking (Harden-Jones 1968), and our general description of shad movements must await additional research at sea to corroborate or correct the proposed migratory cycle. It would seem energetically wasteful for North Atlantic populations to follow the same shoreward route as do Middle and South Atlantic shad. The return of all populations to this region may have historical significance, since shad are believed to have been most abundant in the mid-Atlantic portion of their coastal range (Leim 1924). Variations in life history patterns among populations are generally considered to be adaptive responses (Cole 1954; Murphy 1968; Gadgil and Bossert 1970), and differences in life history characteristics among shad populations in rivers (Carscadden and Leggett 1975b) may also exist at sea. Endocrine-induced differences in the timing of migratory behavior and gonadal maturation may be life history strategies of adaptive significance, considering the species' wide geographical range (21° of latitude). The lengthy period of migration toward the mid-Atlantic coast from offshore by prespawning adults may stem from population-specific responses to photoperiod or temperature cues. Further study on the sensory systems and environmental cues involved in migration is required before a more comprehensive explanation for the migratory cycle of shad is available.

ACKNOWLEDGMENTS

We are indebted to the Resource Surveys Investigation section and other staff members at NMFS, Woods Hole, for their cooperation in this endeavor. Special thanks go to Ralph Mayo for sharing his computer expertise and to Bill Leggett, Emory Anderson, Jon Gibson, Brad Brown, and an anonymous reviewer for reviewing the manuscript. The Massachusetts and Virginia Cooperative Fishery Research Units provided financial support. We dedicate this paper to R. J. Reed for his contributions to the study of American shad biology.

[14]Sholar, T. M. 1977. Anadromous fisheries research program, Cape Fear River System, phase I. N.C. Proj. AFCS 12, 63 p.

[15]Blair, A. B. 1977. American shad culture and distribution studies at Harrison Lake National Fish Hatchery. Proc. Workshop American Shad, Amherst, Mass., Dec. 1976, 10 p.

[16]Johnson, H. B., B. F. Holland, Jr., and S. G. Keefe. 1977. Anadromous fisheries research program, northern coastal area. Section II. N.C. Proj. AFCS 11-2, 41 p.

LITERATURE CITED

BIGELOW, H. B.
1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. 40, 509 p.

BIGELOW, H. B., AND W. C. SCHROEDER
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BLAXTER, J. H. S.
1975. The role of light in the vertical migration of fish - a review. *In* G. C. Evans, R. Bainbridge, and O. Rackham (editors), Light as an ecological factor: II, p. 189-210. Blackwell Sci. Publ., Oxf.

BUMPUS, D. F.
1973. A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6:111-157.

BUMPUS, D. F., AND L. M. LAUZIER
1965. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 7.

CARSCADDEN, J. E., AND W. C. LEGGETT
1975a. Meristic differences in spawning populations of American shad, *Alosa sapidissima*: evidence for homing to tributaries in the St. John River, New Brunswick. J. Fish. Res. Board Can. 32:653-660.
1975b. Life history variations in populations of American shad, *Alosa sapidissima* (Wilson), spawning in tributaries of the St. John River, New Brunswick. J. Fish Biol. 7:595-609.

CHEEK, R. P.
1968. The American shad. U.S. Fish Wildl. Serv., Fish Leafl. 614, 13 p.

CHITTENDEN, M. E., JR.
1969. Life history and ecology of the American shad, *Alosa sapidissima*, in the Delaware River. Ph.D. Thesis, Rutgers Univ., New Brunswick, N.J., 459 p.
1972. Responses of young American shad, *Alosa sapidissima*, to low temperatures. Trans. Am. Fish. Soc. 101:680-685.
1974. Trends in the abundance of American shad, *Alosa sapidissima*, in the Delaware River Basin. Chesapeake Sci. 15:96-103.
1975. Dynamics of American shad, *Alosa sapidissima*, runs in the Delaware River. Fish. Bull., U.S. 73:487-494.
1976. Present and historical spawning grounds and nurseries of American shad, *Alosa sapidissima*, in the Delaware River. Fish. Bull., U.S. 74:343-352.

CHURGIN, J., AND S. J. HALMINSKI
1974. Temperature, salinity, oxygen, and phosphate in waters off United States. NOAA Key to Oceanographic Records, Doc. No. 2:1-166.

CLARKE, G. L.
1940. Comparative richness of zoöplankton in coastal and offshore areas of the Atlantic. Biol. Bull. (Woods Hole) 78:226-255.

COLE, L. C.
1954. The population consequences of life history phenomena. Q. Rev. Biol. 29:103-137.

COLTON, J. B., JR., AND R. R. STODDARD
1972. Average monthly sea-water temperatures, Nova Scotia to Long Island, 1940-1959. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 21.

DODSON, J. J., AND W. C. LEGGETT
1974. Role of olfaction and vision in the behavior of American shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. J. Fish. Res. Board Can. 31:1607-1619.

GADGIL, M., AND W. H. BOSSERT.
1970. Life historical consequences of natural selection. Am. Nat. 104:1-24.

GRICE, G. D., AND A. D. HART
1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287-307.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-35.
1971. Some observations on accuracy of abundance indices derived from research vessel surveys. Int. Comm. Northwest Atl. Fish., Redb. Part III:249-266.

HARDEN-JONES, F. R.
1968. Fish migration. E. Arnold Publ., Lond., 325 p.

HILDEBRAND, S. F.
1963. Family Clupeidae. *In* Fishes of the western North Atlantic, part three, p. 257-454. Mem. Sears Found. Mar. Res. Yale Univ. 1.

HILDEBRAND, S. F., AND W. C. SCHROEDER
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, 366 p.

HILL, D. R.
1959. Some uses of statistical analysis in classifying races of American shad (*Alosa sapidissima*). U.S. Fish Wildl. Serv., Fish. Bull. 59:269-286.

HODDER, V. M.
1966. Two further records of the American shad in Newfoundland waters. Trans. Am. Fish. Soc. 95:228-229.

HOLLIS, E. H.
1948. The homing tendency of shad. Science (Wash., D.C.) 108:332-333.

LAEVASTU, T., AND I. HELA
1970. Fisheries oceanography. Fishing News (Books) Ltd., Lond., 238 p.

LEGGETT, W. C.
1969. Studies of the reproductive biology of the American shad (*Alosa sapidissima*, Wilson). A comparison of populations from four rivers of the Atlantic seaboard. Ph.D. Thesis, McGill Univ., Montreal, 125 p.
1972. Weight loss in American shad (*Alosa sapidissima*, Wilson) during the freshwater migration. Trans. Am. Fish. Soc. 101:549-552.
1973. The migrations of the shad. Sci. Am. 228(3):92-98.
1977. Ocean migration rates of American shad (*Alosa sapidissima*). J. Fish. Res. Board Can. 34:1422-1426.

LEGGETT, W. C., AND R. R. WHITNEY
1972. Water temperature and the migrations of American shad. Fish. Bull., U.S. 70:659-670.

LEIM, A. H.
1924. The life-history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contrib. Can. Biol., New Ser., 2:161-284.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can. Bull. 155, 485 p.

MASSMANN, W. H., AND A. L. PACHECO
1957. Shad catches and water temperatures in Virginia. J. Wildl. Manage. 21:351-352.

MURPHY, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391-403.
NICHOLS, P. R.
1960. Homing tendency of American shad, *Alosa sapidissima*, in the York River, Virginia. Chesapeake Sci. 1:200-201
1966. Comparative study of juvenile American shad populations by fin ray and scute counts. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 525, 10 p.
PARR, A. E.
1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. Bull. Bingham Oceanogr. Collect. Yale Univ. 4(3), 90 p.
REDFIELD, A. C.
1941. The effect of the circulation of water on the distribution of the calanoid community in the Gulf of Maine. Biol. Bull. (Woods Hole) 80:86-110.
SETTE, O. E.
1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II. Migrations and habits. U.S. Fish Wildl. Serv., Fish. Bull. 51:251-358.
SHERMAN, K.
1966. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1964. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 530, 11 p.
STOMMEL, H.
1965. The Gulf Stream. Univ. Calif. Press, Berkeley, 248 p.
SYKES, J. E., AND G. B. TALBOT
1958. Progress in Atlantic coast shad investigations - migration. Proc. Gulf Caribb. Fish. Inst., 11th Annu. Sess., p. 82-90.
TALBOT, G. B.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish Wildl. Serv., Fish Bull. 56:373-413.
TALBOT, G. B., AND J. E. SYKES
1958. Atlantic coast migrations of American shad. U.S. Fish Wildl. Serv., Fish. Bull. 58:473-490.
VLADYKOV, V. D.
1936. Occurrence of three species of anadromous fishes on the Nova Scotian Banks during 1935 and 1936. Copeia 1936:168.
1950. Movements of Quebec shad (*Alosa sapidissima*) as demonstrated by tagging. Nat. Can. (Que.) 77:121-135.
1956. Distant recaptures of shad (*Alosa sapidissima*) tagged in Quebec. Nat. Can. (Que.) 83:235-249.
WALBURG, C. H.
1960. Abundance and life history of the shad, St. Johns River, Florida. Fish Bull., U.S. 60:487-501
WALBURG, C. H., AND P. R. NICHOLS
1967. Biology and management of the American shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 550, 105 p.
WALFORD, L. A., AND R. I. WICKLUND
1968. Monthly sea temperature structure from the Florida Keys to Cape Cod. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 15.
WHITE, M. L., AND M. E. CHITTENDEN, JR.
1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109-123.
WHITELEY, G. C., JR.
1948. The distribution of larger planktonic crustacea on Georges Bank. Ecol. Monogr. 18:233-264.
WILLIAMS, R. O., AND G. E. BRUGER
1972. Investigations on American shad in the St. Johns River. Fla. Dep. Nat. Resour. Tech. Ser. 66, 49 p.
ZINKEVICH, V. N.
1967. Observations on the distribution of herring, *Clupea harengus* L., on Georges Bank and in adjacent waters in 1962-65. Int. Comm. Northwest Atl. Fish., Res. Bull. 4:101-115.

SOURCES AND DISTRIBUTION OF BLUEFISH, *POMATOMUS SALTATRIX*, LARVAE AND JUVENILES OFF THE EAST COAST OF THE UNITED STATES

ARTHUR W. KENDALL, JR.[1] AND LIONEL A. WALFORD[2]

ABSTRACT

Larval bluefish are found offshore somewhere between Cape Cod, Mass., and Palm Beach, Fla., during every season of the year. However, there appear to be two main spawning concentrations—one during spring near the western edge of the Gulf Stream in the South Atlantic Bight and the other during summer over the continental shelf of the Middle Atlantic Bight. Larvae complete development near the surface; juveniles are strongly associated with the surface. Juveniles from the spring spawning remain at sea and are carried northward past Cape Hatteras, N.C., above the edge of the continental shelf. As surface shelf water warms, they move shoreward to spend the summer in estuaries of the Middle Atlantic Bight. Bluefish spawned in summer remain at sea as juveniles or enter estuaries briefly in late summer. In fall, as the water cools, the juveniles move southward out of the Middle Atlantic Bight. It is possible that these two spawnings represent different populations. A smaller fall and winter spawning which occurs offshore south of Cape Hatteras may represent a small population resident to the South Atlantic Bight.

Bluefish, *Pomatomus saltatrix* (Linnaeus), occur in most temperate coastal regions of all world oceans (Briggs 1960). Fowler (1944) erroneously reported them from the eastern Pacific where they do not occur. The earliest descriptions of eggs and larvae of bluefish by Agassiz and Whitman (1885) which have been quoted by other authors, e.g., Padoa (1956) and Salekhova (1959), are erroneous. Colton and Honey (1963), Deuel et al. (1966), and Norcross et al. (1974) correctly described them and showed that bluefish spawn pelagic eggs in the open sea and larval development takes place near the surface. Juveniles generally move from the open sea to coastal areas and estuaries. This pattern has been observed off North America, in the Black Sea, and off South Africa (Irvine 1947; Bigelow and Schroeder 1953; Oben 1957; Smith 1961).

Along the Middle Atlantic Bight, i.e., from Cape Cod, Mass., to Cape Hatteras, N.C., bluefish eggs, larvae, and juveniles have been collected during several ichthyoplankton studies (Sette 1943; Lund and Maltezos 1970; Norcross et al. 1974). Although restricted in sampling area or time, these studies have indicated that spawning and larval development take place offshore from Chesapeake Bay to southern New England in late spring and summer. Juveniles occur in estuaries along the middle Atlantic coast in summer (Clark[3]).

The sources of data for this paper are plankton collections taken by personnel of the National Marine Fisheries Service (NMFS), NOAA, Sandy Hook Laboratory, as part of a study to investigate the importance of estuaries as nursery areas of Atlantic coast fishes. The first part of this study consisted of a survey of ichthyoplankton over the continental shelf, an area thought to be the spawning grounds for many species of fishes. From information gained during this study, we hoped to trace the movement of young stages from spawning grounds and thus evaluate the importance of estuaries as nurseries. From the results of this study, several additional short cruises were conducted to study further the distribution of larval and juvenile bluefish in certain offshore areas at specific times of the year.

In this paper, information from these studies and those of previous workers is presented to help elucidate the times and places of bluefish spawn-

[1]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732; present address: Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]New Jersey Marine Sciences Consortium, Fort Hancock, NJ 07732.

[3]Clark, J. R. 1973. Bluefish. *In* A. L. Pacheco (editor), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic coast estuaries, p. 250-251. Middle Atl. Coastal Fish. Cent., Tech. Publ. 1.

Manuscript accepted September 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

ing along the east coast. Evidence to link the offshore occurrences of bluefish larvae to the estuarine occurrences of bluefish juveniles also is presented. This early life history information relates to what is known of the number and relative sizes of populations of bluefish along the east coast.

MATERIALS AND METHODS

(Table 1, Figure 1)

An ichthyoplankton study of Atlantic continental shelf waters by the Sandy Hook Laboratory began in 1965-66 with a survey from Cape Cod to

TABLE 1.—Bluefish collections from RV *Dolphin* ichthyoplankton surveys and supplemental cruises for young bluefish off the east coast of the United States.

Continental shelf area	Dates	Number of stations	Gear[1]	Bluefish		
				Number of collections	Number	Standard lengths (mm)
Cape Cod to Cape Lookout	3-15 Dec 1965	78	Gulf V			
		35	MWT			
	25 Jan.-9 Feb 1966	86	Gulf V	1	1	8.7
		0	MWT			
	6-22 Apr 1966	92	Gulf V			
		3	MWT			
	12-24 May 1966	92	Gulf V	5	25	3.4-9.1
		63	MWT			
	17-29 June 1966	92	Gulf V			
		59	MWT	2	2	33-37
	5-26 Aug 1966	92	Gulf V	25	1 621	2.4-13.2
		66	MWT	4	8	9-128
	13-18 Sept 1966	30	Gulf V	2	2	4.0-6.7
		15	MWT			
	28 Sept.-20 Oct 1966	92	Gulf V	1	2	3.3-4.0
		77	MWT	1	17	26-219
	9 Nov.-4 Dec 1966	92	Gulf V			
		68	MWT	2	2	49-124
New River, N.C., to Palm Beach, Fla	15-19 Feb 1966	26	Gulf V	1	1	8.0
	7-15 May 1967	80	Gulf V	20	563	2.2-11.6
		80	SMN	11	14	18-34
		80	2-m ring			
	22 July-1 Aug 1967	80	Gulf V			
		80	SMN			
		53	MWT			
	19-26 Oct 1967	80	Gulf V	5	17	3.9-6.9
		80	SMN			
		77	3-m ring			
	27 Jan.-4 Feb 1968	80	Gulf V	2	2	5.1-6.0
		80	SMN			
		50	MWT	2	5	63-92
New York Bight	10-16 June 1969	44	SMN			
		46	MWT	1	1	45.1
		15	Nightlight	1	1	45.9
	15-18 June 1970	44	SMN	3	3	20.8-35.0
		44	2-m ring	1	1	31.3
New Jersey to Maryland	14-18 June 1971	32	SMN	5	8	23.8-33.7
		32	Haedrich	5	7	23.6-32.1
		12	MWT	3	3	27.3-35.7
Virginia to North Carolina	27 Apr.-5 May 1971	58	SMN	19	163	12.6-31.4
		60	Haedrich	27	1 464	3.9-33.5
		19	2-m ring	3	10	4.1-11.3
Cape Hatteras, N.C.	weekly, 11 Apr.-31 May 1972	36	Haedrich	21	1 472	3.5-25.4
New Jersey to Virginia	29 Oct.-1 Nov. 1970	35	SMN	3	3	40.0-48.2
		35	Haedrich	3	4	36.4-34.9
		11	2-m ring	1	3	200
Georgia to Florida	29-31 Jan. 1971	24	SMN			
		24	Haedrich			
		24	MWT			

[1]MWT = midwater trawl; SMN = surface meter net; see text for further details.

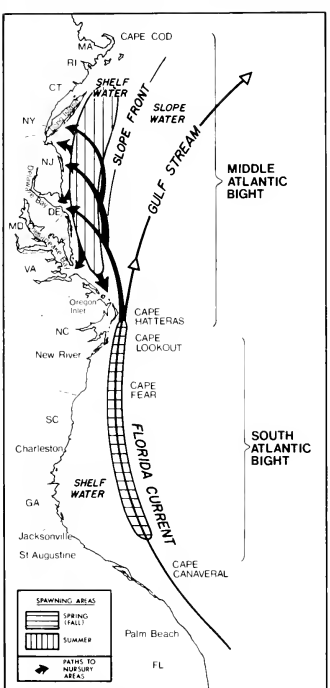


FIGURE 1.—Major features of surface waters and bluefish larval and juvenile distribution off the U.S. east coast.

Cape Lookout, N.C. Over the year, as weather permitted, 92 stations over 14 transects were sampled during 8 cruises. In 1967-68, the study continued, working from Cape Fear, N.C., to Palm Beach, Fla., sampling at 80 stations over 14 transects during each of 4 seasonal cruises. Plankton was sampled with Gulf V samplers (0.52-mm mesh). The 30-min step oblique tows were made at 2.1-2.6 m/s. Two nets were towed simultaneously; one from the surface to 15 m, the other from 18 to 33 m where water depths permitted. Details of gear, procedures, and physical, plankton volume, and juvenile fish data have been published (Clark et al. 1969, 1970).

The same procedures were followed on two additional cruises in 1966. One of these (D-66-2) sampled 26 stations on five transects between Jacksonville, Fla., and Palm Beach in February 1966. The other (D-66-11) sampled 30 stations on the four northernmost transects (Cape Cod to New Jersey) in September 1966.

Collections for pelagic juvenile fishes were made during the cruises in 1965-66 with a scaled-down Cobb midwater trawl (Clark et al. 1969). During the cruises in 1967-68, several nets were towed for juvenile fishes. At each station a surface meter net with 6-mm mesh was towed beside the ship. Subsurface samplers included the scaled-down Cobb trawl, and a 1-m and a 2-m ring net (Clark et al. 1970).

Several offshore cruises from 1969 through 1971 were designed mainly to augment the data on occurrences of bluefish juveniles. A surface meter net and a Haedrich neuston net (Bartlett and Haedrich 1968) were used in paired tows on most of these cruises. Other sampling equipment used at various times included dip nets with nightlights and several types of midwater nets.

In spring 1972, a series of eight weekly cruises near Cape Hatteras aboard a chartered sport fishing boat was conducted working from Oregon Inlet, N.C., out into the Gulf Stream. On each cruise, we made two neuston tows with a Haedrich net near Cape Hatteras. One of these was in the green coastal water, the other in the blue Gulf Stream water, and each tow was within 100 m of the interface between the two water masses. During the return to Oregon Inlet, some 60 km north of Diamond Shoals Light Tower, several additional tows sampled the full range of surface water temperatures occurring in the area. Weather and water temperature data relative to these cruises were gathered from the U.S. Naval Oceanographic Office and the U.S. National Weather Service.

Additional data on bluefish and juveniles and ancillary observations from these collections are available.[4]

[4]Kendall, A. W., Jr., and L. A. Walford. 1978. Data associated with offshore larval and juvenile bluefish collections at Sandy Hook Laboratory, 1965-1972. Unpubl. manuscr., 5 p. Report No. SHL 78-9. Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

We will generally refer to bluefish <10 mm standard length (SL) as larvae and those >10 mm SL as juveniles. Bluefish hatch at about 3 mm SL and by 10 mm SL the fin ray development is nearly complete and in living specimens the body is dark blue on the back and silvery on the sides, as in the pelagic juvenile stage of goatfish and mullet (Norcross et al. 1974).

RESULTS

Hydrographic Features of Middle and South Atlantic Bights

Shelf water characterized by salinities of <35‰, is divided into coastal water (<33.6‰) and shelf edge water (33.6-35.0‰) (Wright and Parker 1976). The Gulf Stream, characterized by salinities >36.0‰ and or temperatures >18 C at 100 m or >15 C at 200 m, flows generally beyond the edge of the continental shelf. The water mass between the shelf water and Gulf Stream, called the slope water, is separated from the shelf water by a strong surface feature, except in midsummer, called the slope front. Surface manifestations such as lines of flotsam, differences in water color, and choppiness of the Gulf Stream are seen on moderately calm days. The shelf water is sluggish and influenced by short-term effects of wind, but generally moves south along the shore. The Gulf Stream moves northward or northeastward at velocities over 100 cm/s (Sverdrup et al. 1942).

Eggs

Bluefish eggs, which share features with pelagic eggs of many other species, were not found in any of our collections. Bluefish eggs have a smooth spherical membrane, a diameter of 0.90-1.20 mm averaging 1.00 mm, a pigmented yolk, a single oil globule about 0.2 mm in diameter, and melanophores in rows on the embryo (Deuel et al. 1966). Even though an egg has all of the above features, it can be identified with certainty as being a bluefish egg only if the oil globule is pigmented and in later development the number of myomeres has become established at 24 to 28.

Two studies have reported occurrences of bluefish eggs along the east coast. Marak and Colton (1961) listed a few of them from late May to early June 1953 in 12.8°C water south of Cape Cod. These data are suspect because: 1) identification was based on inadequate descriptions by Agassiz and Whitman (1885) and Perlmutter (1939); and 2) adult bluefish in spawning condition are not present off southern New England until later in the year when temperatures are considerably warmer. In a second study conducted from 1960 to 1962 off Virginia, Norcross et al. (1974) reported bluefish eggs during the period June through August from near shore to the continental slope. Although none occurred in our collections, from the similarity in distribution of bluefish eggs and larvae seen by Norcross et al. (1974), it seems that an accurate indication of spawning location can be derived from the capture of small larvae.

Larvae

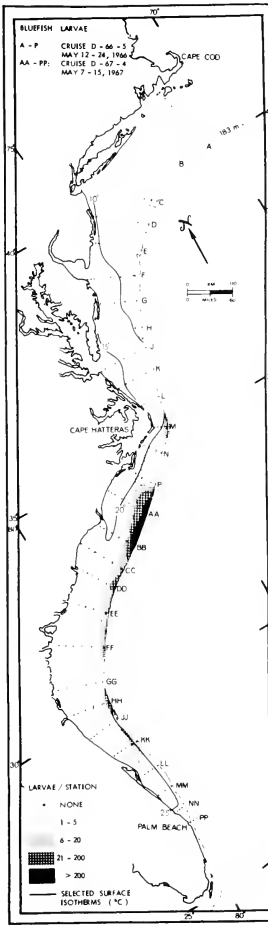
Seasonal-Geographic Distribution

Although bluefish larvae occurred between Massachusetts and Florida during every season, two major geographically distinct concentrations of larvae were found; one south of Chesapeake Bay near the Gulf Stream in spring, and the other north of Cape Hatteras over the middle of the continental shelf in summer.

During spring, bluefish larvae were taken from near Cape Hatteras to Cape Canaveral, Fla. Of the 473 larvae taken at 25 stations during the surveys of May 1966 and 1967, greatest concentrations were between the offings of New River, N.C., and Charleston, S.C., near the edge of the continental shelf (Figure 2). In April and May 1971, we also caught bluefish larvae near Cape Hatteras primarily offshore near the Gulf Stream. From these data, it appeared that bluefish spawned near the edge of the continental shelf in the South Atlantic Bight during spring.

Bluefish dominated the neuston catches near Cape Hatteras during the eight weekly cruises in spring of 1972 (Table 2). They occurred on every cruise and in every water type sampled. The variability in catches between paired tows during this series was too large to permit precise comparison among the dates or sampling areas. However, the largest catches were made in water just shoreward of the Gulf Stream. Most of the specimens taken in or near the Gulf Stream were between 5 and 12 mm SL, whereas the few taken over the shelf ranged from 11 to 21 mm SL.

The numbers of bluefish caught each week gave no indication of relative abundance during spring in this area, partially because weather-influenced



surface temperature patterns affected the catch rate. Large catches just shoreward of the Gulf Stream followed periods of northerly winds which caused a compression of surface isotherms in this area. Following southerly winds the isotherms were spread out and catches were low. It thus appears that the catch rate was related to the width of the band of suitable water, and that in turn was related to wind conditions.

No bluefish larvae were collected in the Middle Atlantic Bight in January, April, May, and June 1966, but they were abundant and widespread in August when their distribution extended from eastern Long Island, N.Y., to Virginia and more or less over the breadth of the continental shelf (Figure 3). They were most abundant off New Jersey and Delaware. Most of these larvae were small (mean, 4.0 mm SL) indicating that spawning had occurred not long before this cruise. The relative number of fish <4 mm SL was greatest at the northern end of the survey area and diminished progressively southward to Delaware Bay (Figure 4). This effect could have resulted from growth of the larvae during our sampling from north to south in this area over a 3-day period. It also might have resulted if bluefish spawning had started in the south and progressed northward. Either or both of these processes may have been involved. There was an 11-day gap in sampling between Delaware Bay (Transect F) and Maryland (Transect G). This might account for our finding so few, but larger larvae south of Delaware Bay.

Bluefish spawning in middle Atlantic waters was almost finished by the end of summer, judging from the paucity of specimens taken during September and October (Figure 5). In September, when we sampled only north of middle New Jersey, we caught two larvae; and in October, when the sampling area extended over the whole Middle Atlantic Bight, we again caught two. We have no information on the southerly extent of bluefish larvae during September, since there was no sampling south of New Jersey then.

Four bluefish larvae were taken during winter cruises, one at each of four stations near the edge of the continental shelf. One was taken off North Carolina (Transect N) and the other three between St. Augustine, Fla., and Palm Beach (Transects Y, KK, and LL).

FIGURE 2.—Distribution of surface temperatures and larval bluefish in May. Transects A-P sampled May 1966; AA-PP sampled May 1967

TABLE 2.—Bluefish catches in paired neuston nets during eight weekly cruises off Cape Hatteras, N.C., April, May 1972.

Item	11 Apr		18 Apr		27 Apr		4 May		11 May		16 May		23 May		31 May	
	Tow 1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Gulf Stream																
Surface temperature (°C)	22.0	ND	23.3	ND	22.5	22.4	23.5	ND	24.0	ND	25.1	ND	ND	ND	25.5	ND
Bluefish catch	0	0	7	0	12	218	8	0	4	0	0	0	0	0	0	0
Mean length (mm SL)			10.9		8.9	10.0	11.6		9.8							
200 m shoreward of Gulf Stream																
Surface temperature (°C)	16.0	ND	19.5	20.6	13.2	22.1	20.0	18.6	20.3	ND	22.6	ND	ND	ND	20.5	19.5
Bluefish catch	4	0	41	14	93	771	3	2	4	0	6	0	0	0	35	217
Mean length (mm SL)	4.8		11.1	10.0	5.5	9.9	12.3	9.1	10.6		12.0				5.9	16.3
Intermediate (shelf) water																
Surface temperature (°C)	12.5	ND	10.6	11.7	ND	ND	15.4	17.0	18.0	16.1	19.4	ND	15.1	ND	17.3	16.3
Bluefish catch	0	0	0	0	0	0	0	1	17	0	2	0	0	0	0	0
Mean length (mm SL)								21.4	12.9		18.7					
Nearshore																
Surface temperature (°C)	13.0	ND	10.8	ND	ND	ND	ND	ND	16.0	ND	19.5	20.0	ND	ND	19.0	ND
Bluefish catch	0	0	0	0	0	0	0	0	5	0	2	0	0	0	0	0
Mean length (mm SL)									10.7		18.8					

ND data

Temperature-Salinity Regimes

During the survey, bluefish larvae occurred in two distinct temperature-salinity regimes. One regime was characterized by surface temperatures of 18°-26°C and salinities of 30-32‰ (Figure 6). These conditions prevailed from late spring through the summer above the thermocline in coastal waters of the Middle Atlantic Bight. Bluefish spawning evidently did not begin there until late July or early August, judging from the small number of large larvae taken in August. Thus, spawning of bluefish in the Middle Atlantic Bight seemed to be influenced partly by features of environment other than temperature and salinity.

The other regime was associated with the inner edge of the Gulf Stream and was characterized by surface temperatures of 20°-26°C and salinities of 35-38‰. As mentioned above, few bluefish larvae occurred in this water during the fall and winter, considerable numbers during the spring, and none during the summer.

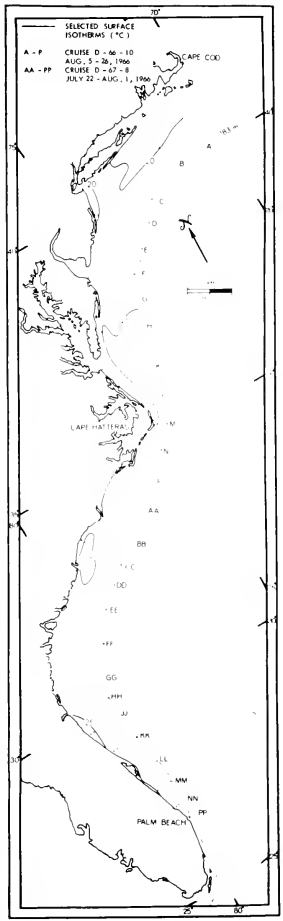
Seasonal Surface Temperature Relations

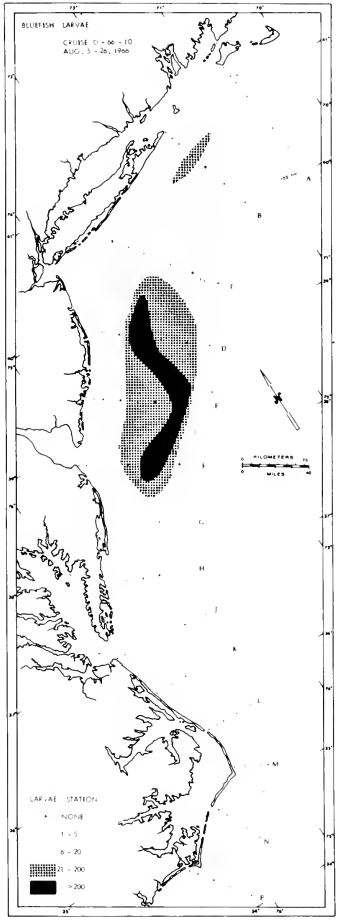
Regardless of season or area, nearly all larvae were taken in waters between 17° and 26°C. Larvae appeared on the shelf throughout the South Atlantic Bight in spring where the surface water temperatures ranged from 19° to 24.5°C. North of Cape Hatteras where we took no larvae in spring, shelf water was <15°C, but near the edge of the Gulf Stream where we did take larvae, temperatures were >15°C. At the stations where bluefish larvae were taken during August, surface temperatures ranged from 18.8° to 25.7°C. Surface water covering most of the Middle Atlantic Bight south of eastern Long Island was within this temperature range (Figure 3). However, south of Cape Hatteras no bluefish larvae were taken in July when temperatures were mostly >26°C. Surface water temperature had decreased between our September and October cruises. The 20°C surface isotherm was off Long Island in September, but had moved south to Virginia by October. The bluefish larvae were taken in 20.3°C water in September and 16.4°C water in October. The few bluefish larvae taken near the edge of the continental shelf off Florida in October were in water <25°C. In winter, all occurrences were in water >20°C, which was limited to the outer portion of the continental shelf from North Carolina to Florida at that time.

Diel Cycles of Vertical Distribution

The number of larvae caught in shallow tows (0-15 m) when compared with deep tows (18-33 m) during day and night provided limited information about diel cycles of vertical distribution. The catch rate was highly dependent on net depth. At the 46 stations where both nets were towed and either caught bluefish larvae, more occurred in the shallow net at 37 stations indicating that the larvae were more abundant in the shallow layer (sign test, $P<0.001$). Nearly all of the catch of the deeper net may have occurred as it passed through the surface layer during setting and retrieving.

FIGURE 3.—Distribution of surface temperatures (left) and larval bluefish (right) in July-August. Transects A-P sampled August 1966, AA-PP sampled July-August 1967.


SELECTED SURFACE ISOTHERMS (°C)
A - P CRUISE D - 66 - 10 AUG. 5 - 26, 1966
AA - PP CRUISE D - 67 - 8 JULY 22 - AUG. 8, 1966
CAPE COD
CAPE HATTERAS
PALM BEACH
70°
60°
25°
30°


BLUEFISH LARVAE
CRUISE D - 66 - 10
AUG. 5 - 26, 1966
KILOMETERS
MILES
LARVAE STATION
NONE
1 - 5
6 - 20
21 - 200
> 200

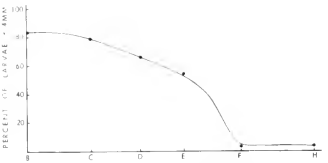


FIGURE 4.—Percent of bluefish larvae <4 mm SL captured on transects B-H (Figure 2) in the Middle Atlantic Bight in August 1966.

Indeed, later studies (Kendall and Naplin[5]) have shown that bluefish larvae occur primarily within 6 m of the surface. The distribution of catches was similar during day and night (Table 3).

Larval Lengths

The length distribution of larvae taken in the shallow tows was not significantly different from that taken in deeper tows (χ^2 $P \sim 0.05$) (Table 4). This result is to be expected if, as indicated above, the catches in the deeper tows can be accounted for by contamination in the surface layer. Fish taken during the day, however, were generally smaller (2.5-4.5 mm) than those taken at night (5.5 mm and larger) (χ^2 $P \leq 0.001$). This effect could result from net avoidance by larger larvae during daytime. The cruises were too infrequent to estimate larval growth.

Juveniles

During the survey cruises we tried to collect pelagic juvenile fishes and during later cruises tried to clarify results from the surveys by sampling in areas and during seasons in which juveniles had occurred earlier. We took bluefish juveniles in several kinds of midwater and surface nets. It is difficult to compare the catches of these several nets or the catches made in different years; nevertheless, this limited information about

[5]Kendall, A. W., Jr., and N. A. Naplin. Diel-vertical distribution of bluefish (*Pomatomus saltatrix*) larvae and that of associated fish eggs and larvae. Manuscr. in prep. Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

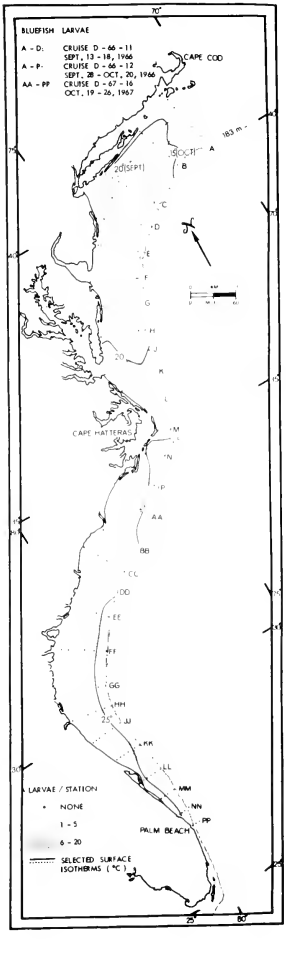


FIGURE 5.—Distribution of surface temperatures and larval bluefish in September-October

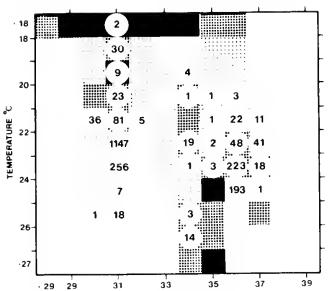


FIGURE 6.—Clustering of catches of larval bluefish by temperature-salinity combination during RV *Dolphin* surveys, 1965-68. Numbers of bluefish larvae superimposed on temperature-salinity combinations where they were caught.

TABLE 3.—RV *Dolphin* 1965-68 ichthyoplankton survey. A comparison of bluefish larval catches during day and night.

Larvae/tow	Number of tows			
	Day	Night	χ^2	
1	12	8	0.309	
2-10	6	7	0.303	
11-100	7	7	0.080	
100	3	2	0.078	
Totals	28	24	0.770	(3 df, P 0.80)

offshore seasonal geographic distribution of bluefish juveniles indicates a complex pattern of movements from offshore spawning areas to coastal and estuarine nursery areas.

In summary we found bluefish juveniles, presumably from the spring spawning, at the surface near the slope front from south of Cape Hatteras to off the Middle Atlantic Bight in April to June (Figure 1). We hypothesize that they move northward along the slope front, then cross the shelf, enter estuaries of the Middle Atlantic Bight and after spending the summer in the estuaries, return to the sea and move southward along the coast and out of the Middle Atlantic Bight. Some juveniles from the summer spawning in the Middle Atlantic Bight remain in coastal waters while some enter estuaries briefly. They too leave the Middle Atlantic Bight in early fall. The following is our evidence for these conclusions.

In May 1967, juvenile bluefish were scattered over the continental shelf in the South Atlantic Bight and north to Cape Hatteras (Figure 7). The largest specimens were from stations near shore.

In April and May 1971, we sampled the offshore area intensively around Cape Hatteras to find any trace of young bluefish which could be attributed to larvae and juveniles such as had appeared previously to the south. During this cruise neuston tows took bluefish juveniles near the edge of the continental shelf (100-fm (183-m) isobath) (Figure 8a). All of the specimens taken were in water >15°C, which occurred all across the shelf south of Cape Hatteras, but only near the edge of the shelf north of there.

In the June 1966 survey, when 59 stations were sampled, bluefish appeared at each of two widely

TABLE 4.—RV *Dolphin* ichthyoplankton surveys 1966-68. Length distributions of larval bluefish collected in Gulf V samples.

Interval midpoint (mm SL)	South Atlantic Bight						Middle Atlantic Bight						All data
	Winter			Spring		Fall	Summer			Shallow tows	Deep tows	Day	Night	
	D-66-1	D-66-2	D-68-1	D-66-5	D-67-4	D-67-16	D-66-10	D-66-11	D-66-12					
2.5					97		231			301	27	266	62	328
3.5				4	205	8	610		2	739	89	689	139	828
4.5					128	6	515	1		602	49	371	280	651
5.5			1	4	15	1	136			145	12	72	85	157
6.5			1	2		2	21	1		22	5	11	16	27
7.5				5			11			14	2	7	9	16
8.5	1	1		8			5			13	2	10	5	15
9.5				2	1		5			7	1	2	6	8
10.5							10			10			10	10
11.5					1		1			2		1	1	2
12.5							1			1			1	1
13.5							1			1			1	1
23.5					1					1			1	1
Total	1	1	2	25	448	17	1,547	2	2	1,858	187	1,429	616	2,045
Mean				6.88	3.63	4.31	4.00			3.98	3.88	3.73	4.51	3.97
Variance				3.55	1.61	0.96	1.31			1.58	1.26	0.84	2.78	1.55

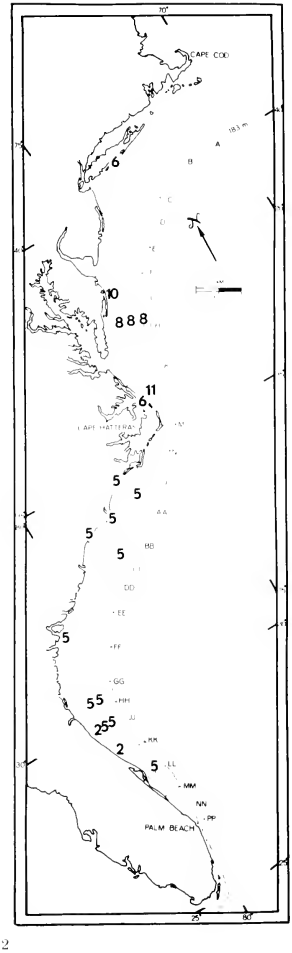


FIGURE 7.—Months of capture (indicated by numerals) of juvenile bluefish at stations sampled by surface meter net and midwater trawl during RV *Dolphin* surveys, 1965-68

separated nearshore stations (Figure 7). The regular presence of bluefish juveniles in offshore waters of the Middle Atlantic Bight in June was observed in three subsequent years. They occurred during 1969 only near shore; during 1970 only near the edge of the continental shelf; and during 1971 they were scattered over the shelf and slope (Figure 8b, c, d). The origin of these juveniles was puzzling, because there was no evidence of bluefish larvae in the Middle Atlantic Bight until midsummer. We had taken larvae and juveniles in April and May from Cape Hatteras south to Florida mainly offshore near the slope front. Apparently these fish become distributed along the slope front off the Middle Atlantic Bight in May and June and then cross the continental shelf in June as surface waters become suitably warm. Surface temperatures on the shelf are generally 15° to 20°C at this time, and most of the juveniles were taken in water >18°C.

The juveniles we caught in August (Figure 7) were presumably products of recent spawning in nearby waters, for only slightly smaller larvae appeared in the plankton tows in the same area. One specimen 128 mm SL taken just outside Chesapeake Bay had probably been spawned in the spring off the South Atlantic Bight.

We collected a few juveniles of widely differing sizes during two surveys in fall 1966. In a cruise conducted in 1970, we confirmed the regular presence of juvenile bluefish in the Middle Atlantic Bight in fall. We then collected juveniles between Delaware and Chesapeake Bays within 13 km of the shore (Figure 8e); and several specimens about 200 mm SL in the same area. The juveniles from these cruises can be attributed to the summer spawning of bluefish in continental shelf waters of the Middle Atlantic Bight; and the fish about 200 mm SL to the southern spring spawning. The latter fish had presumably spent the summer in middle Atlantic estuaries (Wilk[6]) and had returned to the ocean. A 124-mm SL specimen taken in November may have originated from either spawning.

No bluefish juveniles were taken in fall in the South Atlantic Bight and neither larvae nor

[6]Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Sandy Hook Lab. Tech. Ser. Rep. 11, 56 p.

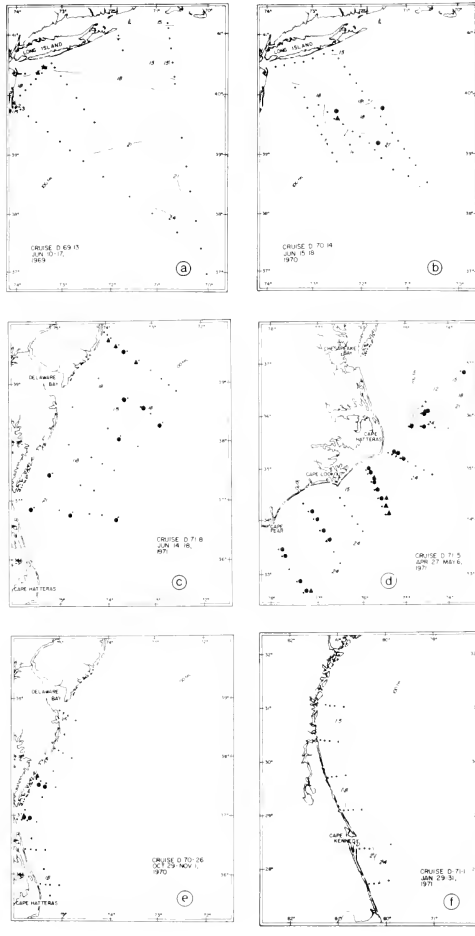


FIGURE 8.—Distribution of juvenile bluefish and surface temperatures during six cruises over portions of the Middle Atlantic Bight. Sampling stations indicated by dots. Presence of juvenile bluefish in surface meter net or Haedrich net indicated by circles, in midwater trawls by triangles, and under nightlight by a star

juveniles were taken in the Middle Atlantic Bight from late fall to June.

In the winter survey, a few juveniles were taken off Florida (Figure 7), but during a follow-up cruise, none were caught (Figure 8f).

DISCUSSION

The patterns of distribution of young stages of bluefish off the east coast can be summarized based on our collections and those of others (Table 5).

From our collections of small larvae, bluefish appear to spawn in two quite different areas—in water just shoreward of the Gulf Stream (Florida Current) from Florida to Cape Hatteras, i.e., the South Atlantic Bight, and in shelf water from Cape Hatteras to Cape Cod, i.e., the Middle Atlantic Bight.

In the South Atlantic Bight, spawning occurs primarily during spring and apparently also to a lesser extent in fall and winter. Most of the larvae we caught were well offshore just shoreward of the Gulf Stream in water which was 20°-26°C and had a salinity of 35-38‰.

Larvae from the spring spawning in the southern area are evidently carried northward past Cape Hatteras in April and May and become spread out along the continental slope off the Middle Atlantic Bight. As shelf waters become suitably warm, generally in mid-June, the young bluefish appear to cross the shelf and enter estuaries, where they spend the summer. There they grow from 25-50 mm SL to 175-200 mm SL (Wilk see footnote 6) and in early fall migrate south along the coast.

Larvae from the fall and winter spawning in southern waters may find their way inshore south of Cape Hatteras as indicated by a few juveniles which we found in Florida in winter.

The spawning in the Middle Atlantic Bight in continental shelf waters occurs in summer. The water in which larvae were found here was 3°C cooler and 5‰ less saline than that in the south-

TABLE 5.—Collections of bluefish eggs, larvae, and juveniles, east coast of United States.

Reference	Sampling period: Years	Sampling period: Months	Sampling area	Occurrences of bluefish	Numbers	Lengths (mm)
Eggs						
Marak and Colton (1961) Marak Foster (1962) Marak Miller (1962)	1951-56	Feb.-June	Ocean off New England	Late May-early June 1953 south of Martha's Vineyard	few	
Norcross et al. (1974)	1959-60	all except Oct.	Ocean off Chesapeake Bay	June, July, August 1960 and 1961		
	1961-62	all	Ocean off Chesapeake Bay	July 1962 nearshore to slope waters	many	
	1962	seasonally	Ocean off Chesapeake Bay			
	1963	July-Aug.	Ocean off Chesapeake Bay			
Larvae						
Sette (quoted by Perlmutter 1939)	1929	Apr.-July	Ocean from Cape Cod-Chesapeake Bay	40 N-Chesapeake Bay, waters near 21°C, mostly outer half of shelf	many	3-21
Herman (1963)	1957-58	all	Narragansett Bay	July 20.7°C	1	3
Lund[1]	1965	May, July-Sept.	Ocean off eastern Long Island	July-Sept. (most in Aug.)	73	5-30
	1966	June-Sept.	Ocean off eastern Long Island		981	5-20
de Sylva et al. (1962)	1956-58	all	Indian River Inlet, Del.	Aug.-Sept.	2	4-28
Pearson (1941)	1929-30	all	Lower Chesapeake Bay	24 July at mouth of bay	4	4-7
Norcross et al. (1974)	1959-60	all except Oct.	Ocean off Chesapeake Bay	May-Aug.	34	3-7
	1961-62	all	Ocean off Chesapeake Bay	July-Sept.	441	3-11
	1962	seasonally	Ocean off Chesapeake Bay	July	34	5-14
	1963	July-Aug.	Ocean off Chesapeake Bay	July-Aug.	93	4-22
Juveniles (< 100 mm)						
Pearcy and Richards (1962)	1959-60	all	Mystic River, Conn.	Seined July-Aug. lower estuary	2	75-94
Perlmutter (1939)	1938	all	Waters around Long Island	Throughout summer—small fish trawl	6	78-96
Lund[1]	1968	July-Sept.	Shinnecock Bay, N.Y.	Throughout summer—seined small (40 mm) fish in July and Aug.	200	40-100
de Sylva et al. (1962)	1958	every other	Delaware River, Del.	Seined June-Sept. lower estuary	130	30-100
Pacheco and Grant (1965)	1957-58	all	White Creek, Del.	Seined May-June, Sept.	45	39-104
Richards and Castagna (1970)	1965-66	all	Eastern shore of Virginia	Trawled at inlets, July, Sept.	5	31-85
Tagatz and Dudley (1961)	1957-60	all	Shoal waters near Beaufort, N.C.	Seined May-July, Oct.-Nov.	37	40-100
Turner and Johnson (1973)	1970	all	Newport River, N.C.	Surface trawled upper river May-July, Oct.	few	45-72

[1]Lund, W.A., Jr. Early life history of the bluefish (*Pomatomus saltatrix* Linnaeus) off the coast of New York and southern New England. Contrib. 64 Mar. Res. Lab., Sounk, Conn., 27 p.

ern area (18°-26° C and 30-32‰). Bluefish larvae have been reported by other authors in this area from May through September, but mostly in July and August (Table 5). Larvae have also been reported in the more saline areas of several estuaries of the Middle Atlantic Bight (Table 5). Although some juveniles from the Middle Atlantic Bight spawning inhabit estuaries in late summer, more seem to remain along the shore. Nevertheless, all appear to move southward and out of the bight in midfall. Their distribution in late fall and winter is still unknown.

From the scarcity of juveniles (i.e., fish 50-150 mm SL) in our samples at sea, and the abundance of these fish in estuarine collections, it appears that bluefish depend chiefly on estuaries for habitat during this stage. Their dependence is determined by the time and place of their spawning. Those from the spring spawning spend most of their first summer in estuaries, while those from the summer spawning spend at most about a month there. Both changes in temperature and seasonal photoperiod influenced the activity and distribution of adult bluefish at least under laboratory conditions (Olla and Studholme 1971, 1972). Thermal edges may act as barriers affecting the distribution of juvenile bluefish, as shown in recent laboratory work (Olla[7]). These factors, and possibly others, probably trigger movements of juveniles from the open ocean to estuaries and back to the open ocean.

In order to assess the relative proportions of the two major spawning areas to the total recruitment of bluefish on the Atlantic coast in any given year, it would be necessary to sample repeatedly during the spring south of Cape Hatteras and during the summer in the Middle Atlantic Bight.

Our present limited understanding of early life history contributes to several other facets of bluefish biology. Population differences of bluefish on the U.S. Atlantic coast have been studied using meristic characters (Lund 1961), migratory patterns, morphometrics, and scale morphology (Wilk see footnote 6). All of these studies indicate that more than one population exists. Scale studies defined two groups of bluefish by the size of fish when the first annual ring forms in May. One group, which reaches about 260 mm by the end of its first winter, evidently represents fish spawned in spring south of Cape Hatteras. The other group, which reaches only about 120 mm by the end of its first winter, represents fish spawned in the summer in the Middle Atlantic Bight. Body proportions of these two groups of fishes are statistically different (Wilk see footnote 6).

Precise information on adult bluefish migration is not available, but general patterns are known (Wilk see footnote 6). Some mature bluefish spawn near the inner edge of the Gulf Stream as they migrate northward from their wintering grounds off Florida. To a lesser extent some bluefish also spawn in the same area in fall and winter, presumably on their return migration. Adult bluefish migrate to coastal waters off the Middle Atlantic Bight in spring and feed there until they migrate south coincident with fall cooling. During their stay in the Middle Atlantic Bight, bluefish spawn on the shelf, and to some extent in mouths of the larger estuaries (Norcross et al. 1974). Although spawning can take place as soon as the adults arrive in the area in May, most seems to occur in July and August, while some continues into September. From the apparent annual variations in timing and amount of this spawning, it is dependent on a combination of several features of the environment including temperature, salinity, photoperiod, and food for the adults.

If each mature fish spawns in both areas and in all seasons, this would indicate that there is a single stock of bluefish on the east coast of the United States. If each fish spawns in only one area, separate populations must exist. Our early life history information is consistent with other information that indicates that there are separate populations. Southern and northern spawnings take place under quite different hydrographic conditions and in quite different current regimens to assist the young fish in movements to nursery grounds. In time these conditions could allow genetically distinct populations to become established. Tagging and fecundity studies would show to what extent this has happened.

Since year-class strength of fishes is determined mainly during their young stages, it is important to understand the factors influencing survival of these stages. In bluefish, the eggs and larvae occur at the surface of the ocean and the juveniles occur in estuaries, areas affected by annual variations in weather-related phenomena and, to an increasing extent, affected by man's activities. It is thus important to monitor these influences and

[7]B. L. Olla, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. August 1978.

develop models to relate them to year-class strength of the various spawnings of bluefish.

ACKNOWLEDGMENTS

John R. Clark, now of the Conservation Foundation, Washington, D.C., while at Sandy Hook Laboratory, supervised the initial work on bluefish larvae from the RV *Dolphin* collections. Several people helped in use of unpublished data in preparation of this paper: Stuart Wilk, NMFS, Sandy Hook, N.J.; David Deuel, NMFS, Narragansett, R.I.; and Sally L. Richardson, Oregon State University. Omie Tillet, Nags Head, N.C., helped make the sampling near Cape Hatteras in spring 1972 pleasurable as well as successful.

LITERATURE CITED

AGASSIZ, A., AND C. O. WHITMAN.
1885. Studies from the Newport Marine Laboratory. XVI. The development of osseus fishes. I. The pelagic stages of young fishes. Mem. Mus. Comp. Zool. Harvard Coll. 14(1), 56 p.

BARTLETT, M. R., AND R. L. HAEDRICH.
1968. Neuston nets and south Atlantic larval blue marlin (*Makaira nigricans*). Copeia 1968:469-474.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BRIGGS, J. C.
1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960:171-180.

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. Data Report I. Northern section, Cape Cod to Cape Lookout. R.V. *Dolphin* cruises 1965-66: Zooplankton volumes, midwater trawl collections, temperatures and salinities. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 28, 132 p.
1970. Studies of estuarine dependence of Atlantic coastal fishes. Data Rep. II. Southern section, New River Inlet, N.C., to Palm Beach, Fla. R.V. *Dolphin* cruises 1967-68. Zooplankton volumes, surface-meter net collections, temperatures, and salinities. U.S. Bur. Sport Fish. Wildl., Tech. Pap. 59, 97 p.

COLTON, J. B., JR., AND K. A. HONEY.
1963. The eggs and larval stages of the butterfish *Poronotus triacanthus*. Copeia 1963:447-450.

DE SYLVA, D. P., F. A. KALBER, JR., AND C. N. SHUSTER, JR.
1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper waters. Univ. Del. Mar. Lab., Inf. Ser., Publ. 5, 164 p.

DEUEL, D. G., J. R. CLARK, AND A. J. MANSUETI.
1966. Description of embryonic and early larval stages of bluefish, *Pomotomus saltatrix*. Trans. Am. Fish. Soc. 95:264-271.

FOWLER, H. W.
1944. Results of the Fifth George Vanderbilt Expedition (1941), (Bahamas, Caribbean Sea, Panama, Galápagos Archipelago and Mexican Pacific Islands). Fishes. Acad. Nat. Sci., Phila., Monogr. 6:57-529.

HERMAN, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.

IRVINE, F. R.
1947. The fishes and fisheries of the Gold Coast. Crown Agents for the Colonies, Lond., 352 p.

LUND, W. A., JR.
1961. A racial investigation of the bluefish, *Pomatomus saltatrix* (Linnaeus) of the Atlantic coast of North America. [Span. Abstr.] Bol. Inst. Oceanogr., Univ. Oriente, Cumana 1:73-129.

LUND, W. A., JR., AND G. C. MALTEZOS.
1970. Movements and migrations of the bluefish, *Pomotomus saltatrix*, tagged in waters of New York and southern New England. Trans. Am. Fish. Soc. 99:719-725.

MARAK, R. R., AND J. R. COLTON, JR.
1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 398, 61 p.

MARAK, R. R., J. B. COLTON, JR., AND D. B. FOSTER.
1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 411, 66 p.

MARAK, R. R., J. B. COLTON, JR., D. B. FOSTER, AND D. MILLER.
1962. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank-Gulf of Maine area, 1956. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 412, 95 p.

NORCROSS, J. J., S. L. RICHARDSON, W. H. MASSMANN, AND E. B. JOSEPH.
1974. Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginian coastal waters. Trans. Am. Fish. Soc. 103:477-497.

OBEN, L. C.
1957. About the drifting approach of fingerling bluefish, *Pomatomus saltatrix* L., to the shores of the Black Sea in the region of the Karadag (1947-1954). Translated from the Russian language by M. J. Koushnaroff and R. J. Mansueti from works of the Daradag Biol. Stn., Acad. Sci. Ukr. USSR 14:155-157.

OLLA, B. L., AND A. L. STUDHOLME.
1971. The effect of temperature on the activity of bluefish, *Pomatomus saltatrix* L. Biol. Bull. (Woods Hole) 141:337-349.
1972. Daily and seasonal rhythms of activity in the bluefish (*Pomatomus saltatrix*). *In* H. E. Winn and B. L. Olla (editors), The behavior of marine animals, Volume 2: Vertebrates, p. 303-326. Plenum Press, N.Y.

PACHECO, A. L., AND G. C. GRANT.
1965. Studies of the early life history of Atlantic menhaden in estuarine nurseries. Part I—Seasonal occurrence of juvenile menhaden and other small fishes in a tributary creek of Indian River, Delaware, 1957-58. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 504, 32 p.

PADOA, E.
1956. Uova, larvae stadi giovanili di teleostai: famiha Z: Pomatomidae. Fauna Flora Golfo di Napoli, Monogr. 38:570-572.

PEARCY, W. G., AND S. W. RICHARDS.
1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. Ecology 43:248-259.

PEARSON, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish Wildl. Serv., Fish. Bull. 50:79-102.

PERLMUTTER, A.
1939. Section I. An ecological survey of young fish and eggs identified from tow-net collections. *In* A biological survey of salt waters of Long Island, 1938, Part II, p. 11-71. N.Y. Conserv. Dep., Suppl. 28th Annu. Rep., 1938, Salt-water Surv. 15.

RICHARDS, E. C., AND M. CASTAGNA.
1970. Marine fishes of Virginia's Eastern Shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235-248.

SALEKHOVA, L. P.
1959. On the development of the bluefish (*Pomatomus saltatrix*) Linne. Tr. Sevastop. Biol. Stn. 11:182-188.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50:149-237.

SMITH, J. L. B.
1961. The sea fishes of southern Africa. 4th ed. Central News Agency, Ltd., South Africa, 580 p.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans. Their physics, chemistry, and general biology. Prentice-Hall, Inc., Englewood Cliffs, N.J., 1087 p.

TAGATZ, M. E., AND D. L. DUDLEY.
1961. Seasonal occurrence of marine fishes in four shore habitats near Beaufort, N.C., 1957-60. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 390, 19 p.

TURNER, W. R., AND G. N. JOHNSON.
1973. Distribution and relative abundance of fishes in Newport River, North Carolina. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 666, 23 p.

WRIGHT, W. R., AND C. E. PARKER.
1976. A volumetric temperature/salinity census for the Middle Atlantic Bight. Limnol. Oceanogr. 21:563-571.

CONTRIBUTION OF 1960-63 BROOD HATCHERY-REARED SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, TO THE COLUMBIA RIVER COMMERCIAL FISHERY

ROY J. WAHLE, REINO O. KOSKI, AND ROBERT Z. SMITH[1]

ABSTRACT

A 4-yr marking program was conducted at Leavenworth National Fish Hatchery, Leavenworth, Wash., to determine the contribution of hatchery sockeye salmon, *Oncorhynchus nerka*, to the Columbia River commercial fisheries and the economic feasibility of hatchery rearing of sockeye salmon. The study involved 1960 through 1963 brood-year fish. During the 4-yr period, 1961-64, a total of 11.5 million fish were released, of which 3.4 million were marked by the removal of the adipose fin and part of one of the maxillary bones—the right maxillary for 1960 and 1962 broods and the left maxillary for 1961 and 1963 broods. Trapping at the lake outlet in the spring for the first 2 yr indicated that less than 50% of the stocked fingerlings migrated. In 1964-67, recovery of marks from the commercial fishery on the Columbia below and the Indian fishery above Bonneville Dam showed that an average of 13.6% of the sockeye salmon catch was composed of fish raised at Leavenworth Hatchery. Adjusting for effects of marking, this represents an average fishery value per brood of $4,274.75. The average potential benefit:cost ratio for the 4 yr of the program was 0.04 to 1. Because preliminary data indicated such a low benefit:cost ratio, sockeye salmon rearing at Leavenworth was radically decreased in 1966 and terminated in 1969.

In the 1930's Grand Coulee Dam was constructed on the upper Columbia River, thus barring anadromous fish runs from 1,835 km of spawning and rearing area. The extreme height of the dam (106 m) precluded building passage facilities for both upstream and downstream migrants. To preserve the runs formerly utilizing the upper basin, a relocation of runs of affected species became necessary.

Basic data on existing fish populations were obtained from 1933 through the time of dam completion in 1941 (Fish and Hanavan 1948). The only relocation areas suitable for spawning and rearing were Columbia River tributaries below Grand Coulee Dam and above Rock Island Dam. The area was less than one-half the extent of that formerly available and on streams which, because of industrial diversion, were for the most part inaccessible to migrating fish. Because of general depletion of all the upriver salmonid runs, correction of fish passage problems was already underway in many areas. With the impetus of the relocation program, further rehabilitation was accomplished.

The sockeye salmon, *Oncorhynchus nerka*, was seriously affected by the habitat changes as its development required a lake-stream environment which has been almost completely eliminated. Annual commercial catches of Columbia River sockeye salmon ranged from ½ to 2 million kg prior to 1900 (Gangmark and Fulton 1952). From then through the early 1920's annual catches varied from about ¼ million to over 1 million kg. Following one more good year in 1926, the ½ million kg figure was never again reached (Figure 1).

Estimates of escapement beyond the fishery were not possible until enumeration of migrating adults began in 1933 at Rock Island Dam, 755 km above the mouth of the Columbia River. An average of about 19,000 adults was counted annually until 1941, when only 949 adults passed upstream. The low escapement was caused by a large commercial catch, low flows, and retention of water behind Grand Coulee Dam (Fish and Hanavan 1948).

The relocation of runs began in 1939 for sockeye salmon as well as chinook salmon, *O. tshawytscha*; coho salmon, *O. kisutch*; and steelhead trout, *Salmo gairdneri*. Adult sockeye salmon were trapped at Rock Island Dam and were transported by tank trucks to the Wenatchee and Okanogan

[1]Environmental and Technical Services Division, National Marine Fisheries Service, NOAA, 811 N.E. Oregon, Portland, OR 97208.

Manuscript accepted September 1978
FISHERY BULLETIN VOL. 77, NO. 1, 1979

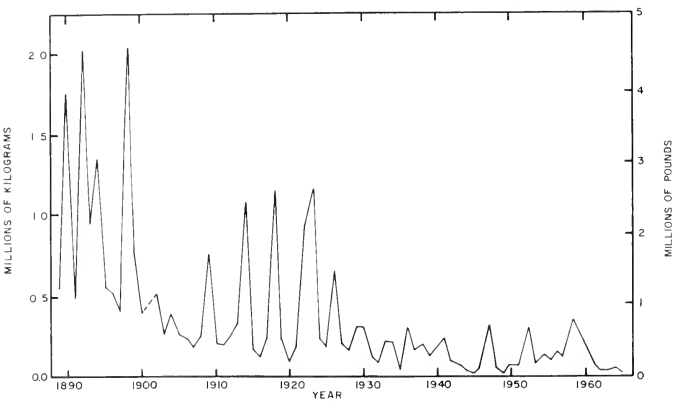


FIGURE 1.—Commercial catch of sockeye salmon in the Columbia River, 1889-1967. [Data for 1889-1936 from Craig and Hacker (1940), for 1937 from Ward et al. (1963) and for 1938-67 from Fish Commission of Oregon and Washington Department of Fisheries (1968).]

Lakes where they were allowed to spawn naturally (Figure 2).

Supplementary to adult relocation, an artificial propagation program was planned. A hatchery was constructed on Icicle Creek, a tributary of the Wenatchee River near Leavenworth, Wash. (Figure 3). Smaller substations were built on the Entiat and Methow Rivers. The sockeye salmon production program was to be concentrated at Leavenworth National Fish Hatchery.

Fish produced at Leavenworth were stocked into Wenatchee and Osoyoos Lakes. Success of the sockeye salmon relocation program was indicated in 1947 when the largest run recorded since 1926 appeared. This raised the question of whether the remaining available spawning habitat was overpopulated, prompting annual inventories that continued for many years (Gangmark and Fulton 1952).

How much of the apparent improvement in sockeye salmon runs was attributable to hatchery production was unknown. Importance of the Wenatchee system for total sockeye salmon production was obvious. Data indicated that an average of 33% of upper Columbia River sockeye salmon homed to the Wenatchee River in the 7 yr just prior to this study (French and Wahle 1965).

Wenatchee System Sockeye Salmon Stock

For over 25 yr Leavenworth Hatchery produced sockeye salmon which were stocked and reared in Wenatchee River tributaries. During this time, five major dams were built on the main Columbia River downstream. These structures, combined with growth and expansion in population and industry, added greatly to existing problems which confronted both downstream migrants and returning adults.

The Wenatchee River system was historically an excellent salmon producing system. It was comparable, for sockeye salmon production, to the Arrow Lakes, Yakima Basin, and Okanogan Lake areas, formerly the primary producers of this species in the basin (Figure 2). In the early 1900's the runs in the Wenatchee became severely depleted because of construction of impassable mill and power dams and unscreened irrigation projects. These conditions prevailed until the early 1930's, at which time about 85% of the Columbia

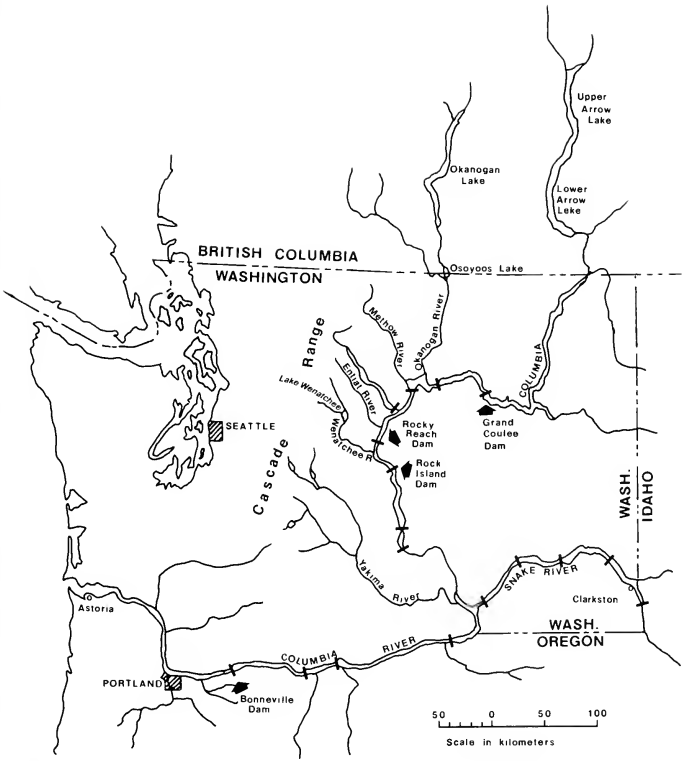


FIGURE 2.—Portion of Columbia River Basin showing areas of past and present importance to sockeye salmon as described in text.

River run was being produced in the Arrow Lakes area (Fulton 1970).

The Grand Coulee Fish-Maintenance Project (Fish and Hanavan 1948) began in 1933. Under this project, obstructions were removed, dams were provided with passage facilities, and irrigation diversions were screened. These measures were necessary to establish suitable habitat for the relocated runs in tributaries between Grand Coulee and Rock Island Dams.

To reintroduce sockeye salmon to the spawning areas above Lake Wenatchee and provide eggs for

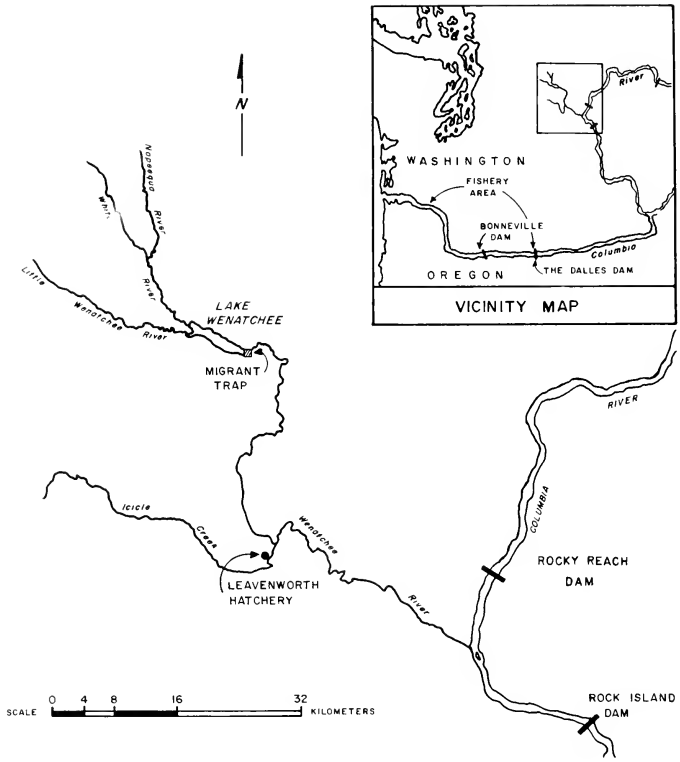


FIGURE 3.—The Wenatchee River system and location of Leavenworth National Fish Hatchery

Leavenworth Hatchery, adult fish were trapped from 1939 through 1943 at Rock Island Dam on the main Columbia. Because the proposed hatcheries would not be available to handle fish until 1940, adults of all displaced species were released for natural spawning in predetermined locations. Separate areas were selected for each species to prevent overcrowding and mixing. Most of the sockeye salmon transplanted undoubtedly originated in the Arrow Lakes, but fish from the Okanogan and Wenatchee systems were certainly included (Fulton 1970).

Under the Grand Coulee Fish-Maintenance Project, sockeye salmon adults were trapped in July and August and hauled by tank truck to Lake Wenatchee, 113 km above Rock Island Dam, where a barrier was installed at the outlet. When spawning time approached, the fish ascended the White and Little Wenatchee Rivers where they spawned. When eggs were later needed for hatchery use, weirs were installed and adults trapped to supply the required ova. Surplus adults were allowed to pass upstream and spawn naturally. The offspring of these natural spawners homed back to the system to establish the new Wenatchee stock.

Spawning occurred in September and October. The fry emerged from the gravel in spring and drifted back down to the lake to rear until the following year. Outmigration occurred in April and May, with a peak reached in early May prior to the heavy spring run-off period (French and Wahle 1959). Following 2, or occasionally 1 or 3, yr at sea, the adults entered the Columbia River in late spring. The run passed Bonneville Dam in late June and early July, and several weeks later ascended the Wenatchee River to renew the cycle.

The Hatchery

Leavenworth National Fish Hatchery was completed in 1940 as the primary station to provide hatchery-reared fish to supplement the newly established natural runs. Sockeye salmon were to be produced there and adults of other species were spawned to obtain stock to supply the satellite stations on the Entiat and Methow Rivers (Figure 2). The hatchery capacity was approximately 3.5 million eggs and 2.4 million fingerlings (Fish and Hanavan 1948).

The source of eggs for the first 5 yr of operation was fish that had been hauled to Lake Wenatchee from Rock Island Dam as part of the relocation project. After this period the adult transportation was terminated and spawning operations continued using fish returning to the lake naturally.

After the eggs were taken and fertilized, usually in September, they were transferred to the hatchery for incubation. Hatching began in January and the fry began to feed about 6 wk later. Initial rearing took place inside the hatchery, and when water temperatures became suitable, they were placed in outside rearing ponds. In September or October, upon reaching an average weight of 9 to 10 g, the fingerlings were trucked to the lake. Survival from egg to stage at release ranged from 62 to 96%. After wintering over until the following April or May, the smolts migrated out of the lake.

From general observations, it appeared that the hatchery operation was a success: proper rearing techniques were followed, hatchery migrants were observed leaving the lake, adults returned to the area in adequate numbers, and fish were available for commercial harvest. Data obtained through spawning surveys and downstream migrant counts at the dams indicated that the sockeye salmon population was being satisfactorily maintained. However, it was not possible to determine whether the wild stock or the hatchery fish contributed most to the runs. Downstream migrant studies by Anas and Gauley (1956) pointed out the impossibility of identifying the separate stocks.

There were indications that the costs of conducting a sockeye salmon hatchery program were significantly higher than the values contributed to the fishery. Despite complexities of measurement of runs, some means of assessment seemed necessary. Thus, a study was designed to evaluate the economic feasibility of continuing artificial propagation of sockeye salmon at the hatchery.

The study involved the marking of a proportion of the hatchery sockeye salmon production for a period of 4 yr, observations on the rearing and migration of the fingerlings, and estimation of the contribution of returning adults to the commercial fishery. An analysis of production costs and the monetary benefits to the fishermen was included.

FIELD OPERATIONS

Estimating Procedures

The procedures used in making estimates of numbers of fish are similar to those described in reports by Worlund et al. (1969) and Wahle et al. (1974). Estimates of the potential contributions and value of hatchery sockeye salmon required four steps: 1) estimation of marked and unmarked hatchery releases, 2) estimation of catch of marked adults, 3) estimation of total contribution of hatchery fish to the catch, and 4) application of dollar values to the estimate of contribution.

Marking and Release Procedure

The study began in July 1961, using 1960-brood fingerling sockeye salmon. Each year, approxi-

mately one-third of the total Leavenworth Hatchery stock was marked. In each year except the first, a circular net pocket with a metal sleeve and a tub sampler were used to obtain a sample of fish for marking. Two types were employed: a 3-pocket sampler which gave an approximate 33.3% sample for marking, and a 10-pocket sampler (Worlund et al. 1969; Wahle et al. 1974) which provided a 10% sample for population estimate. In 1961, the one-third sample was obtained by marking every third pond, and in the other 3 yr the fish to be marked were selected as described above.

In 1961, hatchery personnel marked 1,008,310 1960-brood sockeye by removing the adipose fin (Ad) and part of the right maxillary bone (RM). In 1962, the 1961-brood fish (600,036) were marked by removal of the adipose fin and part of the left maxillary bone (LM). The 1962-brood fish (1,146,485) were marked the same as the 1960-brood, and the 1963-brood (606,578) repeated the 1961-brood mark.

In 1961 the marked and unmarked fish were kept in separate ponds and mortality records kept for each group. The number of unmarked fish for release was estimated by using the number of eggs and the percentage of hatch, and subtracting the number marked plus pond mortality. As the fish were stocked, in order to avoid bias, the marked and unmarked fish were mixed in each truck load.

In the three following years, by knowing the actual number of fish marked for each brood year, and the postmarking mortality, the total population at release time was estimated. Using the 10-pocket sampler on a random group of fish from a pond, a 10% sample was obtained. Repeating this procedure on the 10% sample provided a 1% sample, and a Peterson index of sample size was calculated (Table 1). The fingerlings were transported by tank truck and released into Lake Wenatchee each fall.

TABLE 1.—Numbers of sockeye released into Lake Wenatchee, Wash., during marking program.

Brood	Mark[1]	No marked	No unmarked	% marked	Total released
1960	Ad-RM	1,000,725	1,760,319	36.24	2,761,044
1961	Ad-LM	571,726	1,327,878	30.10	1,899,604
1962	Ad-RM	1,247,755	2,554,809	32.81	3,802,564
1963	Ad-LM	570,735	2,504,344	18.56	3,075,079
Total		3,390,941	8,147,350	29.39	11,538,291

[1]Ad = adipose fin, RM = right maxillary bone, LM = left maxillary bone

In the spring of 1962 and 1963, a trap was operated at the lake outlet to monitor the outmigration. Data obtained at the trap indicated that <50% of the marked fish migrated downstream. This amounted to 38.4% of the marked fish of the 1960-brood and 47.9% of the 1961-brood.

Marked Fish Recovery

Sampling for returning marked adults began in 1964 and continued through 1968. Earlier returns were not expected because prior studies at Lake Wenatchee indicated that few, if any, adults would return in their third year (Major and Craddock 1962). The search for marks was confined to the two commercial fishing areas in the lower Columbia River: zones 1-5, the gill net fishery below Bonneville Dam, and zone 6, the Indian set net and dip net fishery above the dam (Figure 3). Other fisheries were not sampled as Columbia River sockeye salmon rarely occur in the ocean commercial catch and are seldom taken by sport anglers (Koski 1964).

We looked for marked fish during the commercial seasons. The zone 6 catch was monitored at Washington and Oregon Indian fishery buying stations. Commercial canneries in the lower river were sampled for the zones 1-5 gill net catch. Unfortunately for the study, the commercial gill net season in zones 1-5 was closed in 1965 and 1966, and opened only for 5 days in 1964 (Fish Commission of Oregon and Washington Department of Fisheries 1968). The zone 6 catch was also limited by this restriction, severely reducing the total catch (see Table 4). The catch in the 7 yr previous to the study averaged 90,900 fish. During the study period the average was only 22,500 ranging from 4,361 to 56,200 (Figure 4).

Sampling Results

Nearly one-half of the Columbia River commercial sockeye salmon catch was inspected for marks each year, except in 1966 when only a 4.2% sample was obtained because of the erratic nature of landings. The extremely small sample undoubtedly biased the estimation of catch for the brood years involved. For most brood years, the majority of fish were caught in their fourth year (Table 2). For all broods except the 1962 group an average of 94% was caught at age 4_2 (4 - total age, 2 - seaward migration age). This age-group represented only 4% of the total 1962-brood fish caught in 1966, evidence that the age 4_2 fish were almost entirely missed by the fishery, although undoubtedly available.

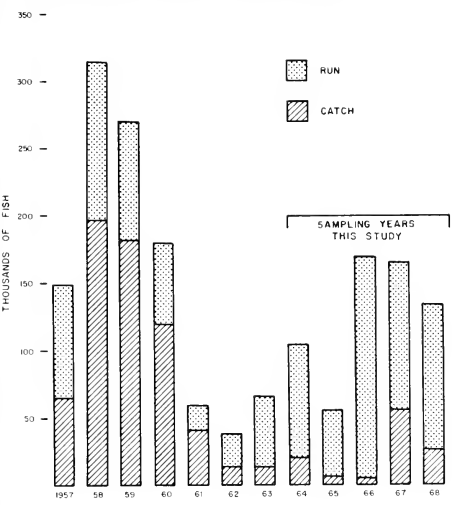


FIGURE 4.—Columbia River sockeye salmon commercial catch in thousands, as part of the total run, 1957-68. [Data from Fish Commission of Oregon and Washington Department of Fisheries (1968).]

TABLE 2.—Sampling rate and marks observed in Columbia River commercial fishery for sockeye 1960-63 broods.

Catch year	Fishery zone[1]	Total catch	Number sampled	Percent sampled	No. of marks observed by brood year			
					1960	1961	1962	1963
1964	1-5	4,950	3,307					
	6	15,820	7,195					
	Total	20,770	10,502	50 6	265	1		
1965	1-5	70	24					
	6	5,773	3,024					
	Total	5,843	3,048	52 2	22	43		
1966	1-5	157	27					
	6	4,204	158					
	Total	4,361	185	4 2		1	8	
1967	1-5	21,218	7,993					
	6	35,002	13,885					
	Total	56,220	21,878	38 9			191	294
1968	1-5	20,300	9,689					
	6	5,000	2,632					
	Total	25,300	12,321	48 7				16
				Total	287	45	199	310

[1]Zone 1-5 (below Bonneville Dam), Zone 6 (above Bonneville Dam)

The number of fish in the catch, the number sampled and the number of marks recovered from zones 1-5 and zone 6, were combined.

CALCULATIONS

Because the marks used to distinguish the groups of hatchery fish have a negative effect on survival, two different steps were employed to calculate the hatchery fish contribution. The determination of the level of contribution required an estimation of the number of hatchery fish in the catch for each year sampled. This was calculated from the estimated number of marked fish plus the estimated number of hatchery unmarked after a correction for differential mark mortality. Potential catch is that which would be expected if marking did not cause postrelease mortalities.

Differential Mark Mortality (Survival Factor)

We suspected that there would be adverse effects on the survival of the fish because of the excised fin and maxillary bone. Foerster (1968) reported that marked sockeye salmon at Cultus Lake had an estimated return of only 38% of the unmarked return.

To obtain a mark survival factor, a modification was made to the procedure for marking the 1961-brood fish. In addition to the group that received an Ad-LM, a second group received only a chemical (tetracycline) mark, while a third had both marks. In sampling returning adults, a comparison of the three groups showed that only 40% of Ad-LM fish expected, returned (Weber and Wahle 1969). Because we believe that tetracycline had no effect on survival, we considered that the difference between returns was caused by mortality due to marking by excision.

Marks in Catch

To calculate the number of marks in the catch for a certain year, the number of n marks in the sample was divided by the sampling ratio:

$$n \text{ marks (catch)} = \frac{n \text{ marks (sample)}}{n \text{ fish (sample)}/n \text{ fish (catch)}}$$

This assumed a random sample of the catch. The mark survival factor was not considered in this equation.

Hatchery Contribution to the Fishery

To determine the percent of sockeye caught in a specific year that originated at Leavenworth Hatchery, the number of (n) unmarked hatchery fish in the catch was estimated by using the number of (n) marked fish in the catch and dividing by the sampling ratio and the marked/unmarked ratio at release, corrected by the mark survival factor. The correction was necessary because this ratio changes from the time of release to time of catch due to the effects of marking:

$$n \text{ unmarked hatchery catch} = \frac{n \text{ marks (catch)}}{\frac{n \text{ fish (sample)}}{n \text{ fish (catch)}} \times \frac{n \text{ marked release}}{n \text{ unmarked release}} \times \text{survival factor}}$$

Summing the marked and unmarked hatchery fish for a catch year and dividing by the total catch gave the estimated percent produced by the Leavenworth Hatchery. For 1964-67, contributions averaged 13.6% of the total catch (Table 3). The 21.6% figure for 1966 may not be representative as the sample size that year was small.

TABLE 3.—Estimated numbers and percent of hatchery sockeye in Columbia River commercial catch.

Catch year	Brood year	Hatchery fish				Total catch all fish
		Marked	Unmarked	Total	%	
1964	1960	517	1,504	2,021		
	1961	2	8	10		
Total		519	1,512	2,031	9.8	20,770
1965	1960	42	123	165		
	1961	82	316	398		
Total		124	439	563	9.6	5,843
1966	1961	24	90	114		
	1962	189	638	827		
Total		213	728	941	21.6	4,361
1967	1962	500	1,692	2,192		
	1963	751	5,443	6,194		
Total		1,251	7,135	8,386	14.9	56,220
1968	1963	31	226	257	(1)	25,300

(1) Not applicable as no 1964 brood hatchery fish were marked

Potential Hatchery Catch

A potential hatchery catch figure is a theoretical number that represents what could have been caught in a given fishery assuming the same effort and no marking program and was required to calculate benefit/cost ratios. It allows for the large number of fish failing to survive because of the mark. Potential hatchery catch (Table 4) was calculated by dividing the number of marks in the catch by the mark survival factor and adding the

TABLE 4.—Potential number and weight of hatchery sockeye by brood year and catch year.

Brood year	Catch year	No. with marks in sample	Hatchery fish in catch		
			Estimated no.	Potential no.	Potential wt[1] (kg)
1960	1964	265	2,021	2,359	4,122
	1965	22	165	192	342
Total		287	2,186	2,551	4,464
1961	1964	1	10	11	16
	1965	43	398	451	802
	1966	1	114	130	234
Total		45	522	592	1,052
1962	1966	8	827	950	1,706
	1967	191	2,192	2,518	4,085
Total		199	3,019	3,468	5,791
1963	1967	294	6,194	6,684	10,733
	1968	16	257	277	479
Total		310	6,451	6,961	11,212
Grand total		841	12,178	13,572	22,519

[1]The average weight of commercially caught sockeye ranged from 1.5 to 1.8 kg during the study.

number of unmarked hatchery fish in the catch:

$$\text{potential hatchery (catch)} = \frac{n \text{ marks (catch)}}{\text{survival factor}} + \text{unmarked hatchery (catch)}.$$

ECONOMIC EVALUATION

A primary purpose of this study was to determine the economic feasibility of rearing sockeye salmon at Leavenworth National Fish Hatchery. An oft-employed measure of financial worth of a program is the benefit/cost ratio which compares the dollar value (benefit) of the fish returned to the amount spent (cost) in their production. Normally a favorable ratio should exceed 1:1.

Cost Accounting

Production costs for each brood of sockeye salmon in this study were derived in the same manner as in Wahle et al. (1974) and consisted of two categories, amortized construction costs or capital costs and operational costs.

The "annual imputed capital charge" was computed by amortizing the capital expenditures at the hatchery into 30 equal annual payments using an interest rate of 3.5%. This rate was the average 3- to 5-yr government bond interest rate weighted by the total annual capital outlay at Columbia River Program Development hatcheries from 1949 to 1970. As the hatchery reared other species in addition to the study fish, the capital charge was apportioned by applying a percentage based on the ratio of manpower time charged specifically to sockeye salmon care.

Operation and maintenance costs were divided into fish food and drugs, and other operational costs. Fish food and treatment costs were apportioned according to the pounds of study fish produced as a percentage of the total production. Other operational costs including labor, personal services, travel, equipment, supplies, and administration were apportioned, as with capital, according to the percentage of time allotted to the care of each brood.

Benefits

In other economic studies involving Columbia River salmonids (Worlund et al. 1969; Wahle et al. 1974) benefits included the accrued values from exvessel prices received by commercial fishermen engaged in the variety of catch methods, i.e., offshore troll, purse seine, gill net, set net, etc. In addition, benefits were calculated for sport-caught fish and for sale of adult carcasses to processors. Our study included only the benefits to commercial fishermen on the Columbia River in the gill net (zones 1-5), and tribal dip net (zone 6) fisheries. Sport catch values were not considered as there are virtually no sockeye salmon caught by anglers in the river.

The simple exvessel price paid to fishermen is a reasonable estimate of benefits as explained by Richards,[2] although some inadequacies exist in more intensive and complicated fisheries. For the minor fishery involved in this study, this method

[2]Richards, J. A. 1969. An economic evaluation of Columbia River anadromous fish programs. U.S. Dep. Int., Fish Wildl. Serv., Bur. Commer. Fish., Working Pap. 17, 274 p.

of valuation seemed satisfactory. The commercial price paid to fishermen during the sampling years ranged from $0.68 to $0.82/kg depending on the area of catch. The benefit/cost ratio averaged 0.039:1, or approximately 4 cents returned for each dollar spent (Table 5).

TABLE 5.—Benefit-cost ratios for Leavenworth sockeye 1960-63 broods

Brood year	Total catch (kg)	Hatchery fish in catch		Production cost ($)	Potential benefit-cost ratio
		Potential wt (kg)	Potential value ($)		
1960	41,327	4,464	3,062	114,123	0.027:1
1961	49,160	1,052	858	86,823	010:1
1962	97,228	5,791	4,456	124,321	036:1
1963	75,579	11,212	8,723	113,541	077:1
Total	263,294	22,519	17,099	438,808	039:1

DISCUSSION

As our results clearly show, hatchery fish did not appear significantly in the commercial catch, averaging only 13.5% of the total harvest. Considering that the hatchery fish may have utilized almost one-half of the natural rearing space available, we expected their contribution would be greater. We also expected a larger proportion of hatchery fish in the returning adult run based on the ratio of hatchery to wild smolts emigrating from Lake Wenatchee. In a concurrent study, Craddock[3] determined that hatchery fish made up 53% and 72% of the 1962 and 1963 total outmigration, respectively.

From the economic viewpoint we feel that the study produced an accurate assessment of the benefits provided to the commercial fishermen by the addition of hatchery fish to their catch. We are confident that the method of determining the production costs of the hatchery sockeye salmon provided a valid estimate for that portion of the benefit/cost ratio.

Benefits as a measure of value in this study applied specifically to those received by the commercial fishery. Not considered were intangible benefits derived from the preservation, maintenance, and enhancement of the Columbia River sockeye salmon. The return of adults to the system for a hatchery egg source is another value. Another unmeasured benefit was the contribution to the Indian subsistence and ceremonial fisheries. In short, the total benefits from the Leavenworth Hatchery sockeye salmon program were obviously greater than the value derived within the specific confines of the study.

From the catch results it is apparent that the study period was one of an abnormally low harvest. The river below Bonneville Dam was closed completely for two of the catch seasons and only 5 days fishing allowed in another, with almost all of the small catch taken in the Indian fishery. As the benefits were based on the number of fish provided the commercial fishery, and the zones 1-5 fishermen were almost completely denied the opportunity to harvest these fish, then little in the way of value could be expected under these conditions. It should be noted that the regulatory measures were in effect specifically for the protection of low runs of summer chinook salmon and summer steelhead trout which can be netted at the same time in the area.

Another indication of the unusually low harvest of sockeye salmon during the study period is noted in catch:escapement ratios (C/E), which in the 5 yr preceding the study were 1/1 - 2.6/1. During the study the ratio did not exceed 0.5/1 and ranged downward to 0.02/1 (Fish Commission of Oregon and Washington Department of Fisheries 1968).

In addition to the low rate of return associated with adult harvest, we suspected that poor survival of the released fish through various stages was a primary cause of low adult returns. Problems confronting the young sockeye salmon are discussed below.

We could not assess any effect on the released fingerlings caused by rearing practices at Leavenworth Hatchery, as there was no comparable rearing of sockeye salmon elsewhere. We assumed that the produced fish were of good quality, as the rearing techniques, disease control, and nutrition in effect at the hatchery were essentially the same at other Columbia River salmon hatcheries raising other species.

A possible hatchery-related effect on the quality of the stocked fish may have been undetected disease. As reported by Guenther et al. (1959), a filterable virus disease transmitted by feeding of sockeye salmon carcasses at Leavenworth Hatchery caused extreme mortalities prior to 1954 when the practice was discontinued. Losses from undetected diseases could have had significant effect on survival following release of the fingerlings. Although kidney disease was not detected at the hatchery, prior to release, the senior author observed it in fish held in saltwater during the mark

[3]D. R. Craddock, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Mukilteo, WA 98272, pers. commun. April 1964.

retention phase of the project. Cumulative long-term effects on outmigrants may have been substantial. Other viral diseases, about which little was known at the time, may have been present.

Lake Existence

A high rate of mortality occurred in Lake Wenatchee during the period of lake rearing, and this was probably spread over the period from stocking until outmigration. Losses similar to the 62 and 51%, found where outmigrants were enumerated, undoubtedly occurred in the 2 yr in which outmigrants were not counted. Foerster (1968) reported that the average smolt migration from British Columbia and Alaska lakes where only fry were stocked was 44% and the survival to return ranged from 11 to 84%. The hatchery rearing at Leavenworth seemed an economic waste, as equal outmigration rates may have been obtained using fry plants.

There is an extensive sport fishery in Lake Wenatchee on Dolly Varden, *Salvelinus malma*, and kokanee, a nonmigrant strain of sockeye salmon. We monitored this fishery in order to determine the effect on released study fish.

Incidental to the trout catch, a fairly large number of sublegal (<6-in) hatchery salmon were taken. This was determined by the presence of marked fish in a sample of sublegal fish in the angler catch. The hatchery fish were caught during the early spring of their second year just prior to their outmigration. Most sublegals were released by the anglers, but mortality undoubtedly resulted from hooking and handling. Additionally, some of the marked sockeye salmon remained in the lake without migrating and were observed throughout the season in the creel checks of legal-sized trout. The percentage becoming resident was unknown, but in 1964 represented 1.4% of the calculated total kokanee sport catch of 17,523 fish.

Sockeye salmon becoming resident in the lake and entering the sport fishery, based on 1964 data, accounted for <1% of the stocked fish. The mortality of sublegal fingerlings from angling was assumed to be small because of their rare occurrence in the sport catch. Health records of the hatchery fish did not indicate any expected loss from disease or parasites. Undoubtedly, the large loss of fingerlings was due to predation by larger fish and possibly starvation.

The heaviest loss of fingerlings in the lake was certainly caused by predation. Although precautions were taken during release, when fish were barged to avoid shoreline concentrations. Thompson and Tufts (1967) reported heavy predation both during and following release periods. Dolly Varden and northern squawfish, *Ptychocheilus oregonensis*, were sampled by gill net and trolling gear. During the weeks of release, the number of captured fish containing sockeye salmon ranged from 58 to 100%. Gangmark and Fulton (1952) during experiments in 1949-51 reported heavy predation by the same species. Our own observations of angler-caught fish from March through July 1962 showed an average of over one sockeye salmon per stomach. No estimate of the total predation loss was possible as the total number of predators was not known.

From our observations and those reported by Allen and Meekin (1973) the zooplankton production in the lake peaked in August and September each year. The hatchery fish, stocked in October, were faced with a declining food supply. Growth apparently stopped during the winter. Fingerlings of the 1961-brood averaged 97 mm FL when stocked in October whereas in the following spring, migrants trapped at the outlet, had a size range of 87-98 mm FL (Weber and Wahle 1969). Low food productivity of the lake, coupled with competition from natural resident fish for food, undoubtedly affected the fitness of the migrant sockeye salmon and possibly caused subsequent losses from stress on the seaward journey.

It is highly improbable that any hatchery production program utilizing an additional rearing period in Lake Wenatchee could succeed. However, even if no loss had occurred during lake residence, thus doubling the number of hatchery outmigrants, no more than a twofold increase in adults could be expected. Even with such an improvement, still more than 10 times that number of adults would be required for a favorable benefit/cost ratio.

Downstream Migrant Problems

With a large portion of the production sacrificed in the lake, the remaining smolts were still faced with great problems. Until recently, little was known of the causes and extent of downstream losses of sockeye salmon, although much information has been obtained for chinook salmon and steelhead trout smolts. Anas and Gauley (1956) studied the seaward migration of sockeye salmon smolts and their data suggested a wide range in

travel time and in size and age of migrants. No estimates of mortality of any given group of sockeye salmon could be made from their data or from other studies conducted at the various dam projects. However, we have assumed that extremely large losses occur in each annual outmigration of sockeye salmon, comparable to those documented for chinook salmon and steelhead trout.

Losses can occur in but a short distance during the seaward journey. Ellis and Noble (1960) reported losses of fall chinook salmon of 12.2 to 29.7% in the Klickitat River in a distance of only 64 km. The Wenatchee stock sockeye salmon smolts had to navigate 844 km in their seaward migration and were subjected to injuries and possible death at each of seven dams, plus the myriad effects of altered flows and water quality.

Major direct causes of mortality in juvenile migrants are gas bubble disease, a result of high dissolved nitrogen concentrations which occur throughout the river and death or injury by passing through turbines (Ebel et al. 1973). At high flows with excessive spill the fingerlings are subjected to the nitrogen problem, while the turbine caused losses are most severe at low flows. Chaney and Perry (1976) reported that the juvenile losses averaged 15 to 20% at each mainstem dam from combined causes. At low flows, cumulative fish losses just from turbine mortality at a series of seven dams may exceed 90%.

Additional mortality can be expected from several other causes. The delay of stream flow in the impoundments has reduced migration rates of juveniles by one-third according to Raymond (1969). The fish are then subject to increased predation, possible loss of marine adaptability, and may become residual in the reservoir. Undoubtedly but a small part of the outmigrants ever reach the sea in some years.

Adult Problems

We surmise that the sockeye salmon suffer losses comparable to the other species in the ocean, but there is no appreciable fishery harvest. The few tagging returns that have been reported for Columbia sockeye salmon (Margolis et al. 1966) indicate a more southerly distribution than for Canadian or Washington sockeye salmon, and there is no inshore marine fishery to intercept the adults.

The relatively few remaining adult sockeye salmon, after surviving the perils of sea life, still must face serious obstacles on the spawning migration. Aside from the commercial harvest, a substantial mortality occurs which cannot be measured precisely. In early reports of upriver fish passage, Schoning (1948) pointed out that annually an average of 36% of the Bonneville Dam count could not be located after subtracting the known harvest. "Fall-back" contributes to the loss and obscures the actual number passing the dam. Later accounts corroborate these losses (Chaney and Perry 1976). Bonneville Dam mortalities would reduce the number of fish available for harvest only in the zone 6 portion of the fishery.

SUMMARY

1. The Columbia River system produced large runs of sockeye salmon prior to 1900, providing an annual commercial harvest reaching 2 million kg.

2. Deterioration of spawning areas and blockage of tributaries caused a severe decline in the sockeye salmon population early in this century.

3. Construction of Grand Coulee Dam in 1941 blocked the sockeye salmon from 1,835 km of spawning and rearing areas, virtually eliminating all natural production.

4. Compensatory measures intended to replace the lost production included relocation of the sockeye salmon runs to suitable areas below Grand Coulee Dam and construction of hatcheries for additional production.

5. Leavenworth National Fish Hatchery on the Wenatchee River was activated in 1940 as the primary fish production station and an annual stocking program of sockeye salmon fingerlings was started.

6. For over 20 yr Leavenworth Hatchery reared sockeye salmon, releasing the fingerlings into the Wenatchee system augmenting the natural production.

7. No assessment had been made of the actual contribution of hatchery fish to the commercial fishery, thus the subject study was initiated using the 1960-63 broods of sockeye salmon.

8. During the initial 4 yr of the study, a total of 11,538,291 fish were released, of which 3,390,941 were marked by removal of the adipose fin and a part of the maxillary bone.

9. The stock used was adult sockeye trapped in tributaries of Lake Wenatchee. Fingerlings were reared at the hatchery until fall, then released into Lake Wenatchee.

10. Surviving smolts migrated out of the lake in the spring. Outmigrant trapping in the first 2 yr

revealed that <50% of the stocked fish migrated downstream.

11. From 1964 through 1968, sampling for marked adults was conducted in the two Columbia River fisheries: the gill net area below Bonneville Dam (zones 1-5), and the Indian set net and dip net fishery above the dam (zone 6). An average of 43.5% of the commercial catch was examined for marks.

12. The commercial harvest was atypical during the study because of regulation restrictions. The average annual harvest for the period was only 22,500 fish compared with average landings of 90,900 for the prior 7 yr. The C/E ratio did not exceed 0.5/1.

13. Almost all hatchery fish in the catch were in their fourth year of life. The average weight of fish in the catch ranged from 1.5 to 1.8 kg.

14. A mark mortality correction factor was included in calculations of hatchery fish in the catch as it was shown that the marked fish survival was only 60.52% of the unmarked fish.

15. During the study, hatchery fish composed an average of 13.6% of the total commercial catch.

16. The exvessel price to fishermen, used to determine benefits in this study, ranged from $0.68 to $0.82/kg.

17. Production costs were determined by a previously developed method utilizing both capital and operational charges.

18. The benefit cost ratio for the study broods was 0.039:1 or about 4 cents returned for each dollar spent.

19. Factors contributing to poor survival of juvenile fish were: high mortality from predation and angling during lake rearing, probable disease and nutritional problems, losses during migration from turbine injury and gas bubble disease, and delay in reservoirs.

20. Reasons for the low return of adults to the fishery include: unknown ocean mortality, losses incurred while ascending Bonneville Dam, and the erratic opportunity of harvest because of season restrictions.

ACKNOWLEDGMENTS

We are grateful for the assistance and cooperation of various individuals and agencies during the course of this study. Special thanks are offered the following individuals: Donald D. Worlund, National Marine Fisheries Service, for development of design and acting as primary consultant; Douglas Weber, Donovan Craddock, and Robert McConnell, National Marine Fisheries Service; Paul D. Zimmer and Eugene Maltzeff, Bureau of Commercial Fisheries; John W. Kincheloe and Steven K. Olhausen, U.S. Fish and Wildlife Service; and Arthur L. Oakley, formerly Fish Commission of Oregon, for their assistance in the design, supervision, and data collection and processing portions of this study. The aid and cooperation of Alfred C. Gastineau and Fredrick W. Bitle and staff of Leavenworth National Fish Hatchery is much appreciated. Helpful editorial comments were contributed by Richard T. Pressey, John I. Hodges, Steve H. Smith, National Marine Fisheries Service; William Sholes, California Department of Fish and Game; Robert Foster, Washington Department of Fisheries; Frederick C. Cleaver, Columbia River Fisheries Council; and F. K. Sandercock, Canadian Fisheries and Marine Service. Our thanks are due Kathleen LaBarge and Vivian Dignan for typing the text and tables for this publication.

LITERATURE CITED

ALLEN, R. L., AND T. K. MEEKIN.
1973. Columbia River sockeye salmon study, 1972. Prog. Rep. Wash. Dep. Fish., 61 p.

ANAS, R. E., AND J. R. GAULEY.
1956. Blueback salmon, *Oncorhynchus nerka* age and length at seaward migration past Bonneville Dam. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 185, 46 p.

CHANEY, E., AND L. E. PERRY.
1976. Columbia Basin salmon and steelhead analysis. Summ. Rep., Pac. Northwest Reg. Comm., 74 p.

CRAIG, J. A., AND R. L. HACKER.
1940. The history and development of the fisheries of the Columbia River. Bull. [U.S.] Bur. Fish. 49:133-216.

EBEL, W. J., D. L. PARK, AND R. C. JOHNSEN.
1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fish. Bull., U.S. 71:549-563.

ELLIS, C. H., AND R. E. NOBLE.
1960. Barging and hauling experiments with fall chinook salmon on the Klickitat River to test effects on survivals. Wash. Dep. Fish., 70th Annu. Rep., p. 57-71.

FISH COMMISSION OF OREGON AND WASHINGTON DEPARTMENT OF FISHERIES.
1968. The 1967 status report of the Columbia River commercial fisheries. Fish. Comm. Oreg. and Wash. Dep. Fish., 91 p.

FISH, F. F., AND M. G. HANAVAN.
1948. A report upon the Grand Coulee Fish-Maintenance Project 1939-1947. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 55, 63 p.

FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Board Can., Bull. 162, 422 p.

FRENCH, R. R., AND R. J. WAHLE
1959. Biology of chinook and blueback salmon and steelhead in the Wenatchee River System. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 304, 17 p.
1965. Salmon escapements above Rock Island Dam, 1954-60. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 493, 18 p.

FULTON, L. A.
1970. Spawning areas and abundance of steelhead trout and coho, sockeye, and chum salmon in the Columbia River basin—past and present. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 618, 37 p.

GANGMARK, H. A., AND L. A. FULTON
1952. Status of Columbia River blueback salmon runs, 1951. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 74, 29 p.

GUENTHER, R. W., S. W. WATSON, AND R. R. RUCKER.
1959. Etiology of sockeye salmon "virus" disease. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 296, 10 p.

KOSKI, R. O.
1964. Management of migratory game fish. Oreg. State Game Comm., Bull. 19(6), 8 p.

MAJOR, R. L., AND D. R. CRADDOCK.
1962. Influence of early maturing females on reproductive potential of Columbia River blueback salmon (*Oncorhynchus nerka*). U.S. Fish Wildl. Serv., Fish. Bull. 61:429-437.

MARGOLIS, L., F. C. CLEAVER, Y. FUKUDA, AND H. GODFREY
1966. Salmon of the north Pacific Ocean—Part VI. Sockeye salmon in offshore waters. Int. North Pac. Fish. Comm., Bull. 20, 70 p.

RAYMOND, H. L.
1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the Columbia River. Trans. Am. Fish. Soc. 98:513-514.

SCHONING, R. W.
1948. Trends of Columbia River blueback salmon populations, 1938-1947. Fish. Comm. Oreg., Res. Briefs 1(2):33-40.

THOMPSON, R. B., AND D. F. TUFTS.
1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. Trans. Am. Fish. Soc. 96:424-427.

WAHLE, R. J., R. R. VREELAND, AND R. H. LANDER.
1974. Bioeconomic contribution of Columbia River hatchery coho salmon, 1965 and 1966 broods, to the Pacific salmon fisheries. Fish. Bull., U.S. 72:139-169.

WARD, D., R. ROBISON, AND A. PALMEN.
1963. 1963 fisheries statistical report. Wash. Dep. Fish., 73d Annu. Rep., p. 127-216.

WEBER, D., AND R. J. WAHLE
1969. Effect of finclipping on survival of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 26:1263-1271.

WORLUND, D. D., R. J. WAHLE, AND P. D. ZIMMER.
1969. Contribution of Columbia River hatcheries to harvest of fall chinook salmon (*Oncorhynchus tshawytscha*). U.S. Fish Wildl. Serv., Fish. Bull. 67:361-391.

RELATIVE ABUNDANCE, BEHAVIOR, AND FOOD HABITS OF THE AMERICAN SAND LANCE, *AMMODYTES AMERICANUS*, FROM THE GULF OF MAINE

THOMAS L. MEYER, RICHARD A. COOPER, AND RICHARD W. LANGTON[1]

ABSTRACT

Meristic characteristics of sand lance taken from Stellwagen Bank indicated the species to be the American sand lance, *Ammodytes americanus*. Bottom trawl data, ichthyoplankton surveys, and diver and submersible observations demonstrated a significant increase in relative abundance of sand lance since about 1975 on Stellwagen Bank; this trend was typical of the Northwest Atlantic from Cape Hatteras, N.C., to the Gulf of Maine. School shapes were constant in appearance, vertically compressed, tightly compacted, and bluntly linear from a dorsal and ventral view. School strengths varied from about 100 to tens of thousands of individuals with the nearest-neighbor distance ranging from ¼ to 1½ body lengths. The swimming motion is sinusoidal in form and eellike in appearance. Swimming speeds varied from 15 to over 120 cm/s. Copepods were the most important food source, constituting 41% of the total weight of food consumed; sand lance feed in school formation between midwater and the surface. Sand lance bury themselves totally or partially in clean sandy substrates when not schooling.

In the Northwest Atlantic, sand lance range from Cape Hatteras, N.C., to Hudson Bay. They occur over sand and fine gravel bottoms and play an important role as a trophic link between zooplankton and commercially important fish such as Atlantic cod, haddock, silver hake, and yellowtail flounder (Scott 1968, 1973; Bowman and Langton 1978). Several species of sportfish (e.g., striped bass and bluefish) also utilize the sand lance as a food source (Bigelow and Schroeder 1953).

Studies of the eggs, larvae, and postlarvae of the American sand lance, *Ammodytes americanus*, have been reported by Covill (1959), Richards (1959, 1965, 1976), Norcross et al. (1961), Williams et al. (1964), and Richards and Kendall (1973). Investigations on the adult sand lance include taxonomic studies by Backus (1957), Richards et al. (1963), Leim and Scott (1966), Reay (1970), Winters (1970), Scott (1972), and Pellegrini[2] and studies on mortality and growth by Graham (1956) and Pellegrini (see footnote 2). Despite these investigations, little is known about the relative abundance, biology, behavior, and food habits of the adult American sand lance.

For the last 10 yr, information has been collected on sand lance during fishery cruises and undersea research programs conducted by the Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass. The purpose of this paper is to describe some aspects of the abundance, behavior, and food habits of the American sand lance based on bottom trawl (groundfish) survey data, observations by scuba divers and from research submersibles with photographic records, and a food-habit study.

MATERIALS AND METHODS

Study Area

The majority of the observations on sand lance were made on Stellwagen Bank, a submarine ridge that rises to within 18 m of the ocean surface on the eastern boundary of Massachusetts Bay (Figure 1). The length of the bank is 39 km (north-south axis) and its greatest width is 13 km (at the southern end). Depths range from 18 to 77 m. Substrate characteristics by depth interval recorded during submersible operations are: 18-43 m—sandy; 43-55 m—sandy bottom with crushed shells; 55-77 m—gravel, rocky with boulders; and below 77 m—mud/silt. Approximately 95% of the bank has a sandy bottom.

Additional observations on sand lance were

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Pellegrini, R. 1976. Aspects of the biology of the American sand lance, *Ammodytes americanus*, from the lower Merrimack River estuary, Massachusetts. Master's problem, Univ. Massachusetts, Amherst, 44 p.

Manuscript accepted September 1978
FISHERY BULLETIN VOL. 77, NO. 1, 1979

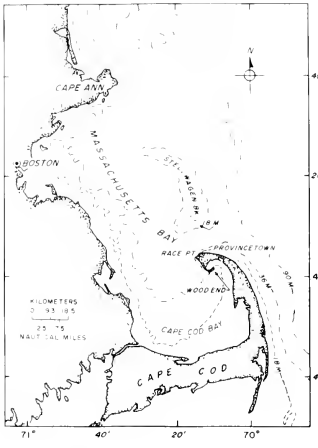


FIGURE 1.—Study area of sand lance observations, Gulf of Maine

made on the Provincetown slope from Race Point to Wood End (Figure 1). Depths over the Provincetown slope range from 0 to 46 m, with a medium-coarse sandy substrate throughout the range. Slope gradients by depth interval are: 0-9 m—5°-15°; 9-46 m—30°-45°. The relatively steep slope begins between 90 and 250 m offshore.

Relative Abundance

Divers using scuba, or observers in submersibles,[3] made in situ observations during various manned undersea research projects from 1968 through 1977 (Table 1, Figure 2). Camera systems aboard the submersible were: 1) a 35-mm Nikon[4] camera using a 55-mm micro lens and an externally mounted MK 150 Subsea stroboscopic light, and 2) a Sony AD 3400 Monochrome video camera and recorder.

TABLE 1.—Dive locations on Stellwagen Bank and Cape Cod (Provincetown, Mass.) with observations[1] on presence (+) or absence (0) of American sand lance. Observations were made using scuba and submersible (sub).

Dates of observations	Dive sites: Provincetown Scuba	Provincetown Sub	Stellwagen Bank Scuba	Stellwagen Bank Sub
1968	1 · 0			
12-16 July · scuba	2 · 0			
1969	1 · 0			
21-25 July · scuba	2 · 0			
	3 · 0			
1970	1 · 0		5 · 0	
06-09 July · scuba	2 · 0		6 · 0	
	3 · 0			
1971	1 · 0	8 · 0	4 · 0	1 · 0
23-25 June · scuba	2 · 0	9 · 0		2 · 0
22 Sept · sub	3 · 0	10 · 0		3 · 0
				4 · 0
				5 · 0
				6 · 0
				7 · 0
1972	1 · 0		4 · 0	
18-21 July · scuba	2 · 0		5 · 0	
24-31 Oct · scuba	3 · 0		6 · 0	
1973	1 · 0		7 · 0	1 · 0
05-10 Oct · scuba	2 · 0		8 · 0	2 · 0
05-09 Oct · sub	3 · 0		9 · 0	3 · 0
			10 · 0	4 · 0
			11 · 0	5 · 0
			12 · 0	6 · 0
				7 · 0
				8 · 0
				9 · 0
				10 · 0
1974	1 · 0			
06-11 July · scuba	2 · 0			
	3 · 0			
1976	1 · · ·	1 · · ·		3 · · ·
16-18 June · scuba	2 · · ·	2 · · ·		
15-18 June · sub	3 · · ·			
1977	1 · · · ·		4 · · ·	
08-11 Aug. scuba	2 · · · ·		5 · · ·	
	3 · · · ·			

[1]Estimates of relative abundance are noted as 0 for no sightings, · for a few sand lance observed, · · for small schools (several hundred individuals per school) with infrequent sightings, and · · · for large schools (thousands per school) and schools observed almost continuously.

Stellwagen Bank is included in one of the sampling strata covered by the spring and fall bottom trawl surveys since 1963 (Grosslein 1969). This stratum encompasses the Massachusetts Bay area, extending from Provincetown to Cape Ann and ranges in depth up to 110 m (Figure 1). Stations were selected randomly within the stratum for each survey and the number of stations actually occupied on Stellwagen Bank on each survey ranged from 0 to 6. Trawl survey results are presented only for 1967-77, the period during which diver and submersible observations were made.

Behavior

Photographic and video records of sand lance behavior were made by scuba divers during a hydroacoustic experiment from RV *Albatross IV*,

[3]Research submersibles were chartered by NOAA's Manned Undersea Science and Technology Program, Rockville, Md.
[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

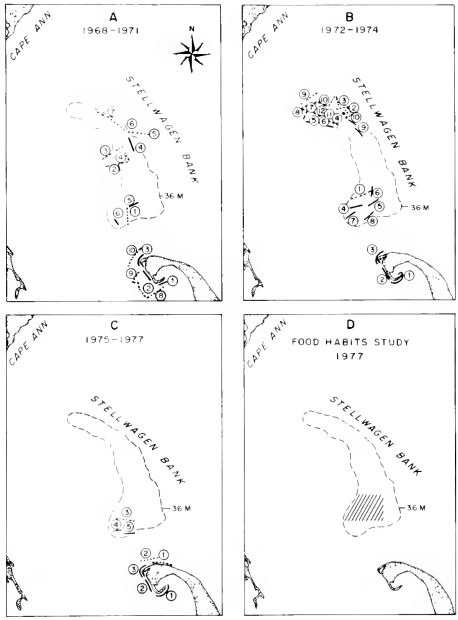


FIGURE 2.—Dive sites and location of 1977 food habits study on Stellwagen Bank and Cape Cod (Provincetown) from 1968 to 1977. Scuba (lines), submersible (dotted lines), 1977 bottom trawl (hatching) sampling areas. See Table 1 for key.

8-11 August 1977, on Stellwagen Bank (scuba dive locations 4, 5) and along the Provincetown slope (scuba dive locations 1-3) (Figure 2C).

Divers, using a Hydro-Products Model 125 television system with a 250-W thallium-iodide light source, filmed sand lance behavior on and near the bottom. The angles and speed at which sand lance entered the bottom substrate and exited from it were estimated from slow-motion video playback.

Schooling behavior was observed and photographed using a Nikonos II underwater camera with a 28- or 35-mm lens and a Subsea MK 150 or 225 electronic strobe. School strength, shape, nearest-neighbor distance, and individual fish size were estimated using in situ observations, photographs, or bottom trawl data. School swimming speeds were estimated at approximately 1 kn by divers swimming parallel to several schools for short distances. A speed of 1 kn is the approximate short-term sustained swimming speed of a diver. All in situ observations by diver scientists were made in daylight between 0900 and 1600 h.

Food Habits

A series of nine tows were conducted from *Albatross IV* on the southwestern edge of Stellwagen Bank over one 24-h period beginning at 1800 h on 9 August 1977 (Figure 2D). The tows were of 5-15 min duration at 3-h intervals and were made with

a Yankee #36 trawl (Grosslein[5]). The cod end and upper belly of the net were lined with 13-mm mesh netting, knot to knot. Only three species of fish were caught in any quantity: spiny dogfish, *Squalus acanthias*; silver hake, *Merluccius bilinearis*; and American sand lance. Sand lance were taken at random from the catch and preserved whole in 10% Formalin for stomach-content analysis.

In the laboratory, the stomachs were dissected out for stomach-content analysis. Ten fish from each of the nine tows were randomly selected from the preserved specimens for analysis. After the stomach was removed from each fish, the contents were examined and washed onto a fine-mesh screen. If the stomach appeared empty or had trace amounts (< 1.0 mg) of food in it, it was rinsed out with seawater directly into a Petri dish. When there was a weighable quantity of prey present, the excess water was drawn off by pressing an absorbent tissue paper to the underside of the screen; the contents were weighed and then washed into a Petri dish. Using a dissecting microscope, the prey of each fish were identified to the lowest possible taxonomic grouping, and the percentage composition of each of the identified groups estimated. The percentage composition and total stomach-content weight were used to calculate the percentage weight for each prey category. The data were also expressed in terms of the percentage occurrence of each prey group in the stomachs.

RESULTS AND DISCUSSION

In the taxonomic studies listed above, morphometric and meristic characteristics were used to distinguish between "inshore sand lance" (*Ammodytes americanus* - *Ammodytes hexapterus*) and "offshore sand lance" (*Ammodytes dubius*), although Bigelow and Schroeder (1953) questioned whether such a distinction could be made.

Because of the question regarding the taxonomic status of *A. americanus* and *A. dubius*, several meristic characteristics were evaluated on sand lance caught on Stellwagen Bank (Figure 2D). Dorsal and anal fin ray counts were made directly on 10 randomly chosen fish ranging from 17.9 to 22.2 cm fork length (FL) and averaging 20.0 cm, SD = 1.24. The anal fin ray count ranged from 30 to 31 with a mean of 30.7, SD = 0.48. The dorsal fin ray count ranged from 60 to 63 with a mean of 61.1, SD = 0.99. The vertebral count, based on radiographs of 20 fish and excluding the hypural complex, ranged from 67 to 72 and averaged 69.25, SD = 1.21. The mean values reported here fell into the *A. americanus* category given by Reay (1970). For the purpose of this paper, the classification of Reay (1970) is accepted.

Relative Abundance

Examination of spring and fall survey data for the past 10 yr, excluding 1967, 1969, 1971, and 1973 for spring and 1971 and 1977 for fall (Stellwagen Bank stations were not sampled), indicates a substantial increase in sand lance abundance on Stellwagen Bank (Figure 3). The relative abundance increased during spring cruises from virtually 0 for the 1967-75 period to 50/tow in 1976 and 10,729/tow in 1977, while increasing during fall cruises from 0 for the 1967-74 period to 4,238/tow in 1975 with a decrease to 5/tow in 1976. Spring cruises (March-May) may give a better indication of sand lance abundance since fall cruises are conducted from October to December, a period of lesser sand lance activity before spawning (Winslade 1974). In the Gulf of Maine, all bottom trawl survey catches <75 sand lance/tow occurred on or along the edge of Stellwagen Bank. The catch rate

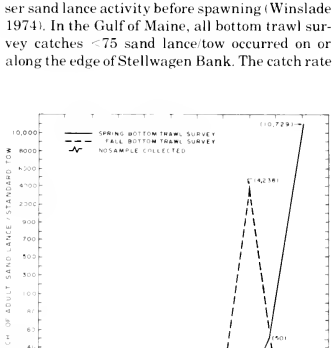


FIGURE 3.—Catch of adult sand lance per standard tow on Stellwagen Bank during the NMFS spring and fall bottom trawl stratified sampling surveys for 1967-77.

[5]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Massachusetts. Lab. Ref. No. 69-02, 34 p.

declined drastically, to <1 sand lance/tow, when not fishing on the bank. In the southwest North Sea, fishermen have also noticed that better catches occur along the edges of larger banks and on the tops of smaller ones (Popp Madsen 1963).

In the last 10 yr, sand lance have shown evidence of a population increase along the Atlantic coast from Cape Hatteras, N.C., to and including the Gulf of Maine. Northeast Fisheries Center spring and fall bottom trawl survey results from 1968 to 1977 show large annual fluctuations in sand lance abundance since 1968 with a definite upward trend beginning in 1975 (Figure 4). The magnitude of this increase is considerably less than that recorded on Stellwagen Bank for the same period, but the yearly trends are similar.

One area of concern in attempting quantitative sampling is net avoidance. Livingstone (1962) documented on film that adult sand lance were able to escape in <2.5 s from the cod end of a Yankee Modified #41 trawl net with a cod end mesh of 114 mm, knot to knot, and a 38-mm cotton webbing covering. These films also showed the ease with which individuals and small schools were able to avoid the trawl net. In areas where abundance is high, the ability to avoid trawl nets may be less effective. Scott (1973) found it unusual to catch adult sand lance in nets except in areas where they were very abundant.

Relative abundance of sand lance on Stellwagen Bank and Provincetown slope, based on diver and submersible observations, has increased significantly since 1976 (Table 1). Although numerous diving programs have been carried out over the study area since 1968, it was not until the spring of 1976 that schools of sand lance were first observed. However, it is very likely that relatively small numbers of sand lance were present in the study area prior to 1976 but not noticed by the divers. This increase in sightings coincides with an increase in number of sand lance caught per tow during the bottom trawl survey cruises.

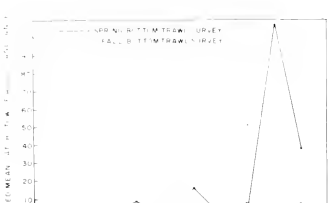


FIGURE 4.—Changes in the relative abundance of adult *Ammodytes* spp. in the Northeast Fisheries Center spring and fall bottom trawl surveys from 1968 to 1977 in the area extending from Cape Hatteras northward (Data from Grosslein et al. in press, table 3.2.)

Sand lance larvae studies, conducted by the Boston Edison Company[6] showed sand lance larvae were among the most abundant fish larvae occurring in ichthyoplankton sampling surveys conducted in Cape Cod Bay, Mass., during 1974-77. They were more abundant in the eastern portion of the bay and were considerably more abundant in 1976 than in the previous 2 yr. This increase in sand lance larvae was also observed during the Northeast Fisheries Center spring ichthyoplankton surveys conducted in the area from Cape Hatteras to the Gulf of Maine for the past 4 yr (Figure 5). For example, the mean sand lance catch/10 m^2 area in spring 1977 was 9 times greater than in spring 1974.

Bottom trawl survey results, diver and submersible observations, and ichthyoplankton survey results all indicate that there is a relatively large concentration of sand lance inhabiting a small section of the Gulf of Maine, i.e., Stellwagen Bank and outer Cape Cod (Provincetown slope), and that this population has increased considerably since 1975; this increase in population is typical of the Northwest Atlantic from Cape Hatteras to the Gulf of Maine.

Behavior

School Structure

Schools of sand lance observed on the Provincetown slope were relatively small in numbers of fish, ranging from about 100 to several thousand individuals and were usually found in depths ranging from 6 to 20 m. From photographs it was calculated that individual fish on Provincetown slope ranged from approximately 12 to 17 cm long, with a mean of 15 cm. Sand lance schools observed on Stellwagen Bank were relatively large in numbers, ranging from about 500 to tens of thousands

[6]Boston Edison Company. 1974-77. Marine ecology studies related to operation of Pilgrim Station. Boston Edison Co., 800 Boylston Street, Boston, MA 02199

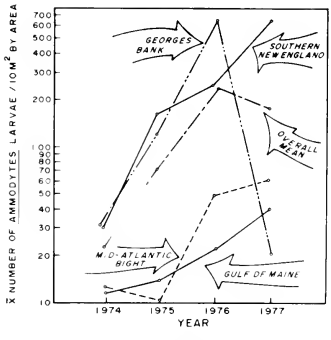


FIGURE 5.—Changes in the relative abundance of larval *Ammodytes* spp. in the Northeast Fisheries Center spring ichthyoplankton surveys from 1974 to 1977 in the area extending from Cape Hatteras northward. Data from Smith, W. G., and L. Sullivan. 1978. Annual changes in the distribution and abundance of sand lance, *Ammodytes* spp., on the northeastern continental shelf of the U.S. from the Gulf of Maine to Cape Hatteras. Northeast Fish. Cent., Sandy Hook Lab., Sandy Hook, NJ 07732. Lab. Ref. No. SHL 78-22.

of individuals. Individuals varied from 7.4 to 24.0 cm FL (measurements from bottom-trawl catches), with a mean length of 18.2 cm. Sand lance within a given school were of similar size; slightly larger fish were observed in positions at the head or central "core" of the school, with the smaller individuals occurring at the periphery. This distribution by size within the school was observed in both study areas. Schools were observed on the surface, at mid-depth, and near the bottom.

Inshore school strengths described by Kühlmann and Karst (1967) for European sand lance species *Hyperoplus lanceolatus* and *Ammodytes lancea* were commonly 30-100 or 200-300 individuals. These smaller schools joined up to form schools of from 500 to ~1,000 fish and headed offshore for deeper water in the early morning. We observed schools of this size primarily in the Provincetown slope area. However, because the individual size of the fish and school strengths on Stellwagen Bank were larger, it is unlikely that these schools formed in the Provincetown slope area and moved out to the bank.

School Shape

The shape of sand lance schools, where individuals were not engaged in feeding, was constant in appearance. As a school moved undisturbed through the water it appeared vertically compressed, tightly compacted, and bluntly linear from the lateral view (Figure 6). Provincetown slope schools were 1-5 m wide, 0.5-1.5 m high, and 3-20 m long; these measurements depended on school strength. This school form, where the height-width-length ratio was approximately 1:3:10 (having more individuals situated ahead, alongside, and behind than above or below), is called a stratified school (Wahlert and Wahlert 1963). This school formation was, in general, independent of school strength. The "nearest-neighbor" distance between fish was approximately ½-¾ body length (BL) (Figure 6). This distance became greater along the school's flanks. The "nearest-neighbor" distance decreased to ¼ BL when the school exhibited a fright reaction to divers. The fishes leading the school and ones along the flanks usually swam the deepest. School shapes described by Kühlmann and Karst (1967) were similar to the measurements reported in this study, but a significant difference appeared in the school height and length measurements. Kühlmann and Karst (1967) listed their school height as 15-50 cm, and their school length as ≥40 m. Sand lance schools encountered in our study were more than double the height and shorter in length. The European study took place in water depths of 1-6 m, and in this relatively shallow water, there may be a tendency for a school to flatten out and increase its length.

Movement

The swimming motion of sand lance is sinusoidal in form and eellike in appearance from the dorsal and ventral views. Sidewise undulations begin at the head and run along the body toward the tail (Figure 7). Schools swimming undisturbed, and not engaged in feeding, maintain an estimated speed of 30-50 cm/s. Schools exhibiting feeding behavior usually swim at about half the speed of undisturbed schools, or about 15-25 cm/s, and spread out to a little over double the normal schooling distances so that the nearest neighbor is approximately 1-1½ BL away. Smaller schooling groups were observed to swim faster than larger schools. When approached by divers, schools ac-

FIGURE 6.—School of sand lance encountered on Provincetown slope. Note lateral view of sand lance leaving the bottom to join school above.

celerated to one side or split to avoid the divers at the part of the school closest to the divers. The forward portion of the school continued on in its original direction, while the rear portion generally reversed direction. These avoidance maneuvers were made at about 70-120 cm/s, over double the original undisturbed speed, and lasted for only a few seconds before the divided sections regrouped and slowed down to their original speed. Feeding schools were observed in midwater and near the surface, but not on the bottom.

Kühlmann and Karst (1967) recorded the escape speed of larger sand lance to be 300-500 cm/s for at least a few seconds. During our study, there were many occasions when the swimming speed appeared to be >120 cm/s, but the actual speed was not calculated.

Behavior Within and Near the Ocean Floor

Sand lance were found in substrates conducive to burrowing, such as clean sandy bottoms, sand bottoms with crushed shells, and fine-graveled bottoms. Substrates of mud, mud/silt, medium to coarse gravel, and rock/boulder were avoided. This preference for loose porous substrate facilitates entry and exit and may relate to a sufficient supply of dissolved oxygen within at least the first few centimeters of interstitial water. Oxygen is continually replenished by tidal currents of 32-47 cm/s (0.62-0.91 kn) measured at 1 m above the bottom on Stellwagen Bank (Padan 1977).

Sand lance usually disappear into the bottom in small groups. The initial penetrating angle was estimated as 60°-75° from the horizontal and con-

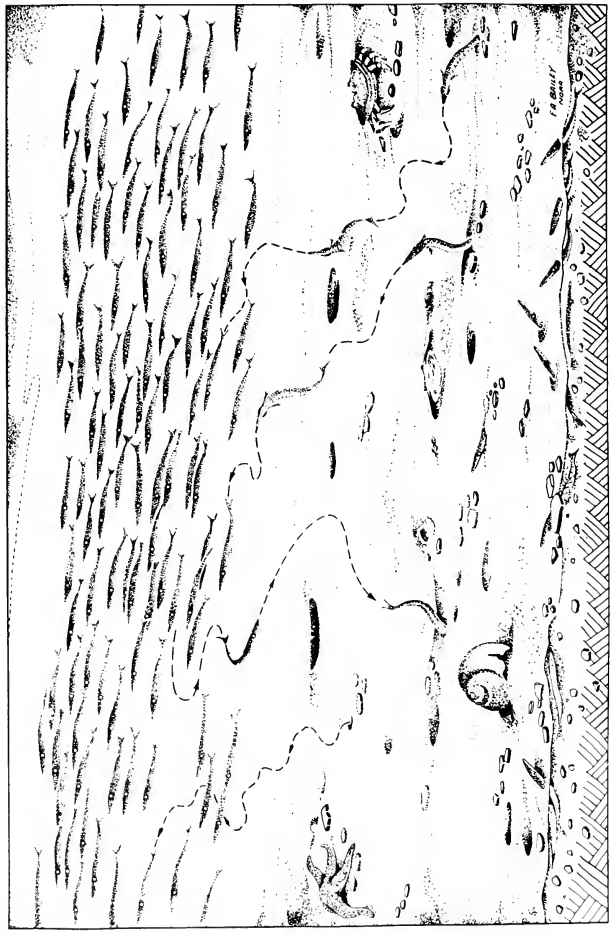


FIGURE 7.—Artist's rendition of sand lance behavior within and near the ocean floor.

sisted of a continuance of their sinuous movement until one-quarter of the body was buried, at which point the remaining three-quarters of the body was brought to a 20°-40° angle to allow the animal to settle into its normal resting position (Figure 7). Once in a resting position, the sand lance would partially emerge headfirst if disturbed (Figure 7). Sand lance on Stellwagen Bank, exhibiting this partial-emergence behavior, would retract back into the bottom when further disturbed. In contrast, sand lance encountered along Provincetown would usually leave the substrate. Kühlmann and Karst (1967) observed similar behavior and noted on several occasions that, after pulling back into the bottom, sand lance could turn, move laterally through the substrate, and emerge some distance away. This behavior was not observed in our study area.

Sand lance leaving the bottom exited at an angle between 20° and 60° with an initial speed of 50-80 cm/s, which increased up to 120 cm/s within the first 1.5 m from the bottom (Figure 7). As divers proceeded along the bottom, sand lance would exit from the substrate and either school or swim to the end of the diver's visual range.

Food Habits

The results of the stomach-content analysis for *A. americanus* collected on Stellwagen Bank are given in Table 2. The data are presented as both the percentage occurrence of prey in the stomachs and as the percentage weight of the total prey consumed. It is evident that copepods were the most important prey, occurring in 37.8% of the stomachs examined and making up 41.4% of the total weight of the prey. The other identifiable prey groups, such as hyperiid amphipods, mysids, euphausiids, chaetognaths, salps, and animal eggs, were much less important, usually occurring in only 1-2% of the stomachs. Of these groups only the chaetognath *Sagitta* contributed significantly to the diet on a percentage weight basis (39.9%). This was because the stomach of one fish was quite distended with chaetognaths. "Animal remains," which are unidentifiable prey, were the most frequently occurring prey category; however, on a weight basis they were much less significant.

The food habits of a number of different species of sand lance have been studied in Atlantic and Pacific waters. In general the diets are all very similar, with copepods being the major prey in almost every instance (Reay 1970). Around Japan,

TABLE 2.—Stomach contents of American sand lance collected on Stellwagen Bank, August 1977. The data are expressed as both the percentage frequency of occurrence of prey and as the percentage weight of the total quantity of prey consumed.

Prey	Occurrence (%)	Weight (%)
Copepods		
Calanoida	3.3	0.81
Calanus	8.9	9.55
Centropages	10.0	2.57
Pseudocalanus	17.8	6.28
Temora	17.8	8.06
Tortanus	17.8	6.27
Metridia	1.1	1.22
Cyclopoida		
Oithona	2.2	0.05
Unidentified	28.9	6.62
Copepod subtotal	37.8	41.43
Hyperiid amphipods	1.1	0.09
Mysids	1.1	0.32
Meganyctiphanes norvegica	1.1	0.41
Sagitta elegans	2.2	39.91
Salpidae	1.1	0.04
Animal eggs	1.1	0.01
Trematodes	3.3	0.01
Animal remains	84.4	17.79
No. stomachs examined	90	
No. stomachs empty or trace	32	
Mean wt of contents/stomach	15.3 mg	
Mean fish length	18.2 cm, SD 1.8	

for example, both Senta (1965) and Sekiguchi (1977) have shown that *A. personatus* is a plankton feeder relying heavily on copepods. In the North Sea, Roessingh[7] found that copepods were the major prey of *A. marinus* and occurred in roughly the same proportions in the stomachs as they did in the plankton. Macer (1966) examined the stomach contents of five species of sand lance from the North Sea. In all cases the sand lance were found to be plankton feeders, with copepods being the dominant prey for at least three of the five species. Only for *A. lanceolatus* was it conclusively shown that copepods were less significant as prey, being replaced by fish eggs, larvae, or small fish, particularly small *Ammodytes*. Two species of sand lance are reported to occur along the Atlantic coast of North America, and only a small amount of information is available on their food habits. Richards (1963) examined the stomachs of 290 *A. americanus* in Long Island Sound; as for most other species of sand lance, copepods were the major prey. *Centropages* were preyed upon by 80% of the fish, *Acartia* by 55%, and *Temora* by 42%. Other prey included barnacle cyprids, fish eggs, dinoflagellates and diatoms, mysids, and sand lance larvae. Scott (1973) studied the food habits of

[7]Roessingh, M. 1957. Problems arising from the expansion of the industrial fishery for the sand eel, *Ammodytes marinus* Raitt, towards the Dutch coastal area. Near Northern Seas Committee, Int. Counc. Explor. Sea.

A. dubius in the Canadian northwest Atlantic. Again, copepods, especially *Calanus finmarchicus*, were the most important prey. Other prey included crustacean larvae, invertebrate eggs, polychaete larvae, larvaceans, fish eggs, pteropods, and barnacle cyprids. Comparison with plankton tows made at the time the fish were caught showed that *A. dubius* had a definite preference for the larger zooplankton such as copepods. From the data in Table 2, it is clear that the diet of *A. americanus* from Stellwagen Bank is typical for this family of fishes. There are, however, several small differences from other published results which are worth noting. For example, chaetognaths occurred rarely in the stomachs (2.2%) but on a weight basis were only slightly less important than copepods. It would appear that chaetognaths are readily consumed if available. One notable exception to the list of prey is phytoplankton. Both Richards (1963) and Scott (1973), as well as Senta (1965) and Macer (1965), reported finding diatoms or dinoflagellates in the guts of the fish they examined. In our study, no phytoplankton was observed as part of the stomach contents. It is possible that at certain times of the year the occurrence of phytoplankton would be much more apparent in the guts, as might also be expected for other prey such as crustacean larvae, barnacle cyprids, and larval polychaetes.

SUMMARY

1. The meristic counts of sand lance reported are in agreement with published data and fall into the category of *Ammodytes americanus*, the American sand lance.

2. Data on the relative abundance of sand lance from Northeast Fisheries Center spring and fall bottom trawl survey cruises indicate that there has been a substantial increase in sand lance abundance on Stellwagen Bank over the last 10 yr. This trend was also reflected by an increase in the numbers of sand lance larvae occurring in the spring ichthyoplankton results measured in the Gulf of Maine over the last 4 yr. This increasing trend in larval and adult sand lance abundance in the Gulf of Maine was typical of the northwest Atlantic from Cape Hatteras northward.

3. Sand lance encountered within the Provincetown slope area ranged from 12 to 17 cm long (mean = 15 cm), and school strength numbered from about 100 to several thousand individuals. In contrast, individuals on Stellwagen Bank ranged from 7.4 to 24.0 cm FL (mean = 18.2 cm), while school strengths ranged from about 500 to tens of thousands of individuals.

4. School shapes were constant in appearance, vertically compressed, tightly compacted, and bluntly linear from a dorsal and ventral view. Provincetown slope schools were 1-5 m wide, 0.5-1.5 m high, and 3-20 m long depending on school strengths. The nearest-neighbor distance between fish swimming in an undisturbed school was approximately ½-¾ BL; between fish swimming in a school exhibiting a fright or avoidance reaction, ¼ BL; and between fish swimming in a school engaged in feeding, approximately 1-1½ BL.

5. The swimming motion of sand lance is sinusoidal in form and eellike in appearance. Schools swimming undisturbed and not engaged in feeding maintain an estimated swimming speed of 30-50 cm/s; during feeding they maintain an estimated speed of 15-25 cm/s; and during avoidance maneuvers, 70-120 cm/s. Feeding schools were observed in midwater and near the surface, but not on the bottom.

6. Sand lance were found to prefer clean sandy substrates conducive to burrowing. Sand lance usually disappear into the substrate in small groups, initially penetrating at an angle of 60°-75° from the horizontal, and continuing their sinuous movement until one-quarter of the body is buried, at which point the remaining three-quarters of the body is brought to a 20°-40° angle to allow the animal to settle into its resting position. Sand lance encountered on Stellwagen Bank were occasionally observed to partially emerge from the substrate headfirst and retract back into the bottom if approached. In contrast, sand lance along Provincetown slope would exit from the bottom when approached. Sand lance leaving the bottom exited at an angle of between 20° and 60° with an initial speed of 50-80 cm/s and built their speed up to 120 cm/s within the first 1.5 m from the bottom. Individual fish exiting would show schooling behavior if another fish was exiting at the same time.

7. Copepods were the most important prey of *A. americanus*, occurring in 38% of the stomachs examined and making up 41% of the total weight of prey consumed.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the assistance of the National Marine Fisheries Service, Woods Hole, Survey Unit for bottom trawl survey

data; the laboratory scientific illustrator, Frank Bailey, for his many hours of patient craftsmanship; and Rosalind Cohen and Nancy Kohler for their assistance with the stomach-content analysis.

LITERATURE CITED

BACKUS, R. H.
1957. The fishes of Labrador. Ammodytidae. Bull. Am. Mus. Nat. Hist. 113:307-308.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BOWMAN, R. E., AND R. W. LANGTON.
1978. Fish predation on oil-contaminated prey from the region of the ARGO MERCHANT oil spill. *In* In the wake of the ARGO MERCHANT, p. 137-141. Univ. R.I., Cent. Ocean Manage. Stud.

COVILL, R. W.
1959. Food and feeding habits of larvae and postlarvae of *Ammodytes americanus*, 1952-1955. *In* Oceanography of Long Island Sound, p. 125-146. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).

GRAHAM, J. J.
1956. A mortality of sand launce, *Ammodytes americanus*. Copeia 1956:192-194.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

GROSSLEIN, M. D., R. W. LANGTON, AND M. P. SISSENWINE.
In press. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relationship to species interactions. *In* Symposium on the Biological Basis of Pelagic Fish Stock Management No. 25.

KUHLMANN, D. H. H., AND H. KARST.
1967. Freiwasserbeobachtungen zum Verhalten von Tobiasfischschwarmen (*Ammodytidae*) in der westlichen Ostsee. Z. Tierpsychol. 24:282-297. (Also issued as Transl. Mar. Lab., Aberdeen (1392).)

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

LIVINGSTONE, R., JR.
1962. Underwater television observations of haddock (*Melanogrommus aeglefinus* [Linnaeus]) in the cod-end. J. Cons. 27:43-48.

MACER, C. T.
1965. The distribution of larval sand eels (Ammodytidae) in the southern North Sea. J. Mar. Biol. Assoc. U.K. 45:187-207.
1966. Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Minist. Agric., Fish. Food (G.B.) Fish. Invest., Ser. II, 24(6), 55 p.

NORCROSS, J. J., W. H. MASSMANN, AND E. B. JOSEPH.
1961. Investigations of inner continental shelf waters off lower Chesapeake Bay. Part II. Sand lance larvae, *Ammodytes americanus*. Chesapeake Sci. 2:49-59.

PADAN, J. W. (editor).
1977. New England Offshore Mining Environmental Study (Project NOMES). U.S. Dep. Commer., NOAA Spec. Rep. NOAA ERL 1977.

POPP MADSEN, K.
1963. Tobis pa algehaet. Fiskeridir. Skr. Ser. Teknol. Unders. 1963:46-47.

REAY, R. J.
1970. Synopsis of biological data on North Atlantic sand eels of the genus *Ammodytes*, *A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*. FAO Fish. Synop. 82, 42 p.

RICHARDS, S. W.
1959. Pelagic fish eggs and larvae of Long Island Sound. *In* Oceanography of Long Island Sound, p. 95-124. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).
1963. The demersal fish population of Long Island Sound. Bull. Bingham Oceanogr. Collect., Yale Univ. 18(2), 101 p.
1965. Description of the post larvae of the sand lance (*Ammodytes*) from the east coast of North America. J. Fish. Res. Board Can. 22:1313-1317.
1976. Mixed species schooling of post larvae of *Ammodytes hexopterus* and *Clupea horengus horengus*. J. Fish. Res. Board Can. 33:843-844.

RICHARDS, S. W., AND A. W. KENDALL, JR.
1973. Distribution of sand lance, *Ammodytes* sp., larvae on the continental shelf from Cape Cod to Cape Hatteras from R.V. *Dolphin* surveys in 1966. Fish. Bull., U.S. 71:371-386.

RICHARDS, S. W., A. PERLMUTTER, AND D. C. MCANENY.
1963. A taxonomic study of the genus *Ammodytes* from the east coast of North America (Teleostei: *Ammodytes*). Copeia 1963:358-377.

SCOTT, J. S.
1968. Morphometrics, distribution, growth, and maturity of offshore sand launce (*Ammodytes dubius*) on the Nova Scotia banks. J. Fish. Res. Board Can. 25:1775-1785.
1972. Morphological and meristic variation in northwest Atlantic sand lances (*Ammodytes*). J. Fish. Res. Board Can. 29:1673-1678.
1973. Food and inferred feeding behavior of northern sand lance (*Ammodytes dubius*). J. Fish. Res. Board Can. 30:451-454.

SEKIGUCHI, H.
1977. Further observation on the feeding habits of planktivorous fish sand-eel in Ise Bay. Bull. Jpn. Soc. Sci. Fish. 43:417-422.

SENTA, T.
1965. Nocturnal behavior of sand-eels, *Ammodytes personatus* Girard. Bull. Jpn. Soc. Sci. Fish. 31:506-510.

WAHLERT, G. V., AND H. V. WAHLERT.
1963. Beobachtungen an Fischschwarmen. Veroff. Inst. Meeresforsch. Bremerhaven 8:151-162.

WILLIAMS, G. C., S. W. RICHARDS, AND E. G. FARNWORTH.
1964. Eggs of *Ammodytes hexapterus* from Long Island, New York. Copeia 1964:242-243.

WINSLADE, P.
1974. Behavioural studies on the lesser sandeel, *Ammodytes marinus* (Raitt). I. The effect of food availability on activity and the role of olfaction in food detection. II. The effect of light intensity on activity. III. The effect of temperature on activity and the environmental control of the annual cycle of activity. J. Fish Biol. 6:565-599.

WINTERS, G. H.
1970. Meristics and morphometrics of sand lance in the Newfoundland area. J. Fish. Res. Board Can. 27:2104-2108.

SEASONAL DISPERSAL AND HABITAT SELECTION OF CUNNER, *TAUTOGOLABRUS ADSPERSUS*, AND YOUNG TAUTOG, *TAUTOGA ONITIS*, IN FIRE ISLAND INLET, LONG ISLAND, NEW YORK[1]

BORI L. OLLA, ALLEN J. BEJDA, AND A. DALE MARTIN[2]

ABSTRACT

Results of field observations examining seasonal movements in the cunner, *Tautogolabrus adspersus*, and young tautog, *Tautoga onitis*, showed a small portion of a resident population located off Fire Island, N.Y., to disperse seasonally. Dispersal was from habitats which provide cover for both species throughout the year to seasonal habitats occupied primarily during summer. While both species exhibit a high degree of association with cover, results of experimental transfers of young tautog, monitored either ultrasonically or directly by divers with self contained underwater breathing apparatus, showed that fish will leave a suboptimal habitat even though cover is present. Dispersal and habitat selection are discussed in relation to seasonal changes in the environment and ecological requirements of the fish

Association with and dependence on cover by marine fishes have been observed for a wide variety of species, exemplified by those which reside on coral reefs (e.g., see: Hobson 1968, 1972, 1973; Sale 1969a, 1971, 1972, 1977; Smith and Tyler 1972, 1973). Although the number of species is much less, similar associations with cover also occur in temperate waters (e.g., see: Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976; Olla et al. 1974, 1975).

In both tropical (Hobson 1968, 1972) and temperate regions a major behavioral trait of the family Labridae is that members show a strong association with cover. Field studies on two temperate-water labrids of the northwest Atlantic, cunner, *Tautogolabrus adspersus* (Olla et al. 1975), and young tautog, *Tautoga onitis* (Olla et al. 1974), have demonstrated their close association with cover. Under laboratory conditions similar associations have been observed for both species (cunner, Olla and Bejda unpubl. obs.; young tautog, Olla and Studholme 1975).

Over several years, incidental sightings of cunner and young tautog always found them in association with cover. However, it was apparent that a substantial number of fish were in areas in which cover was present only seasonally, e.g., macroalgae and mussel beds. This suggested to us that there must be movement to these areas sometime after emergence from winter torpor (Olla et al. 1974, 1975) in March or April and movement away from these areas in the fall as the cover provided at these areas diminished. The possibility of seasonal dispersal and habitat selection appeared likely. At least for adult tautog changes in habitat requirements with season have been established, as evidenced by the fact the fish migrate offshore to overwinter (Cooper 1966; Olla et al. 1974).

In this study we have examined seasonal movements in cunner and young tautog, basing our observations on trapping and tagging, as well as surveying shelter sites seasonally by direct observation with scuba or mask and snorkel. We also performed a series of transfer experiments to examine certain aspects of habitat selection.

MATERIALS AND METHODS

Based on previous scuba observations, six study sites (A, B, C, D, E, and F; Figure 1) within Fire Island Inlet, Long Island, N.Y., were selected at which to monitor the seasonal movements of cunner and young tautog. One site (A) was inhabited throughout the year and will be referred to as a perennial site. The five other sites (B, C, D, E, and F) were utilized only during late April through

[1]This work was supported, in part by a grant from the U.S. Department of Energy No. EX76-A-28-3045-A010.

[2]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

Manuscript accepted October 1978
FISHERY BULLETIN VOL. 77, NO. 1, 1979

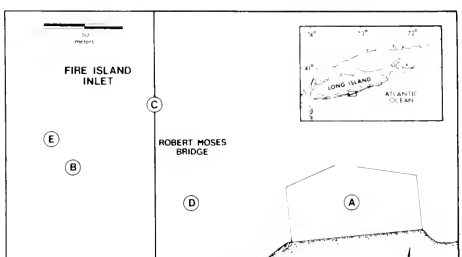


FIGURE 1.—Location of study sites for cunner and young tautog within Fire Island Inlet, Long Island, N.Y. (see text for site descriptions).

October and will be referred to as seasonal sites. A description of each site follows.

Site A was the boat basin at the Fire Island Coast Guard Station, an open pentagon (110 × 52 × 47 m), constructed of tongue-and-groove planks, steel sheeting, and piles (Olla et al. 1975). Along the outer perimeter was a zone of riprap (0.2–0.4 m in diameter), 3 m wide and 2 m high. The mean water depth ranged from 2.4 to 8.8 m. Beds of the mussel, *Mytilus edulis*, were located along the walls, piles, and bottom.

Site B was a 20.3-cm diameter drain pipe originating at the Fire Island water treatment plant. Located at a mean depth of 7.5 m, a 1.5-m section of the pipe was exposed and paralleled the bottom at a distance of 1 m. Beds of mussels surrounded the pipe in about a 6-m radius.

Site C was one of the support piers for the Robert Moses Bridge, consisting of quarried stone and reinforced concrete. The mean water depth was 7.5 m. The pier was incrusted with mussels to a depth of 2 m below the high water mark.

Sites D and E each consisted of an exposed vertical mud bank about 6 m long and 1 m high. Irregularly spaced along the face of each bank were approximately 35 to 50 holes, apparently a result of erosion, varying in size from 12 to 20 cm wide and 5 to 15 cm deep. Small clumps of mussels were distributed along the top of each bank. Site D was at a mean depth of 6.0 m and Site E at 7.6 m.

Site F was a grass bed which bordered a rocky shore line for 75 m and extended out from the shore 13-20 m. During the late spring and summer, the area typically consisted of dense growths of eelgrass, *Zostera marina*, and algae (*Codium* spp., *Enteromorpha* spp., *Polysiphonia* spp., and *Ulva* spp.). Beds of mussels were interspersed between the vegetation. Water depth throughout the area varied from 0.3 to 1.5 m.

A seventh area, a small cove at the mouth of Fire Island Inlet, not designated in Figure 1, was the site of two transfer experiments involving experimental cover. This site had a barren sand bottom, primarily dredge spoil, at a mean depth of 3.7 m.

Three methods, trapping, direct visual counts, and tagging, were used to monitor, for both cunner and tautog, the periods and limits of movements as well as the types of habitats utilized. Fish traps were placed at Sites A, B, C, D, and E with two traps at Site A from March through November, one trap at Site B from May through November, and one trap each at Sites C, D, and E from June through November. Traps at each site were pulled at regular weekly intervals throughout the study and the number of cunner and tautog recorded. To compare the catch of the traps at the perennial site with the catch at the seasonal sites, we calculated the mean number of fish caught per trap per week for each habitat type. Traps captured cunner ranging in size from 3.9 to 25.0 cm ($\bar{x}$ = 14.5 cm) and tautog from 7.3 to 35.0 cm ($\bar{x}$ = 16.9 cm). Traps also provided the fish for the tagging portion of the study, as well as one means of recapture.

Visual counts of cunner and tautog were made at Site F from the end of February through October. A series of six transects the length of the site and 3 m wide were swum by divers, counting all

tautog and cunner observed within each transect with the sum of the six transects being the total count.

Cunner and tautog (≥14.0 cm) trapped at Sites A, B, C, D, and E were tagged throughout the study with Floy-67C[3]anchor tags. Tags were consecutively numbered allowing identification of individual fish and their release site. Each tag was printed with a request for fishermen catching tagged fish to return the tag, accompanied by information as to the location and date the fish was caught. Fish were recaptured either in our traps or by recreational fishermen.

Ultrasonic tracking was employed for short-term monitoring of movement and cover association of young tautog residing at both a perennial (Site A) and seasonal (Sites B and F) habitats. Four fish (two at Site A, one at Site B, and one at Site F) were individually tracked using the same procedures previously described by Olla et al. (1974, 1975) for capturing, handling, and tracking.

A series of transfer experiments was conducted to examine habitat selection in young tautog. All fish were captured at Site A and released at either existing, seasonal habitats (Sites B and C) or at experimental habitats which we established (see below). Fish were transferred by boat in 100-l barrels of aerated seawater with the time to travel from capture to release sites ranging from 5 to 15 min. Four fish (three at Site B and one at Site C) were separately released at the seasonal habitats and tracked ultrasonically. Five transfers were made to the experimental habitats. One transfer was a single fish, released and monitored ultrasonically. The other transfers consisted of four group releases with 10 fish/group. The response of the fish in these releases was monitored directly using scuba. While lying motionless, 5 m from the release site, the observer recorded at 1-min intervals the number of fish present. Cover at the experimental habitats consisted of masonry structures constructed from standard cement blocks (20 × 20 × 40 cm) positioned in a manner which laterally exposed the central cavities (7 × 13 × 20 cm) of each block. Cement blocks had been shown to be readily acceptable as cover by young tautog in the laboratory (Olla and Bejda unpubl. obs.). The structure for the single fish release was a four-block cube (40 × 40 × 40 cm). Two structures were used in the group releases. They were identical 12-block rectangular prisms (120 × 40 × 40 cm).

RESULTS

Catch and Direct Sightings at Seasonal and Perennial Habitats

It was apparent from catch data and direct underwater sightings that a majority of the habitat sites were utilized only seasonally by both cunner and young tautog. Throughout the summer, substantial numbers of fish were captured at Sites A-E (Table 1) or sighted directly at Site F (Table 2). In September, there was a gradual decline in the catch of cunner and in October a sharp decline in both cunner and tautog at Sites B-E (Table 1). At Site F, direct visual counts indicated the same general trend (Table 2). However at Site A, while there was little change in catch during September, the catch of both species increased in October (Table 1). In November, Sites B-F were observed directly with scuba and no fish were sighted. At Site

TABLE 1.—Mean monthly catch of cunner and young tautog at perennial (A) and seasonal (B-E) sites

	Mean catch/unit effort[1]			
	Cunner		Tautog	
Month	Perennial site	Seasonal sites	Perennial site	Seasonal sites
March	11.0	ND[2]	6.5	ND
April	36.0	ND	2.7	ND
May	6.8	9.5	2.5	9.2
June	19.7	8.5	1.3	10.6
July	13.8	5.3	0.6	11.9
August	21.8	6.1	6.2	9.8
September	21.9	2.8	8.6	8.0
October	34.0	3.0	14.9	1.0
November	9.7	0	3.8	0

[1]Unit effort = one trap fished 1 wk
[2]ND = no data

TABLE 2.—Visual counts using scuba or mask and snorkel of cunner and young tautog at seasonal Site F

		Total number				Total number	
Date		Cunner	Tautog	Date		Cunner	Tautog
Feb	28	0	0	July	21	53	7
Mar	4	0	0		8[2]	165	60
	12	0	0		9[2]	93	27
	20	0	0		10[2]	89	16
	25	0	0		15	107	29
Apr	2	0	0		16[2]	42	13
	28	17	3		29	44	24
May	20	29	11	Aug	12	63	20
	22	74	20		13	169	71
	29	60	15	Sept	3	42	7
June	5	65	14		24	34	6
	11	79	19	Oct	2	0	0
	18	10	0		20	0	0
	26	69	12		29	0	0

[1]Mean of two counts
[2]Mean of three counts

[3]Reference to trade names does not imply endorsement of commercial products by the National Marine Fisheries Service NOAA

A, although large numbers of fish were sighted, the catch was declining (Table 1). The decline in catch at Site A may be related to lowered activity associated with decreasing temperature with the fish overwintering in torpor at this site (Olla et al. 1974, 1975). Although traps were not in place in Sites B-E earlier than May, no fish were sighted directly in these areas or at Site F (Table 2) prior to mid- or late April. The presence of fish at Site A throughout the year led us to term this a perennial habitat, while Sites B-F, where fish were only seen seasonally, we defined as seasonal habitats.

Recaptures

Tagged fish showed limited movements, with 91.3% of the cunner and 73.2% of the tautog recaptures occurring at the same site at which they were released (Table 3). For the remainder of the fish, i.e., those recaptured at other sites, there were seasonal differences in where they were captured. From May through August, recaptures were at seasonal as well as perennial sites (Table 3). But then from September through November, all recaptures were from sites which would be considered perennial, including ones outside the study area (Table 3).

Movements and Association with Cover of Young Tautog at Seasonal, Perennial, and Experimental Habitats

In an earlier study, we had established that young tautog remained within several meters of cover (Olla et al. 1974). Specifically, the cover referred to in that study was Site A, identified in this study as a perennial habitat. To reconfirm the observation of the previous study, two fish (no. 1, 2; Table 4) were ultrasonically tracked for 48 h at Site A. Agreeing with the earlier results, both fish remained within several meters of the site.

The question we next addressed was whether young tautog showed a similar association with cover at seasonal habitats. To answer this question, we captured and released two fish affixed with ultrasonic tags at Sites B (no. 4; Table 4) and F (no. 3; Table 4). The results of tracking showed the two fish to have a similar affinity to these sites as the fish had to the perennial one, remaining within 3 to 6 m of cover.

The area over which the fish ranged varied with the size of the site. For example, when fish no. 3 was released at Site F, which consisted of beds of algae and eelgrass measuring about 15 × 75 m, it moved freely throughout the habitat, but never more than several meters beyond its perimeter. On the other hand, fish no. 4 released at Site B where cover was highly limited (0.2 × 1.5 m) exhibited less movement, while again remaining within several meters of cover. It appeared that the close association to cover was the same at both seasonal and perennial habitats.

Thus far, all of the fish that were tracked had been released at the same site at which they were captured. Our next question was whether fish that were displaced from where they were captured

TABLE 4.—Size, capture and release sites (Figure 1), and period monitored for nine young tautog ultrasonically tracked.

Number	TL (cm)	Capture site	Release site	Tracking duration (h)
1	22.5	A	A	48
2	24.0	A	A	48
3	20.2	F	F	24
4	24.5	B	B	48
5	21.5	A	B	48
6	22.8	A	B	72
7	23.0	A	B	48
8	24.0	A	C	48
9	22.5	A	(1)	24

(1) Experimental cover

TABLE 3.—Number and location of recaptures of cunner and young tautog tagged and released at perennial and seasonal sites

					No. recaptured at other sites			
					May-August		September-November	
Species	Release site	No. released	Total no. recaptured	No. recaptured at release site	Perennial sites	Seasonal sites	Perennial sites	Seasonal sites
Cunner	A	875	176	166	5	1	4	0
	B	83	13	7	0	3	3	0
	C	15	0	0	0	0	0	0
	D	54	6	5	0	0	1	0
	E	10	0	0	0	0	0	0
	Total	1 037	195	178	5	4	8	0
Tautog	A	245	25	20	0	1	4	0
	B	283	29	18	0	5	6	0
	C	72	12	11	0	0	1	0
	D	123	3	2	0	0	1	0
	E	41	2	1	0	1	0	0
	Total	764	71	52	0	7	12	0

would accept and remain at a different site. Four fish captured at Site A, the perennial habitat, were affixed with ultrasonic tags and released at either of two seasonal sites. Three fish were released separately at Site B (no. 5-7; Table 4) and a fourth at Site C (no. 8; Table 4) and individually tracked for 48 to 72 h. The fish appeared to accept the transfer to a different habitat with all four fish remaining within several meters of the release site.

The close association with cover exhibited by fish ultrasonically monitored at both perennial and seasonal habitats indicated the possibility that the apparent dependence on cover might be such that a fish would remain at any object that afforded cover. To examine whether the presence of cover was the sole determinant of habitat acceptance, we transferred a fish from Site A to a structure constructed of cement blocks, measuring 40 × 40 × 40 cm, and located on a sand bottom 50 m from a habitat with which fish were associated (Site F). The fish (no. 9; Table 4), during the first 5 min after release, circled the structure and moved farther away with each circuit, showing little, if any, attraction. When about 10 m from the structure, it swam shoreward and reached Site F about 5 min later. The fish remained at this site during the next 24 h, showing the same degree of movement exhibited by fish no. 3 (Table 4) which had been previously captured and released at this site.

It was possible that the fish moved from the structure because of its proximity to a natural habitat, therefore affording it a choice. It was also possible that social factors related to the release of a single fish rather than a group may have played a role in the rejection of the structure as a habitat. To control for these factors, we next released fish in a group of 10, 4.5 km from their home range and 100 m from the nearest natural habitat at which conspecifics were present. To broaden the scope of our queries we included the possible influence of factors such as food and naturally occurring cover on habitat selection. Two cement block structures (120 × 40 × 40 cm) were placed 10 m apart. Both were identical except that while one consisted simply of bare cement blocks, the other contained clumps of mussels and algae (*Ulva* sp.), naturally occurring food and shelter material. Two groups of 10 fish each (15-23 cm) captured at Site A, were released together at each habitat while being observed with scuba. Within 5 min of being released, the fish left both structures, swimming away in various directions.

The habitats were then modified by the addition to each of a fish trap. To the habitat which contained mussels and algae the trap added was overgrown with various fouling organisms and had been in continuous use over a period of 4 to 5 mo, capturing both tautog and cunner. The fact that this trap captured fish consistently led us to conclude that it provided an attractive stimulus or set of stimuli. The trap added to the bare structure was new. A group of 10 fish (10-25 cm), captured at Site A, was released at each habitat. As previously, the fish left the bare habitat within 5 min. Dispersal from the other habitat was more gradual with the last fish leaving about 60 min after release. In all instances, the fish departed, indicating that factors in addition to those provided were necessary for mediating habitat selection.

DISCUSSION

It was clear from the results of trapping, tagging, and direct underwater observation that some portion of the cunner and young tautog populations dispersed in late spring. The dispersal was from the boat basin (Site A, which we termed a perennial habitat) to habitats that were utilized only seasonally. Once adopting a seasonal habitat, the fish appeared to remain there until fall. Then there was a general movement back to a perennial habitat, but as was evident from the capture of tagged fish at perennial sites outside of the study area, not necessarily the one from which they dispersed in the spring. Once arriving at a perennial habitat, the fish remained to overwinter in torpor, not emerging until sometime in early spring when the temperature reached 5° to 6°C (Olla et al. 1974, 1975).

Supporting our findings for seasonal movement, Briggs (1977) found a marked increase in the number of young tautog captured during the fall at the Kismet artificial reef, 6 km from our study area. This increase, we surmise, also reflects the movement of fish from seasonal habitats to one which appears to be perennial.

In attempting to define habitat requirements for both species, it is apparent that cover is a critical factor. During the day when these fish are active, they remain within several meters of cover, and at night when quiescent and unresponsive, they are either in, against, or under cover (Olla et al. 1974, 1975). Once becoming torpid in winter, they remain under cover until spring. It seems reason-

able to assume that dependence on cover is related to protection from predation. Large adult tautog, not as vulnerable to predation because of their size, move away sometimes considerable distances from cover each day to feed (Olla et al. 1974).

With such a strong tendency to remain in proximity to cover, the question arises as to what causes a portion of the population to disperse. It is clear that environmental factors are changing with season as are the requirements of the fish. Both species in the spring have emerged from 3 to 4 mo of torpor, which has required them to live on stored energy reserves. The need for food arising from winter deprivation, coupled with the increased metabolic requirements resulting from the increase of temperature in late spring, might stimulate feeding and the competition for food. At least until June, the major dietary component for both species is *Mytilus edulis* (Olla et al. 1975), and thus competition for food would be both intra- and interspecific.

The spawning season for cunner also peaks during June (Dew 1976). Thus we can expect that competition for participation in either group spawning (Wicklund 1970) or pair spawning (Pottle and Green[4]) would increase. This increase would relate either to participation in gamete release or male territoriality as related to pair spawning. Although the majority of tautog studied were immature and would generally not be involved in the reproductive competition, it is possible that the arrival from offshore of adults that are in spawning condition (Olla et al. 1974) and which we know to be highly aggressive (Olla and Samet 1977; Olla et al. 1977) may also play a role in the dispersal of the smaller fish.

Competition in both species is manifested through aggression (for tautog, Olla and Studholme 1975; Olla et al. 1977, 1978; for cunner, Olla and Bejda unpubl. field and laboratory obs.). The increase in aggression that may occur at the perennial habitat as a result of competition could cause this site to become suboptimal, at least for some portion of the population. Seasonal changes in levels of aggression within a population might result in corresponding seasonal changes in the carrying capacity of the habitat.

[4]Pottle, R. A., and J. M. Green. 1978. Field observations on the reproductive behaviour of the cunner, *Tautogolabrus adspersus* (Walbaum), in Newfoundland. Unpubl. manuscr., 27 p. Department of Biology and Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9.

Support for the idea that fish will leave a suboptimal habitat is reflected in the results of the transfer experiments where young tautog left the cement block structures provided for them. Similar results were obtained with juvenile cunner (Olla unpubl. obs.). In attempting to examine the mechanism for habitat selection in the manini, *Acanthurus triostegus sandvicensis*, Sale (1969b) performed a series of laboratory experiments and concluded from these that there was a higher intensity of exploratory behavior exhibited when animals were subjected to an inadequate environment. Similarly, it could be concluded that young tautog were showing greater exploratory behavior when they left the experimental cover provided for them. A portion of the fish that disperse will be lost, with the probability of survival decreasing as the amount of time taken to find a suitable habitat increases. Nevertheless, through this mechanism, fish are able to utilize seasonally available resources.

The return to perennial habitats from seasonal ones in the fall may also be related to these becoming suboptimal for the fish, but for different reasons than those which caused dispersal in the spring. At habitats which exist only seasonally, as in the case with macroalgae and eelgrass beds, the actual cover that these beds provide begins to wane as they start to die back in the fall. Although some sites were structurally more permanent, such as Site B (the submerged pipe), the animals did not use them as perennial habitats, and the changes which were occurring to render them suboptimal were not obvious. Besides changes in the environment, of prime importance for consideration is the change in the animals' requirements for cover. What served adequately in summer is not adequate for winter.

In observing cunner and young tautog in the field during winter torpor, both species were found in deep recesses and often buried under several millimeters of sand, farther under cover than observed during nighttime quiescence in summer. This afforded them greater protection during the winter. The seasonal sites studied did not provide cover equivalent to that at perennial ones, which have numerous deep crevices and holes.

Laboratory studies on adult tautog confirm the change in cover requirements during winter torpor (Olla et al. 1977; Olla and Studholme 1978). As temperature declined, the fish began to show an affinity for those structures which would serve as cover during the winter at least 1 to 2 wk before

torpor was observed at which time the fish actually burrowed under them being almost completely covered by sand. These structures differed from the ones the fish used throughout the rest of the year at night. In the field, the offshore movement of the adults begins 4 to 8 wk before they would encounter temperatures that would induce torpor (Olla et al. 1974), indicating a change in habitat requirements with season. About the same time that adult tautog are moving offshore, cunner and young tautog are moving to perennial sites.

Association with cover is no doubt a strongly motivated behavior for young tautog and cunner, but one for which there is a considerable range of adaptation. Under seasonally changing conditions or when habitats are simply suboptimal as in the transfer experiments, the animals will disperse, leaving cover at the risk of predation until alternate sites are found (as discussed earlier). On the other hand, a closer association results from transient environmental causes, such as the presence of predators resulting in young tautog fleeing to cover (Olla et al. 1974). Similarly, elevated temperature stress causes young tautog to associate more closely with cover, at least under laboratory conditions (Olla and Studholme 1975).

ACKNOWLEDGMENTS

We wish to thank the personnel of the U.S. Coast Guard, Fire Island Station, N.Y., for their assistance and cooperation.

LITERATURE CITED

BRAY, R. N., AND A. W. EBELING
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRIGGS, P. T.
1977. Status of tautog populations at artificial reefs in New York waters and effect of fishing. N.Y. Fish Game J. 24:154-167.

COOPER, R. A.
1966. Migration and population estimation of the tautog, *Tautoga onitis* (Linnaeus), from Rhode Island. Trans. Am. Fish. Soc. 95:239-247.

DEW, C. B.
1976. A contribution to the life history of the cunner, *Tautogolabrus adspersus*, in Fishers Island Sound, Connecticut. Chesapeake Sci. 17:101-113

HOBSON, E. S.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgol. wiss. Meeresunters. 24:361-370.

HOBSON, E. S., AND J. R. CHESS
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

OLLA, B. L., A. J. BEJDA, AND A. D. MARTIN
1974. Daily activity, movements, feeding, and seasonal occurrence in the tautog, *Tautoga onitis*. Fish. Bull., U.S. 72:27-35.
1975. Activity, movements, and feeding behavior of the cunner, *Tautogolabrus adspersus*, and comparison of food habits with young tautog, *Tautoga onitis*, off Long Island, New York. Fish. Bull., U.S. 73:895-900.

OLLA, B. L., AND C. SAMET
1977. Courtship and spawning behavior of the tautog, *Tautoga onitis* (Pisces: Labridae), under laboratory conditions. Fish. Bull., U.S. 75:585-599.

OLLA, B. L., C. SAMET, A. J. BEJDA, AND A. L. STUDHOLME.
1977. Social behavior as related to environmental factors in the tautog, *Tautoga onitis*. *In* The behavior of marine organisms, plenary papers, p. 47-99. Mar. Sci. Res. Lab. Tech. Rep. 20, Memorial Univ. Newfoundland.

OLLA, B. L., AND A. L. STUDHOLME
1975. The effect of temperature on the behavior of young tautog, *Tautoga onitis* (L.). *In* H. Barnes (editor), Proceedings of the ninth European marine biology symposium, p. 75-93. Aberdeen Univ. Press.
1978. Comparative aspects of the activity rhythms of tautog, *Tautoga onitis*, bluefish, *Pomatomus saltatrix*, and Atlantic mackerel, *Scomber scombrus*, as related to their life habits. *In* J. E. Thorpe (editor), Rhythmic activity of fishes, p. 131-151. Academic Press, Lond.

OLLA, B. L., A. L. STUDHOLME, A. J. BEJDA, C. SAMET, AND A. D. MARTIN.
1978. Effect of temperature on activity and social behavior of the adult tautog *Tautoga onitis* under laboratory conditions. Mar. Biol. (Berl.) 45:369-378.

SALE, P. F.
1969a. Pertinent stimuli for habitat selection by the juvenile manini, *Acanthurus triostegus sandvicensis*. Ecology 50:616-623.
1969b. A suggested mechanism for habitat selection by the juvenile manini *Acanthurus triostegus sandvicensis* Streets. Behaviour 35:27-44.
1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces; Pomacentridae). Copeia 1971:324-327.
1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology 53:741-744.
1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337-359.

SMITH, C. L., AND J. C. TYLER
1972. Space resource sharing in a coral reef fish community. *In* B. B. Collette and S. A. Earle (editors), Results of the tektite program: Ecology of coral reef fishes, p. 125-170. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.
1973. Direct observations of resource sharing in coral reef fish. Helgol. wiss. Meeresunters. 24:264-275.

WICKLUND, R. I.
1970. Observations on the spawning of the cunner in waters of northern New Jersey. Chesapeake Sci. 11:137

BIOLOGY OF WALLEYE POLLOCK, *THERAGA CHALCOGRAMMA*, IN THE WESTERN GULF OF ALASKA, 1973-75

STEVEN E. HUGHES AND GEORGE HIRSCHHORN[1]

ABSTRACT

Data on the stock composition, growth, mortality, and abundance of walleye or Alaska pollock, *Theragra chalcogramma*, in the western Gulf of Alaska were collected during six demersal trawl surveys in 1973-75. Over 102,000 km² of continental shelf and slope were surveyed; most of this area was covered during spring and summer.

Using the area-swept technique and catchability coefficients of 1.0 and 0.5, the exploitable pollock biomass in the survey region was between 610,000 and 1,220,000 metric tons. The percentage of larger and older fish increased to the west. Sexual maturity was reached at age 3. Growth completion rates ranged from 0.2 to 0.4. Natural mortality was estimated (assuming natural mortality equals growth completion rate) at 0.33 for males and 0.30 for females. Variations in growth completion rates within year class and variable recruitment strength indicated a probable east-west separation of pollock spawning populations near Kodiak.

The National Marine Fisheries Service conducted six trawl surveys of walleye or Alaska pollock, *Theragra chalcogramma*, and other groundfish resources in the western Gulf of Alaska from Cape Cleare, Montague Island, west to Unalaska Island during each spring and summer of 1973-75 (Figure 1). These surveys have provided information on the geographic and bathymetric distribution and densities of species within the groundfish commmunity (Hughes and Parks 1975).

An additional goal of these surveys and subject of this report was the collection of pollock life history data for management purposes.

METHODS

Six cruises were completed. Five were conducted from the 28-m NOAA RV *John N. Cobb*, employing 400-mesh Eastern otter trawls with 30-m footropes. During these five surveys, fishing was conducted following a predetermined, stratified random survey pattern (Grosslein[2]). Fishing densities varied from one 30-min trawl/1,370 km² in strata of anticipated low densities (depths of 90 m or less) to one 30-min trawl/515 km² in the remaining depth strata of 91-180 m, 181-270 m, 271-360 m, and 361-450 m. The other cruise was conducted from the 26-m chartered trawler *Anna Marie*, with similar but larger modified Eastern and Norwegian-style otter trawls with about 34-m footropes. Because the purpose of the *Anna Marie* survey was to determine commercial production potentials (Hughes and Parks 1975), fishing was concentrated where fish schools were detected by echo sounding; no predetermined survey pattern was followed. Consequently, the *Anna Marie* data (Sanak-Unalaska, May-June 1974) were not used for pollock density or biomass studies.

Stretch mesh measurements (1 knot included) of all trawls ranged from 10.2- to 14.0-cm mesh in the intermediate and cod end sections. Trawls measured by scuba divers at depths of 15 m indicated vertical heights of 2-3 m and horizontal spread of 11-13 m.

Methods of selecting random samples of pollock for collection of biological data were consistent during all surveys (Hughes 1976a). Length-frequency fork length (FL) measurements to the nearest centimeter by sex were randomly collected from each catch with the desired sample size being 300 pollock. While processing pollock for length-frequency data, stratified subsamples of otoliths (10/sex per cm) and individual fish weights (5/sex per cm) were taken (±5 g). Otoliths were stored in ethanol in plastic boxes (Hughes 1976b) and ages were later determined as described by LaLanne (in press).

Length-frequency distributions determined

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Grosslein, M. D. 1969. Some observations on accuracy of abundance indices derived from research vessel surveys. Unpubl. manuscr. Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979

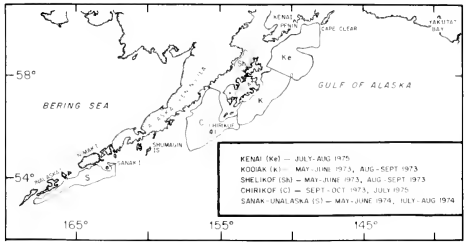


FIGURE 1.—Western Gulf of Alaska regions where trawl surveys were completed, 1973-75.

from the five standard resource assessment surveys were weighted by catch magnitude and area within sampling strata, whereas data collected during the commercial fishing (Sanak-Unalaska, May-June 1974) trials were weighted only by catch magnitudes. Length-age data from the stratified otolith collections of sexed pollock in each survey region (Figure 1) were compiled into age-length keys.

The proportions of observed ages on each length interval above 19 cm were applied to the weighted length frequencies. For this we used a computer program by Allen (1966) modified to exclude extrapolations beyond the aged length range and to include the calculation of mean length at age, as well as numbers at age. Thus numbers and size of pollock in the fishable population were estimated by region, age, and sex.

Resulting analysis provided weighted age composition data and mean length-at-age data for growth studies. Von Bertalanffy growth-in-length parameters and length-weight data were determined for each region.

An area-swept technique (Alverson and Pereyra 1969) was employed to estimate the pollock exploitable biomass, using the relation $\bar{P}w = (\text{CPUE})(A)/(c)(\bar{a})$ where $\bar{P}w$ is equal to the average standing stock, in weight, of the catchable population. A is the total area; $\bar{a}$ is the average bottom area covered by the trawl per standard tow; and c is a coefficient related to the effectiveness of the trawl in capturing pollock.

Whereas earlier studies of Alaskan pollock assumed $c = 1.0$ (Alverson and Pereyra 1969), pollock were often acoustically detected off the sea bottom and above the trawl's headrope. Estimates of c given for some gadoid species of the northeastern Atlantic Ocean indicated c may not exceed 0.51 (Edwards 1968). In this report, values of both 0.5 and 1.0 provide a conservative range of biomass estimates.

RESULTS

The surveys resulted in 144 fishing days on the grounds and 368 successful trawl hauls. Over 455,000 kg of groundfish were sampled, including 49,912 pollock which were processed for biological data.

Size and Age Composition

In the three regions where spring and summer surveys were conducted during the same year (Shelikof Strait 1973; southeast Kodiak 1973; and Sanak-Unalaska 1974), seasonal variations in size and age composition were attributed to fish measuring ≥ 28 cm which represented the 1- and 2-yr-old juvenile segment of the population (Figures 2, 3). However, substantial differences between regions indicate that size and age of adult pollock consistently increased when moving from the southeast Kodiak and Shelikof Strait regions westward through the Chirikof region and into the Sanak-Unalaska region.

The age composition data also indicated that Gulf of Alaska pollock display strong variations in year-class strength. Both 1967 and 1970 year classes showed unusually strong recruitment. Indication of a strong 1967 year class, sampled as 6-yr-olds, was noted during the May-June 1973 surveys of the southeast Kodiak and Shelikof regions. The relative strength of this year class was again noted 3 mo later during the August-September survey of southeast Kodiak and, particularly, of Shelikof Strait. Farther west, in the October 1973 Chirikof

FIGURE 2.—Weighted length-frequency distributions of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75

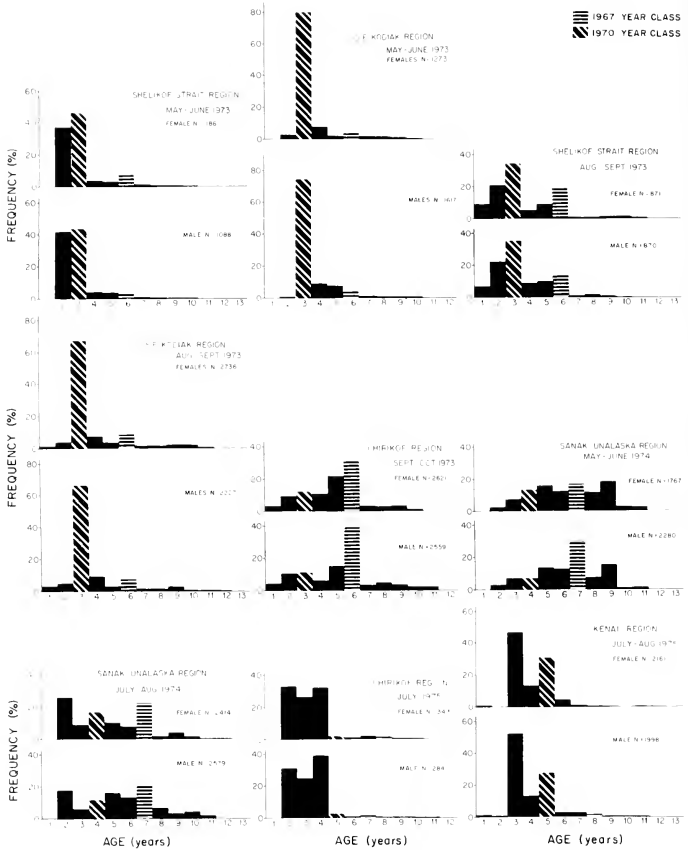


FIGURE 3.—Weighted age-frequency distributions of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

survey, 6-yr-old pollock were dominant. One year later, in the most westward region (Sanak-Unalaska 1974), the prominence of the 1967 year class as 7-yr-olds was apparent during both the May-June and July-August surveys.

During the May-June and August-September 1973 surveys of southeast Kodiak and Shelikof Strait, 3-yr-old pollock (1970 year class) were dominant. The unusual strength of this year class was again noted 2 yr later east of Kodiak as 5-yr-olds during the 1975 Kenai survey. However, recruitment of the 1970 year class was not successful west of Kodiak, as shown by the low relative abundance of 3-yr-olds in the Chirikof region in 1973, of 4-yr-olds in the Sanak-Unalaska region in 1974, and of 5-yr-olds in the Chirikof region in 1975.

Maturity and Sex Composition

Most adult pollock (>85%) had spawned prior to our earliest sampling (May). Based upon a subjective evaluation of gonad condition from pollock collected during May, it appeared that prime spawning periods were March and April. Ripe males and females were obtained as late as August, but these represented <0.1% of samples. Both sexes were fully recruited to the spawning population at age 3. Mature or recently spent age 2 males were encountered but represented <5% of that age-group. Mature or spent age 2 females were not encountered; however, minor gonad enlargement was noted. Means of lengths at first maturity in spring surveys were 29-32 cm for males and 30-35 cm for females.

Our data indicate that sex composition fluctuates around 50% at 20-45 cm FL but that females become progressively more dominant with larger size (Figure 4). As will be shown later, the point of major difference in sex ratio (45 cm) is composed primarily of age 4, 5 females and age 5, 6 males.

Length-Weight

Pollock length-weight data by sex were collected during the May-June and August-September surveys of the southeast Kodiak and Shelikof Strait regions in 1973. Data were also collected during the September-October 1973 survey of the Chirikof region. Length-weight relations were determined for these survey regions and periods (Figure 5) by fitting the logarithmic form of the equation ($W = aL^d$), where W is body weight in grams and L is fork length in centimeters, to the mean weight per centimeter-length interval.

Comparison of these curves indicates that female pollock measuring >33 cm weighed considerably less than males of equal length during the May-June postspawning survey. Female weight gain during summer was more rapid than in males, and differences in weight-at-length in the Shelikof Strait, southeast Kodiak, and Chirikof regions were negligible during the August-October sampling.

Regional differences during spring-summer periods were also noted. Shelikof Strait pollock were heavier than southeast Kodiak pollock of equal length during spring and considerably lighter during summer. This difference may be due to a more rapid weight gain in the southeast Kodiak region or to migration of the most healthy fish out of Shelikof. An additional factor suggesting migration was that samples of male pollock in Shelikof actually showed a weight loss from spring to summer.

Density Distribution and Estimates of Standing Stock

Pollock were distributed over depth intervals of 50-360 m (Table 1). Highest densities occurred at depths of 91-270 m during spring and summer. Geographically, densities were highest at Sanak-Unalaska (181-270 m), followed by southeast Kodiak (91-180 m). Spring-summer 1973 assessment surveys of Shelikof Strait and southeast Kodiak indicated highest densities during summer.

The summer biomass of pollock exceeding 20 cm FL was estimated as 610,000-1,200,000 metric tons (t) of whole fish (Table 1). Regional biomass estimates were greatest in the Chirikof region, followed by Sanak-Unalaska, southeast Kodiak, Kenai, and Shelikof Strait.

Growth

Length-age data from the nine surveys were fitted by the von Bertalanffy relation $l_t = L_\infty \{1 - \exp k(t - t_0)\}$ following computational procedures by Fabens (1965). Because variation in age range affects comparability of parameters (Hirschhorn 1974), curve fits over original age ranges were supplemented: 1) with fits over a standardized age range of 2-8 yr, 2) with an artificial data point (0,0

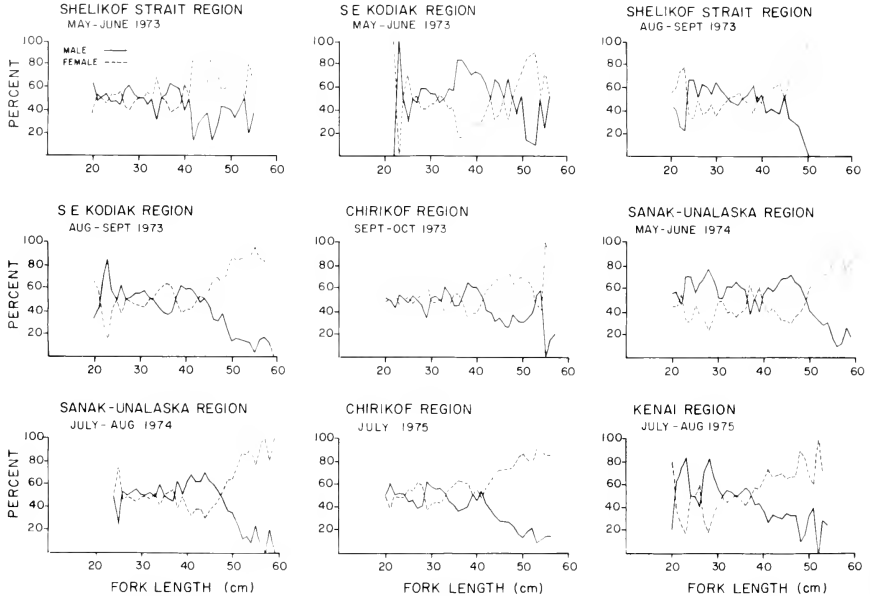


FIGURE 4.—Walleye pollock sex composition plotted as a function of increasing fish length by survey region and season in the western Gulf of Alaska, 1973-75.

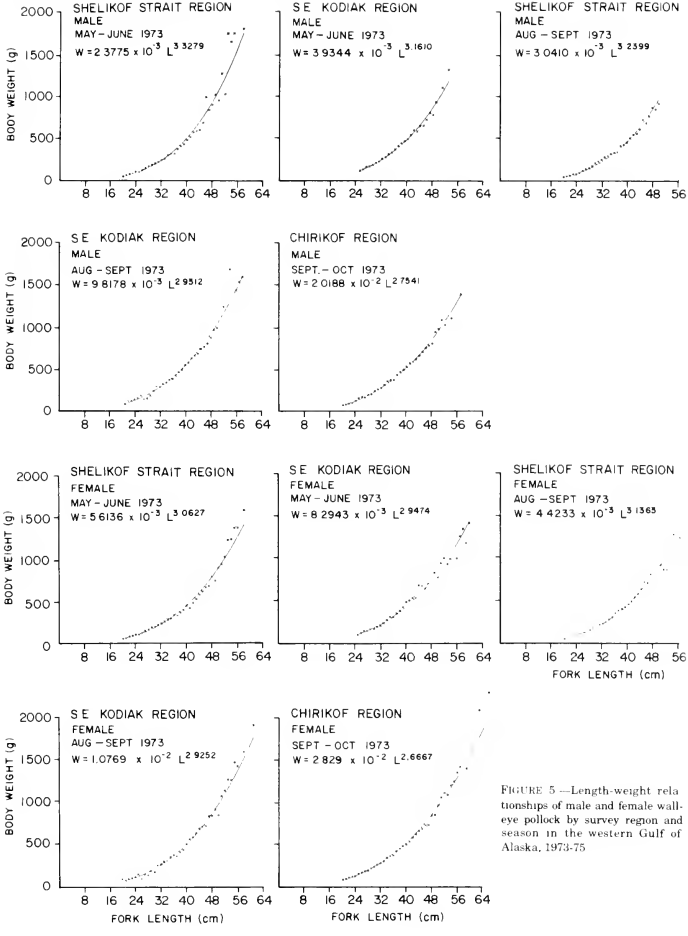


FIGURE 5.—Length-weight relationships of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75

TABLE 1.—Summary of exploitable walleye pollock biomass and density by depth strata and survey regions in the western Gulf of Alaska. Catchability coefficients 1.0 and 0.5 are used to produce a range of pollock biomass and density. Biomass estimates were calculated from the summer survey period due to limited spring survey coverage.

Survey region and period	Depth strata (m)	Area surveyed (km^2)	Density (t/km^2)		Exploitable biomass (t)	
			$c = 1.0$	$c = 0.5$	$c = 1.0$	$c = 0.5$
Summer						
Kenai Peninsula	91-180	19,183	4.1	8.2	77,742	155,485
(148.-152 W)	181-270	8,026	2.8	5.6	22,230	44,460
July-Aug 1975	271-360	796	0.2	0.4	186	371
Regional total		28,005			100,158	200,316
SE Kodiak	55-90	7,302	2.2	4.4	16,180	32,360
(152.-154 W)	91-180	6,143	16.1	32.2	99,042	198,085
Aug-Sep 1973	181-270	1,475	9.9	19.8	14,706	29,412
	271-360	737	0	0	0	0
Regional total		15,657			129,928	259,857
Shelikof Strait	55-90	381	0.2	0.4	89	178
(Aug-Sep 1973)	91-180	3,341	5.8	11.6	19,480	38,960
	181-270	2,713	1.0	2.0	2,610	5,221
Regional total		6,435			22,179	44,359
Chirikof	55-90	9,439	1.0	2.0	9,082	18,163
(154.-159 W)	91-180	12,749	13.6	27.2	173,583	347,168
July 1975	181-270	11,661	0.2	0.4	11,220	22,440
Regional total		33,849			193,885	387,771
Sanak-Unalaska	50-90	6,647	2.7	5.4	18,060	36,120
(162.-168 W)	91-180	8,935	13.1	26.2	117,096	234,192
July-Aug 1974	181-270	912	31.8	63.6	29,107	58,214
	271-360	703	0	0	0	0
	361-450	322	0	0	0	0
Regional total		17,519			164,263	328,526
Survey total		101,465			610,413	1,220,826
Spring						
SE Kodiak	50-90	4,778	0.4	0.8	—	—
(148.-152 W)	91-180	4,496	2.0	4.0	—	—
May-June 1973	181-270	737	0.4	0.8	—	—
Regional total		10,011				
Shelikof Strait	50-90	381	0.2	0.4	—	—
(May-June 1973)	91-180	3,982	0.7	1.4	—	—
	181-270	11,558	0.6	1.2	—	—
	271-360	1,008	0.3	0.6	—	—
Regional total		16,929				
Survey total		26,940				

added on the assumption that at age 0 length is near 0 (Alverson and Carney 1975), and 3) with nominal ages or ring counts incremented by the fraction of a year between middates of spawning and sampling (Δt in Table 2).

Because each growth pattern in Figure 6 represents a synthetic cohort, i.e., a composite of year classes, the departures from the pattern, generated by members of the 1967 and 1970 year classes, were examined in detail. According to the age composition discussed earlier, both year classes were encountered in relatively high abundance at one extreme of the survey range (Figure 3) and in low abundance at the other (the 1967 year class was prominent at Sanak-Unalaska, the 1970 year class at Kenai). To examine the evidence for a growth-density relation, the size differences between the synthetic growth curves and observed mean lengths of the sampled age-groups of these year classes were calculated (lower part of Table 2).

The results are shown along a schematic east-west axis in Figure 7. In the easternmost region (Kenai), the strong 1970 year class indicates negative departures from expectation (at age 5), whereas corresponding departures are positive for the relatively weak year class of 1967 (at age 8). In the westernmost region, the relative strengths of these year classes seemed to be reversed, and the direction of departures of their mean lengths at ages 4 and 7 also reversed. By this criterion, the segregation of the two components of each year class was most pronounced at the extremes and least so in the intermediate Kodiak-Shelikof region where the lines cross.

Age-specific observed lengths of the 1970 and 1967 year classes were also compared directly with those of others, apparently weaker year class-

TABLE 2.—Mean length (centimeters) at age of western Gulf of Alaska *Theraga chalcogramma* by survey and sex; growth parameters (L_∞, K, t_0) for original and "selected" data sets, with standard deviation (σ) of departures from fit; departures of 1967 and 1970 year class mean lengths at age, from fit (Δ67YC, Δ70YC).

		Sanak				Chirikof				Kodiak			
		May-June '74		July-Aug '74		July 1975		Sept.-Oct. '73		May-June '73		Aug.-Sept. '73	
		M	F	M	F	M	F	M	F	M	F	M	F
Item		— (0.17)[1]			(0.42)		(0.25)		(0.50)		(0.17)		(0.42)
Years of age (t)	1	—	—	20.00	—	—		19.49	20.02	—	—	23.07	23.09
	2	25.52	24.36	29.55	29.75	24.70	24.99	27.15	27.99	25.24	26.21	29.51	29.50
	3	35.19	35.20	38.51	36.04	31.54	32.18	35.01	35.74	30.24	30.38	33.44	33.85
	4	39.59	40.17	41.16	42.14	33.88	34.98	39.32	40.58	38.77	38.44	40.37	41.48
	5	43.68	44.63	44.07	45.18	38.41	40.07	40.18	42.63	40.30	43.55	41.70	44.32
	6	45.16	46.81	45.01	47.05	42.10	43.05	41.36	43.82	43.26	45.15	43.37	45.91
	7	47.02	48.70	44.69	47.02	42.59	44.98	43.84	48.44	47.66	50.62	46.47	48.73
	8	47.50	51.01	47.27	51.65	44.67	48.02	47.37	48.37	48.04	53.04	46.97	50.16
	9	48.27	50.74	48.34	53.51	49.84	52.86	46.85	49.39	46.67	51.62	46.41	50.77
	10	53.16	55.25	47.74	52.05	50.86	54.21	46.04	52.73	46.03	57.03	48.00	49.52
	11	50.11	55.56	48.13	46.79	50.57	53.85	—	—	—	—	54.10	54.00
	12	—	—	—	57.00	—	54.00	—	—	—	—	55.07	—
Parameter sets for original data	L_∞	50.06	55.22	48.14	53.03	52.36	58.40	47.26	54.37	48.21	66.25	58.69	56.34
	K	−0.47	−0.37	−0.47	−0.42	−0.25	−0.21	−0.38	−0.28	−0.38	−0.18	−0.19	−0.24
	t_0	0.68	0.63	0.29	0.61	−0.30	0.42	0.10	−0.09	0.26	−0.61	−1.18	−0.75
	σ	1.63	1.58	0.94	2.94	2.52	1.45	1.32	1.31	1.87	1.70	2.30	1.40
Parameter sets for ages 0.-2-8	L_∞	51.649	57.855	48.948	54.288	47.651	52.515	49.848	51.970	52.271	59.788	48.496	53.118
	K	−0.328	−0.265	−0.396	−0.328	−0.323	−0.284	−0.319	−0.315	−0.302	−0.256	−0.383	−0.331
	t_0	−0.036	−0.052	−0.019	0.012	0.011	0.023	0.004	−0.015	0.021	0.062	0.018	0.021
	σ	1.228	1.429	1.349	1.246	0.940	1.013	1.603	1.132	1.363	1.686	1.157	1.074
	Δ70 YC	−0.96	+1.25	−0.65	+0.66	0.49	−0.53	+1.46	−0.91	−1.85	2.47	1.88	−2.02
	Δ67 YC	−0.24	−0.59	−1.69	−2.48	−0.34	−0.59	−2.23	−1.50	−0.86	−2.16	−0.95	−0.82

		Shelikof				Kenai	
		May-June '73		Aug.-Sept. '73		July-Aug. '75	
		M	F	M	F	M	F
Item		(0.17)		(0.42)		(0.33)	
Years of age (t)	1	—	—	20.71	20.74	21.92	21.23
	2	23.95	24.04	28.30	29.38	26.47	29.00
	3	30.37	30.64	32.71	33.52	31.84	32.58
	4	35.75	36.37	36.86	37.48	36.43	38.13
	5	38.86	40.34	38.71	39.20	37.94	39.65
	6	41.42	44.18	40.06	42.09	43.04	45.65
	7	49.01	46.50	45.32	47.51	[2]43.33	50.37
	8	49.41	49.29	43.94	46.52	51.06	51.32
	9	46.49	47.82	45.21	47.77	51.72	54.10
	10	47.00	49.85	45.60	48.39	53.00	—
	11	—	—	—	44.00	53.45	53.22
	12	—	—	—	—	—	55.44
Parameter sets for original data	L_∞	49.48	52.92	46.62	46.50	62.63	57.60
	K	−0.34	−0.28	−0.33	−0.39	−0.10	−0.22
	t_0	0.26	0.05	−0.31	0.06	−1.50	−0.71
	σ	2.42	0.90	1.16	2.29	1.72	1.88
Parameter sets for ages 0.-2-8	L_∞	55.974	56.041	45.010	47.592	54.591	54.274
	K	−0.253	−0.255	−0.405	−0.386	−0.274	−0.312
	t_0	0.042	0.019	0.018	0.031	0.089	0.069
	σ	1.846	0.466	1.561	2.002	2.832	2.579
	Δ70 YC	0.23	0.31	−0.94	−1.21	−3.66	−4.11
	Δ67 YC	−2.68	−0.18	−1.57	−1.46	−2.18	−1.17

[1]Age, increment (Δt) for sample date

[2]Extreme frequencies eliminated in computing mean length at age 7

es to see whether differences agree, in direction, with those generated by use of synthetic cohort growth curves. In this comparison, only early season samples were considered. Both year classes indicated lower mean lengths than other year classes sampled at like ages.

Growth completion rates (K) were 0.34 in males and 0.28 in females, from surveys indicating prominence of the 1967 or 1970 year classes (Figure 3). A similar averaging of length-at-age in all remaining data gave higher K-values (0.40 and 0.35, respectively), possibly reflecting lower relative year class strengths. We also ranked relative percent frequency at each age within range 2-8 yr, then fitting lengths of ages within ranks, thus replacing the original time-area classifications. Extreme K-values (males 0.25, 0.38; females 0.24, 0.40) were associated with extreme ranks; however, at intermediate ranks fluctuations were considerable. The K-ranges from this rearrangement of the data are similar to those shown in Table 2 for the original data configurations by survey (males,

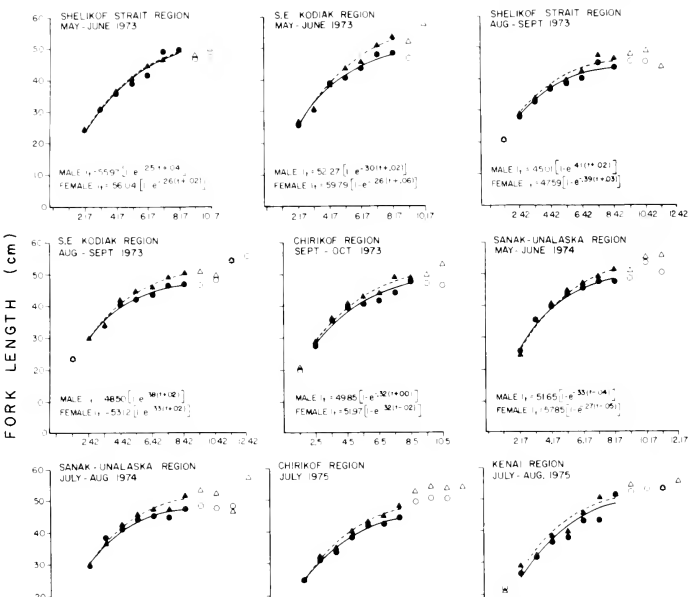


FIGURE 6.—Growth curves of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

0.25, 0.41; females, 0.26, 0.39). The arithmetic means of K in Table 2 (ages 2-8) are 0.33 and 0.30 and the geometric means of L_∞ 50.39 and 54.06 cm for males and females, respectively. Significant negative correlation between $\ln L_\infty$ and $|K|$ was found in both sexes. The highest observed ages in each survey lie, on the average, between those ages when growth is theoretically between 95 and 97.5% complete, according to the growth parameters for ages 2-8 in Table 2. Similarity in this regard is considered essential in estimating average natural mortality rates from empirical data (Alverson and Carney 1975).

Yield Relations

For management purposes natural mortality (M) as well as growth rate is needed for recogni-

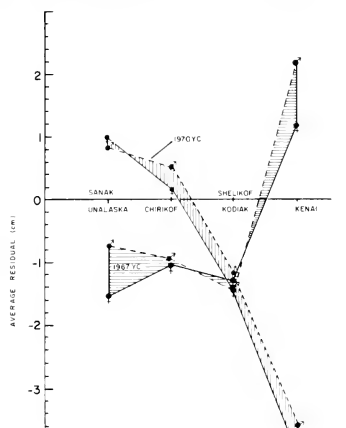


FIGURE 7.—Average of residuals from fit of observed mean length-at-age, taken over all age-groups of the 1967 and 1970 year classes of walleye pollock sampled in the western Gulf of Alaska by region and sex, 1973-75

tion of optimality in biomass relations. Since no independent estimates of M are available for Gulf of Alaska pollock, we shall assume $M = K$. Yield relations based on this assumption have been examined in detail by Alverson and Carney (1975) for cases where the third Bertalanffy parameter (t_0) is close to zero. In the preceding section and Table 2, such growth estimates were provided.

As indicated earlier, means of observed female lengths at first maturity ranged from 30 to 35 cm, comparable to 32-37 cm when length at this stage is considered as two-thirds of the final length (L_∞) associated with the extreme growth completion rates for females in Table 2 (0.386, 0.255). Use of this constant was discussed and examined by Holt (1962). Corresponding ages at first maturity (T_{mat}) ranged from 2.84 to 4.30 yr, and ages of maximum (unfished) biomass per unit input (T_{mb}) ranged from 3.60 to 5.45 yr, according to equation 5 of Alverson and Carney (1975). The differences ($T_{mb} - T_{mat}$) at each extreme imply two annual pre-T_{mb} spawnings in the low-K cohort compared to one in the high-K cohort. The maximum production per unit input from the low-K (0.255, L_∞ = 56.04) cohort exceeds that for the high-K (0.386, L_∞ = 47.59) cohort by 64% assuming a cubic length-weight relation. Under the assumption $M = K$, any environmental or fishing conditions tending to reduce growth completion rate (and increase L_∞) would be expected to increase cohort productivity as well as delay the achievement of maximum biomass per unit input. Such a delay also implies an increased number of spawning opportunities for females prior to the age at maximum biomass.

DISCUSSION

Pollock size and age composition, size and age at first maturity, sex composition, length-weight relationship, density distribution by depth and area, estimate of exploitable biomass, in addition to growth and yield relationships in the western Gulf of Alaska have been described. The survey area, Cape Cleare to the western end of Unalaska Island, carries an exploitable pollock biomass that we have calculated at 0.6-1.2 million t. Compared with the 54,000 t of exploitable pollock in the central and eastern portions of the Gulf of Alaska (Ronholt et al.[3]), the resource described in this report represents over 90% of pollock in the Gulf of Alaska.

Agreeability of size, age, and growth data between surveys over the 3-yr study period indicated that assessment techniques were reliable. Weighting size and age composition data by catch rate and square miles within each depth sampling stratum is regarded as desirable when dealing with a species which displays bathymetric preference. Such weighting procedures coupled with the collection of otoliths over all depths and areas appear to provide accurate descriptive information for a large region. It is possible that pollock display bathymetric variations in growth rate as Westrheim (1973) has shown for Pacific ocean perch. However, our data did not allow such de-

[3]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1976. An assessment of demersal fish and invertebrate resources of the northeastern Gulf of Alaska, Yakutat Bay to Cape Cleare, May-August 1975: NEGOA Annual Report. Unpubl. manuscr., 184 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112

tailed examination, and the above sampling and analytical procedures would average this phenomenon if it does occur.

Data presented indicate that at least 87% of the pollock resource resides at depths 91-270 m during the summer with greater bathymetric dispersement during the spring. Densities were lowest in the Kenai region (eastern extreme) and highest in the Sanak-Unalaska region (western extreme). Except for the Kenai and Shelikof regions, where densities were notably low relative to other regions, regional biomass estimates are a function of both pollock density and available shelf or slope area at depths of 91-270 m.

Age and size composition data indicated that strong variations in year-class strength occur and recruitment of year classes is not uniform over the western Gulf. Whereas such geographic variations in year-class strength could be caused by environmental conditions, neither of two prominent year classes (1967 and 1970) indicated similar relative abundance over the entire east-west range of these surveys. Rather, the 1967 year class appeared in high density only west of southeast Kodiak and the 1970 year class, only at southeast Kodiak and eastward. These geographic density differences were accompanied by observed growth differences (size at age) and by negative departures of observed size at age in these year classes from expected size based on growth curve fits (Figure 7).

Analysis of all the growth information from these surveys indicated an inverse relation of growth completion rate (K) to relative year-class strength as well as to final estimated fish length (L_∞). From the differences in K values obtained and assuming $M = K$, it is inferred that optimally timed harvests per unit input would be larger in low-K cohorts than in high-K cohorts. Optimal timing from the yield standpoint also implies enhancement of the reproductive potential of low-K cohorts.

In conclusion, the western Gulf of Alaska pollock stock has been described and biological parameters reported for management. It is suggested that an east-west separation of spawning stocks may occur near Kodiak and that management should be applied accordingly.

LITERATURE CITED

ALLEN, K. R
1966 Determination of age distribution from age-length keys and length distributions, IBM 7090, 7094, Fortran IV. Trans. Am. Fish. Soc. 95:230-231

ALVERSON, D. L., AND M. J. CARNEY
1975. A graphic review of the growth and decay of population cohorts. J. Cons. 36:133-143.

ALVERSON, D. L., AND W. T. PEREYRA.
1969. Demersal fish explorations in the northeastern Pacific Ocean—an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26:1985-2001.

EDWARDS, R. L.
1968. Fishery resources of the North Atlantic area. *In* D. W. Gilbert (editor), The future of the fishing industry of the United States, p. 52-60. Univ. Wash. Publ. Fish., New Ser. 4.

FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

HIRSCHHORN, G.
1974. The effect of different age ranges on estimated Bertalanffy growth parameters in three fishes and one mollusk of the northeastern Pacific Ocean. *In* T. B. Bagenal (editor), The aging of fish, p. 192-199. Unwin Bros. Ltd., The Gresham Press, Old Woking, Surrey, Engl.

HOLT, S. J.
1962. The application of comparative population studies to fishery biology - an exploration. *In* E. D. LeCren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 51-71. Blackwell Sci. Publ., Oxf.

HUGHES, S. E.
1976a. System for sampling large trawl catches of research vessels. J. Fish. Res. Board Can. 33:833-839.
1976b. Simple container for the collection and storage of otoliths. Calif. Fish Game 62:306-307.

HUGHES, S. E., AND N. B. PARKS.
1975. A major new fishery for Alaska. Natl. Fisherman 55(13):34-40.
In press. The validity and consistency of age determinations from otoliths of walleye pollock (*Theragra chalcogramma*). Int. North Pac. Fish. Comm., Annu. Rep. 1978.

WESTRHEIM, S. J.
1973. Age determination and growth of Pacific ocean perch (*Sebastes alutus*) in the northeast Pacific Ocean. J. Fish. Res. Board Can. 30:235-247.

NOTES

ZOOPLANKTERS THAT EMERGE FROM THE LAGOON FLOOR AT NIGHT AT KURE AND MIDWAY ATOLLS, HAWAII

Many zooplankters in nearshore marine habitats are in the water column at night, but spend the daytime sheltered on or near the sea floor (Emery 1968; Glynn 1973; Porter 1974). The diel movements these organisms make between the water column and the sea floor are major features of nearshore ecosystems, and strongly influence many of the fishes in these habitats (Hobson 1968, 1973, 1974, 1975; Hobson and Chess 1976, 1978). Some of these zooplankters are holoplanktonic forms that swarm close to bottom structures by day and disperse above the reef at night. Included are various calanoid copepods (e.g., *Acartia* spp.), cyclopoid copepods (e.g., *Oithona* spp.), mysids (e.g., *Mysidium* spp.), and larval fishes (Emery 1968; Hobson and Chess 1978). Although such forms often occur in caves and other reef openings large enough to accommodate their free-swimming habit, they should be distinguished from the many meroplanktonic forms that by day live in or on the substrate (although this distinction between meroplankton and holoplankton is not always clear-cut).[1] At least some of these neritic holoplankters seem just loosely associated with specific substrata. For example, by day the calanoid *A. tonsa* swarmed close to coral reefs in the tropical Atlantic (Emery 1968) and to kelp forests in the warm temperate eastern Pacific (Hobson and Chess 1976), and also occurred in open waters offshore (Fleminger 1964). The meroplanktonic forms which by day characteristically assume what is essentially a benthonic mode have a much stronger affinity to specific nearshore substrata, and these are the major topic of this paper. Included are various polychaetes, ostracods, copepods, mysids, cumaceans, tanaids, isopods, gammarid amphipods, and various larval forms (Hobson and Chess 1976, 1978, in prep.).

Two recent studies, one on the Barrier Reef (Alldredge and King 1977) and the other in the Philippine Islands (Porter et al 1977; Porter and Porter 1977), have attempted to quantify the emergence of zooplankters from various coral-reef substrata. These are important papers because they draw attention to what unquestionably is a highly significant and long-neglected aspect of nearshore ecosystems. We suspect, however, that there are problems with these studies. If so, the problems should be promptly recognized because undoubtedly they will spawn similar investigations by other workers elsewhere (e.g., see Randall et al. 1978). Alldredge and King collected their samples in Plexiglas[2] traps that rested on the bottom and retained organisms that rose into the water column; however, zooplankters from the surrounding water had access to these traps through gaps between the traps' rigid lower edges and irregularities on the sea floor. Earlier (Hobson and Chess 1978), we stated that these collections need to be repeated with this possibility of error eliminated. Obviously, if many zooplankters entered the traps from the surrounding water column, the samples cannot be considered measures of the organisms that emerged from the underlying substrata. The Porter group used traps that were tethered above the sea floor, and so would seem to have offered even greater access to zooplankters from the surrounding water. In fact, the probability that such forms entered the traps seems to us so great that we would have expected that their intent was simply to sample zooplankters near the reef. And yet, in prefacing their findings with statements like (p. 107)". . . volumes of plankton produced per m^2 per hour by different reef substrates during the day and during the night are given in Table 1." they clearly implied that each trap sampled only those organisms that had risen from the substrate directly below it.

Our doubts about these studies, however, were moderated by limitations in our own knowledge of the phenomenon. We had worked extensively with these activity patterns as they relate to fishes (Hobson 1968, 1974; Hobson and Chess 1976, 1978) and had made inferences about the daytime modes of nocturnal zooplankters in nearshore habitats. Still, we had not satisfactorily distin-

[1] We define meroplankton as those zooplankters that are in or on the substrate during part of the diel cycle, and holoplankton as those that are in the water column at all hours. As pointed out earlier (Hobson and Chess 1976), these terms have carried different meanings for different authors.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

guished the forms that by day assume essentially a benthonic existence on or in the bottom, from the forms that by day aggregate close to, yet free of, the substrate, or which migrate to deeper water. To increase our understanding of these activities and to acquire a firmer base upon which to assess other studies, we trapped zooplankters that emerged from various substrata in the lagoons of Kure and Midway Atolls, Hawaii during August 1977, making special effort to exclude forms from the surrounding water column.

Methods

Midway and Kure Atolls are about 90 km apart at the northwestern end of the Hawaiian Archipelago. They are very similar, each having a lagoon that is relatively small (diameter about 8 km) and shallow (maximum depth about 15 m). All our study sites were in approximately 5 to 7 m of water near the outer leeward reefs.

We made seven paired collections, each pair at a different location. One of each pair sampled the organisms that rose from the substrate during the day, and the other sampled the organisms that rose from the same spot during the night. Of the substrates sampled, three were sand (two at Midway, one at Kure), two were a mixture of sand and coral rubble (one at Midway, one at Kure), and two were small heads of both living and dead coral

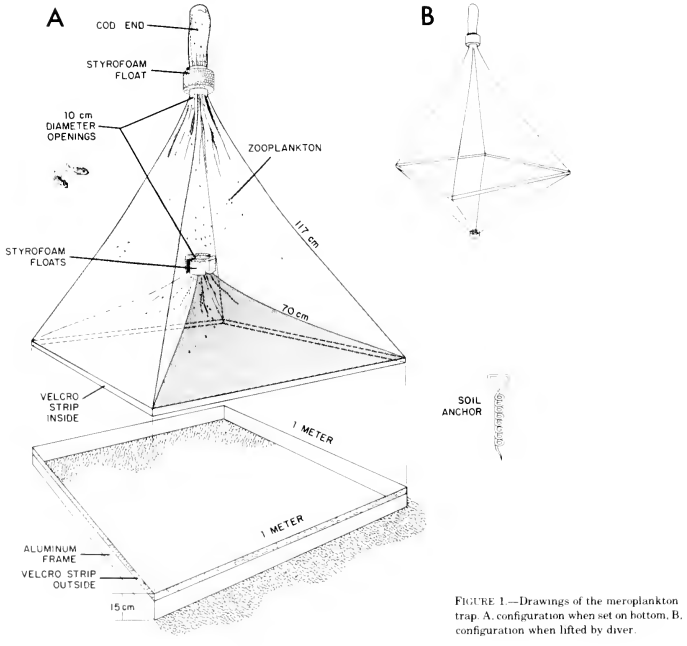


FIGURE 1.—Drawings of the meroplankton trap. A, configuration when set on bottom; B, configuration when lifted by diver.

(about 0.25 to 0.40 m^2) surrounded by sand and coral rubble (one at Midway, one at Kure).

It was not our intent to characterize the meroplankton from each substrate—the collections were too few for this; rather, we sought only a general understanding of the types and numbers of organisms that emerge from the lagoon floor.

To begin each set of collections, we placed our trap (Figures 1, 2) in position between sunrise and 0800 h. First we buried the lower portion of the metal frame in the sand and secured it with soil anchors. A tight seal around the base of the trap was judged critical to prevent entry by organisms from the surrounding water. Next we attached the net (which had a 0.333-mm mesh) to this base and allowed it to remain in position throughout the day. We retrieved the net between 1730 h and sunset, washed all materials into the cod end, then removed the materials, and placed them in 10% Formalin. The net, with an empty cod end in place, was then reattached to the frame and left in place throughout the night. The following morning, again between sunrise and 0800, the entire trap—base as well as net—was retrieved, and the collected organisms placed in preservative as before. Having thus completed one set of collections, we moved to another site and repeated the procedure. (We would have reversed the order of collections in some sets, e.g., nighttime first, if appreciable numbers of organisms had been taken by day; as it turned out, however, essentially all organisms were taken in the nighttime samples, as detailed in the Results.)

FIGURE 2.—The meroplankton trap in place to sample organisms that emerge from sand in the lagoon of Midway Atoll. If the trap had not been designed to exclude holoplankters, we believe the collections would have included, among other holoplankters, calanoid copepods (*Acartia* sp.) that swarmed close to the adjacent reefs by day, including at their bases, and dispersed throughout the area at night.

Our trap worked as follows: Organisms rising from the substrate inside the trap swam upward through the small upper opening of the inner cone and entered the space within the larger outer cone (Figure 1A). Some may have continued up into the cod end, which floated above, but this had no bearing on the collections. When the organisms returned toward the sea floor all except those that happened to descend through the small orifice of the inner cone were trapped where the two cones converged at their common base. In retrieving the net, we reached in under the edge attached to the metal frame and grasped the inner cone around its smaller orifice, thus closing it. We then pulled this out, thus everting the inner cone and producing a diamond-shaped bag (Figure 1B) with the orifice closed in our grasp at one end and the cod end at the other. We then towed the net back to the boat, still enclosing the smaller orifice in our grasp, so that, as we swam, all materials inside were swept back into the trailing cod end.

Results

The organisms collected by our trap, day and night, are listed in Table 1. The general absence of organisms in the daytime collections was predictable, based on the many reports which have concluded that the diel emergence of such forms is primarily a nocturnal phenomenon (see references listed above). Among organisms we observed swarming close to reef structures in the vicinity of our trap during the day were calanoid copepods (most of them *Acartia* sp.), mysids, and larval fishes. Although such forms disperse in the water column at night (Emery 1968; Hobson and Chess 1976, 1978), their absence from our trap collections is consistent with the contention that the holoplanktonic forms associated in varying degree with the reef are distinct from those organisms that live by day in or on the substrate.

TABLE 1.—Organisms trapped by day and night at Kure and Midway Atolls.

Zooplankton category	Day ($n = 7$)		Night ($n = 7$)	
	Percent occurrence	Mean no individuals	Percent occurrence	Mean no individuals
Foraminiferans[1]	43	2.9	100	18.9
Polychaetes[2]	29	0.5	100	7.3
Gastropods[3]	57	0.1	100	7.0
Ostracods[4]	0	0.0	86	1.7
Calanoid copepods[5]	0	0.0	100	17.7
Cyclopoid copepods	0	0.0	43	1.4
Harpacticoid copepods[6]	0	0.0	100	31.0
Mysids	0	0.0	14	0.1
Cumaceans	0	0.0	29	0.6
Tanaids[7]	0	0.0	86	11.9
Isopods[8]	0	0.0	71	3.0
Crinpedian larvae	0	0.0	29	0.6
Gammarid amphipods[9]	0	0.0	100	40.1
Caprellid amphipods	0	0.0	43	1.0
Candean larvae	0	0.0	43	60.9
Candean adults and juveniles	0	0.0	86	18.4
Reptantian zoea	0	0.0	57	17.0
Brachyuran megalops	0	0.0	71	6.3
Anomuran glaucothoe	0	0.0	43	1.3
Chaetognaths[10]	0	0.0	57	5.9
Ascidian larvae	0	0.0	14	1.0

[1] All foraminiferans were either *Tretomphalus* sp. (72%) or *Amphistigina* sp. (28%).

[2] The major polychaete was *Polyophtnalmus* sp.

[3] Included one 8-mm dorid opisthobranch; the rest were prosobranchs 3 mm long.

[4] The major ostracod was a species of Cylindroleberidnae.

[5] All identifiable calanoids were *Paramisophria* sp., probably undescribed (Abraham Fleminger, Scripps Institution of Oceanography, La Jolla, CA 92038 pers. commun. April 1978).

[6] All identified harpacticoids were of a species of the family Peltididae.

[7] All the tanaids appeared to be of a species of *Leptochelia* close to *L. dubia* (see Hobson and Chess 1976).

[8] Major isopods were *Cirolana* sp. *Ianiropsis* sp. *Munna* sp. anthurids and cryptoniscid larvae.

[9] Gammarids included *Aproides* sp. *Dexaminoides orientalis Lilgeborgia* sp., a eusirid, an oedicerotid, and a phoxocephalid.

[10] All chaetognaths were *Spadella gaetanoi* (A. Alvarino, Fishery Biologist Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. commun. Sept. 1978).

Discussion

Our collections and collecting sites were too few to comprehensively quantify the zooplankters that emerge from the lagoon substrata at Kure and Midway Atolls. Despite its limitations, however, this study increases our understanding of the kinds of organisms that have this habit. Furthermore, it indicates there may be serious problems with the more extensive studies of Alldredge and King (1977), Porter et al. (1977), and Porter and Porter (1977).

Certainly some of the differences between their samples and ours are unrelated to sampling problems. We assume, e.g., that the zooplankton fauna at Kure and Midway Atolls is distinguishable from the zooplankton fauna in the more tropical latitudes of the western Pacific Ocean where the Alldredge and Porter groups studied. It is unlikely, however, that zoogeographic variations can account for certain of the more striking differences between their samples and ours. The predominant forms in their collections were calanoid and cyclopoid copepods. Alldredge and King (1977) calculated that during the night a mean of 6,679 calanoids emerged from each square meter of the reef face, and Porter et al. (1977) reported that over 10,000 calanoids emerged during the night from each square meter of branching coral in their study area. In comparison, our night-long collections from a variety of substrata, including coral, yielded a mean of only 17.7 calanoids/m^2. Of course, we did not sample a well-developed reef. Only two of our sites included living coral, and these were isolated heads (our traps required a bed of sand). So habitat features could have contributed differences between the collections. Nevertheless, if one considers the species of calanoids and cyclopoids collected by Alldredge and King, there are strong indications that the large numbers reported were inflated by holoplanktonic forms. The only calanoids and cyclopoids they identified were *Acartia* spp. and *Oncaea* spp. Species of these two genera are exceedingly numerous in the water column during both day and night (see Emery 1968; Hobson and Chess 1976), and we question whether they could in fact assume a benthonic mode. As stated (Hobson and Chess 1978:149) "We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher." Although the Porter group did not identify their calanoids and cyclopoids to lower taxa, they too sampled western Pacific reefs and so the copepods that similarly dominated their collections may well have been the same, or very similar, to those taken by Alldredge and King. All our calanoids, on the other hand, appeared to be referable to the little known genus *Paramisophria* (Abraham Fleminger, Associate Research Biologist, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978). This fact agrees with our contention that zooplankters which periodically enter the substrate should be morphologically distinctive. If the diurnal benthic mode of this species is a generic characteristic, which seems probable, then its poorly known status likely stems from failure to be sampled by standard plankton-collecting techniques.

During a marine survey of the Palau Islands, Randall et al. (1978) attempted to measure the zooplankters that emerged from the sea floor using traps ". . . built according to the design of Porter

and Porter (1977)." Their samples, taken above coral and sand substrata, included far fewer copepods than the Alldredge and Porter collections (but many more than ours); nevertheless, they recognized the presence of holoplanktonic forms (e.g., siphonophores, crustacean and fish eggs, and fish larvae), which they assumed ". . . either swam (or were carried) under the base of the trap from the open water . . .."

So we believe that the studies by the Alldredge and Porter groups are flawed by the unrecognized occurrence in their samples of organisms from the surrounding water column. At Enewetak Atoll (Hobson and Chess 1978), we concluded that many of the zooplankters above lagoon reefs at night are visitors from the deeper water. If this circumstance existed where Alldredge and Porter set their traps, then their collections probably included deep-water forms. If so, the figures presented as measures of zooplankters that emerge from defined areas of particular nearshore substrata probably include not only holoplankters associated by day with other nearshore substrata but also holoplankters from outside the nearshore realm.

We consider our collections conservative estimates of the numbers of organisms that emerge from the sampled substrata. It may be that some forms which ordinarily rise into the water column were inhibited by our trap, and undoubtedly some that rose into the trap found their way back to the sea floor. But we feel our trap should have been as effective in capturing emerging zooplankters as those used by the Alldredge and Porter groups. Possibly some strictly benthic forms entered our samples by climbing up the inside of the trap. The few prosobranch gastropods that were taken may have been trapped this way, although they were small enough to have been swept up into the water column by surge, or perhaps to possess some flotation device that periodically permits a planktonic mode, as is the case with certain foraminiferans (e.g., *Tretomphalus* and perhaps *Amphistegina*). Significantly, most of the organisms collected belong to groups that include forms we have collected in the water column at night elsewhere: e.g., the foraminiferan genus *Tretomphalus* (at Majuro and Enewetak Atolls: Hobson and Chess 1973, 1976); the polychaete genus *Polyophthalmus* (at Enewetak Atoll: Hobson and Chess 1978); and the ostracod subfamily Cylindroleberdinae, the tanaid genus *Leptochelia*, the isopod genera *Cirolana* and *Munna*, and family Anthuridae, the gammarid genus *Aoroides*, and families Eusiridae, Oedicerotidae, and Phoxocephalidae (at Santa Catalina: southern California: Hobson and Chess 1976, in prep). The forms that predominated in our collections belong to groups that were only relatively minor elements in the Alldredge and Porter collections. Most, in fact, were lumped by Porter et al. (1977) in their summarizing Figure 2 as "miscellaneous." This is not because they took fewer of these forms than we did, but rather because copepods and larvaceans so dominated their collections.

We believe that the major difference between our collections and those of the Alldredge and Porter groups is that we excluded organisms from the surrounding water column. Alldredge and King (1977) were aware that outside organisms could enter through the gaps around the base of their traps, but seemed more concerned about organisms inside that might have escaped. They dismissed both possibilities as significant sources of error with the statement (p. 318 ". . . as many plankters may also enter the trap through these gaps as escape through them." But because these devices were, after all, traps, probably many more zooplankters came in than went out. And if in fact zooplankters entered the traps through these gaps, it seems certain that forms from the surrounding water, including holoplankters, were continuously captured. Porter et al. 1977 reported about 1.5 to 2 times as many zooplankters as did Alldredge and King. They attributed this difference to more effective methods and equipment, but their traps, tethered above the reef, may simply have been more readily entered by holoplankters. This would also account for the relatively large numbers of zooplankters they trapped by day. Both studies may have suffered from a misconception about the movements of these organisms. Alldredge and King doubted that many escaped through the gaps around the bases of their traps because they assumed (p. 318 ". . . emerging plankton swim primarily upward . . .." The Porter group would seem to have based their trap design —inverted cones tethered above the bottom—on the same assumption. But while these animals certainly rise progressively higher in the water column after emerging from the sea floor, generally they swim—some flit—in short, irregular tangents more horizontal than vertical (based on our direct observations of a wide variety of forms in many locations). In any event if holoplankton did enter these traps in significant numbers, then

the samples taken should not be presented as measurements of the forms that emerged from the underlying substrata.

Acknowledgments

We thank Richard S. Shomura and his staff at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, and Robert T. B. Iverson, Southwest Region, National Marine Fisheries Service, for their cooperation and logistic support. We also thank Robert Johanness, Hawaii Institute of Marine Biology; Abraham Fleminger, Scripps Institution of Oceanography; and Alan R. Emery, Royal Ontario Museum, Canada, for helpful comments on the manuscript. Kenneth Raymond, Southwest Fisheries Center La Jolla Laboratory, drew Figure 1 and Alice Jellett, Southwest Fisheries Center Tiburon Laboratory, typed the manuscript.

Literature Cited

ALLDREDGE, A. L., AND J. M. KING
1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 41:317-333.

EMERY, A. R.
1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13:293-303.

FLEMINGER, A.
1964. Distributional atlas of calanoid copepods in the California current region, Part I. Calif. Coop. Oceanic Fish. Invest., Atlas 2, 313 p.

GLYNN, P. W.
1973. Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope. Part II. Plankton community with evidence for depletion. Mar. Biol. (Berl.) 22:1-21.

HOBSON, E. S.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.
1973. Diel feeding migrations in tropical reef fishes. Helgol. wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.
1975. Feeding patterns among tropical reef fishes. Am. Sci. 63:382-392.

HOBSON, E. S., AND J. R. CHESS
1973. Feeding oriented movements of the athernid fish *Pranesus pinguis* at Majuro Atoll, Marshall Islands. Fish. Bull., U.S. 71:777-786.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.
1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull., U.S. 76:133-153.

PORTER, J. W.
1974. Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavenosa*. Proc. Second Int. Coral Reef Symp. 1:111-125.

PORTER, J. W., AND K. G. PORTER.
1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol. Oceanogr. 22:553-556.

PORTER, J. W., K. G. PORTER, AND Z. BATAC-CATALAN.
1977. Quantitative sampling of Indo-Pacific demersal reef plankton. Proc. Third Int. Coral Reef Symp. 1:105-112.

RANDALL, R. H., C. BIRKELAND, S. S. AMESBURY, D. LASSUY, AND J. R. EADS.
1978. Marine survey of a proposed resort site at Arakabesan Island, Palau. Univ. Guam Mar. Lab. Tech. Rep. 44, 66 p.

EDMUND S. HOBSON
JAMES R. CHESS

Southwest Fisheries Center Tiburon Laboratory
National Marine Fisheries Service, NOAA
3150 Paradise Drive
Tiburon, CA 94920

A SURVEY OF HEAVY METALS IN THE SURF CLAM, *SPISULA SOLIDISSIMA*, AND THE OCEAN QUAHOG, *ARCTICA ISLANDICA*, OF THE MID-ATLANTIC COAST OF THE UNITED STATES

Since the mid-1940's, two varieties of clams have become increasingly important to the seafood industry, the surf clam, *Spisula solidissima*, and the ocean quahog, *Arctica islandica*. Surf clams and ocean quahogs are marketed primarily by the canning industry in chowders or as minced clams, as well as in a number of specialty products, such as cakes, patties, and dips. Prior to World War II, however, these clams had been used only as animal feed or fertilizer. A commercial surf clam fishery developed rapidly with an annual harvest of 51.4 million pounds of meats in 1977 (Hutchison[1]) and a peak harvest of 96.1 million pounds of meats in 1974 (Bell and Fitz Gibbon 1977). The ocean quahog fishery developed more slowly. It was not until the 1970's that a vigorous commercial ocean quahog fishery developed, primarily to supplement the dwindling supplies of more desirable clams, in particular, the hard clam, *Mercenaria mercenaria*; the soft-shell clam, *Mya arenaria*; and the surf clam (Anonymous 1971). The ocean quahog harvest in 1977 of 16.4 million

[1]Roger Hutchison, U.S. Department of Commerce, Economic and Marketing Research Division, Washington, D.C., pers. commun. February 1978.

pounds of meats (Hutchison see footnote 1), however, represents a small fraction of an estimated sustained yield of 86 million pounds of meats annually (Rinaldo[2]).

Since surf clams and ocean quahogs have replaced many traditional species, studies are needed that reflect their economic importance. It is well documented that many molluscs, including surf clams and ocean quahogs, concentrate heavy metals (Brooks and Rumsby 1965; Pringle et al. 1968; Waldichuk 1974). Boyden (1973) stated that one of the nutritious qualities of shellfish may be their high metal content. However, heavy metals exhibit toxic effects that affect all life stages of shellfish, especially development stages (Calabrese et al. 1973; Calabrese and Nelson 1974; Thurberg et al. 1975). Considerable research has been done on effects of heavy metals on more popular species of bivalve molluscs, especially the American oyster, *Crassostrea virginica*, hard clams, and soft-shell clams (Calabrese et al. 1973; Calabrese and Nelson 1974; Thurberg et al. 1974). However, until recently, there has been little interest in surf clams or ocean quahogs. Concentrations and concentration factors for a number of metals, including cadmium, chromium, copper, lead, nickel, and zinc, have been given by Pringle et al. (1968) and Pringle and Shuster[3] for surf clams taken from Atlantic coast waters (Maine through North Carolina). Thurberg et al. (1975) exposed larval, juvenile, and adult surf clams to sublethal doses of silver and measured both physiological responses and bioaccumulation. Researchers at the U.S. Environmental Protection Agency (EPA), Narragansett, R.I., have exposed ocean quahogs to low concentrations of cadmium and monitored toxicological, biological, and histopathological effects, as well as bioaccumulation (Zaroogian[4]). Bioaccumulation distribution patterns associated with industrial and sewage sludge dumpsites southeast of Delaware Bay have been monitored in ocean quahogs by scientists at the EPA, Annapolis, Md. (Lear and Pesch 1975). Awareness, then, of the importance of these species is developing, but clearly more research is needed for such an important commercial shellfishery.

Nine metals were chosen for analysis: arsenic, cadmium, chromium, copper, lead, mercury, nickel, silver, and zinc. Based upon estimates of global metal production and oceanic sedimentation rates, Bowen (1966) divided 38 metals into their pollution potentials. He categorized cadmium, chromium, copper, lead, mercury, silver, and zinc as very high potential pollutants and arsenic and nickel as moderate. Goldberg (1972) emphasized the need for measurement in benthic organisms of the most potentially hazardous trace metals.

Materials and Methods

Sampling

The area of this survey extended from approximately Montauk Point, N.Y., to Cape Hatteras, N.C., and seaward to approximately the 20-fathom contour. The survey encompassed the southern distribution of both surf clams and ocean quahogs in the United States. Samples were collected at 151 stations for chemical analysis (Figure 1) in June and August 1974, aboard the NOAA ship *Delaware II* (MARMAP[5]). A small hydraulic surf clam dredge, modeled closely after larger commercial dredges, was used throughout the survey. At each station 4-6 clams of marketable size were dissected, using stainless steel equipment. The foot was removed from each animal, drained, then combined and frozen in plastic bags. At the laboratory the tissues were homogenized in an electric blender equipped with a glass jar and stainless steel blades then stored for analysis in plastic ointment jars. All containers and equipment were acid-washed prior to use.

Analysis

Mercury analysis was performed on a Perkin-Elmer Model 305[6] atomic absorption spectrophotometer fitted with a 25 × 150 mm absorption cell with silica end windows, using the flameless method of Greig et al. (1975).

Arsenic analysis, performed on a Perkin-Elmer Model 403 atomic absorption spectrophotometer,

[2]Rinaldo, R. G. 1977. Atlantic clam fishery management plan. Environmental impact statement: Mid-Atlantic and New England Regional Fisheries Management Councils. Available Fisheries Management Division, National Marine Fisheries Service, NOAA, State Fisheries Pier, Gloucester, MA 01930.

[3]Pringle, B. H., and C. N. Shuster, Jr. 1967. A guide to trace metal levels in shellfish. USDHEW, Public Health Serv., Shellfish Sanit. Tech. Rep., 18 p.

[4]Gerald E. Zaroogian, U.S. Environmental Protection Agency, Environmental Research Laboratory, Narragansett, RI 02882, pers. commun. February 1976.

[5]MARMAP. 1974. Surf clam survey, cruise report, NOAA ship *Delaware II*, 13-28 June 1974 and 5-10 August 1974, 9 p.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

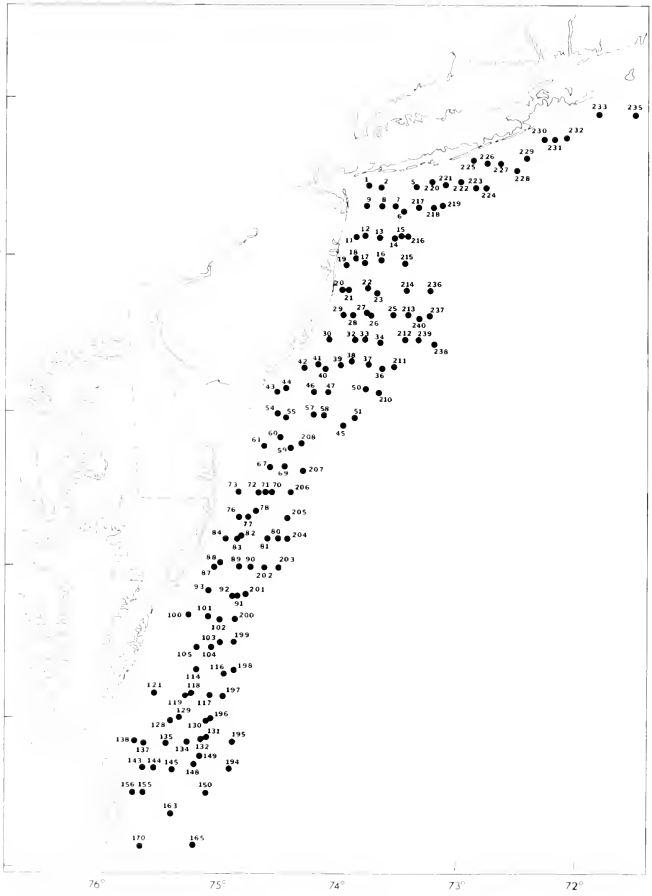


FIGURE 1.—Station location and number relative to the mid-Atlantic coast of the United States.

using a nitrogen/hydrogen flame, required an improvisation of two simple interconnecting adapters. The first, attached directly to the instrument, consisted of the female portion of a polyethylene quick disconnect (Nalgene 6150) and a nylon elbow hose connector threaded to fit the auxiliary inlet of the burner assembly. The second consisted of the male portion of the quick disconnect and a gas outlet adapter (Kontes K-183000). Both adapters were assembled with minimum length and bore of Nalgene tubing. The following procedure was used: A 5-g sample of tissue was placed into a 250-ml beaker to which 10 ml $Mg(NO_3)_2 \cdot 6H_2O$ (200 g/l) and 10 ml concentrated HNO_3 (Baker 9603) were added. The mixture was covered with a watchglass and evaporated to dryness on a hot plate (130°-140°C). It was then placed into a cool muffle furnace and the temperature raised in steps, first to 250°C for 3 h, then to 400°C for 3 h, and finally to 550°C for approximately 15 h. After the beaker was completely cool, 15 ml of concentrated HCL (reagent grade) were added and the resulting solution transferred to a 25-ml volumetric container and brought to volume with distilled water. A 10-ml aliquot of this solution was placed into a 24/40 jointed, 50-ml Erlenmeyer reaction flask and 2 ml of 15% (wt/vol) freshly made KI solution and 2 ml of freshly made $StCl_2$ solution (20% [wt/vol] in 1:1 concentrated HCL:water) were added, waiting 2 min after each addition. Then 10 ml of distilled water were added. Five (5.00) grams of granular (20 mesh, no fines) low arsenic zinc (Fisher Z-15) were placed into the elbow of the second adapter, as noted above, and attached to the first adapter. This assembly was quickly inverted while attaching it to the reaction flask. The arsine generated was then analyzed at the instrument, which was equipped with a 3-slot burner and background corrector. Use of a recorder combined with full noise filtration and slow gas evolution contributed to a smooth and reproducible peak upon which calculations were based. The reaction flask and the first adapter can be quickly removed for cleaning and reuse.

Analysis of the remaining metals, also performed on the Perkin-Elmer Model 403, resembled that of Middleton and Stuckey (1954): A sample of tissue (10 g wet weight) was weighed into a 250-ml beaker and 10 ml of concentrated HNO_3 (Baker 9603) were added. The beaker was covered with a watchglass and heated to approximately 130°-140°C on a hot plate until the liquid evaporated. One to two milliliters of concentrated HNO_3 was added and the evaporation repeated. Again, 1-2 ml of acid was added but evaporated at 350°C or more. The hot plate was cooled and the latter acid addition and evaporation was repeated until ashing was complete. The residue was dissolved in and taken up to 25 ml with 10% (wt/vol) reagent grade HNO_3 after filtration through Whatman No. 2 paper. The solution was then analyzed directly in an air/acetylene flame by conventional atomic absorption spectrophotometry.

Results

Greater average concentrations of silver, arsenic, cadmium, copper, and zinc (122, 44.5, >230, 56.0, and 10.9% greater, respectively) were found in ocean quahogs than in surf clams for the entire survey (Table 1). Concentrations of several metals in both clams decreased southward. Concentrations of silver decreased steadily from 2.62 to 0.58 ppm in ocean quahogs and 1.63 to 0.19 ppm in surf clams. This is a 4.5- and 8.6-fold decrease, respectively, from the northernmost range of latitude to the southernmost. Concentrations of arsenic also decreased steadily, 1.6-fold, from 3.90 to 2.41 ppm in ocean quahogs. Although a steady decrease in arsenic concentrations was noted for a full 2.5° of latitude, a distinctive trend for the entire range of latitude was not evidenced. Copper concentrations in ocean quahogs decreased 2.5-fold from 7.16 to 2.84 ppm and zinc concentrations in surf clams decreased 2.0-fold from 18.5 to 9.1 ppm. Concentrations of cadmium and zinc in the ocean quahog and copper in the surf clam did not exhibit any statistically significant trends, while the data for the remaining metal-clam combinations were insufficient for statistical analysis (Table 2).

The results of Pringle and Shuster (see footnote 3) for cadmium and zinc (<0.20, 12.39 ppm, wet weight, respectively) in surf clams are in general agreement with the mean results of our study. Their result for copper (2.39 ppm) was lower, while chromium and nickel (2.57, 1.22 ppm, respectively) were higher. The collection area of the former study was defined only as Maine through North Carolina; hence, geographic variations might be expected. In addition, neither the number of stations nor of surf clams analyzed was stated.

Conclusions

While the Food and Drug Administration (FDA)

TABLE 1.—Average[1] heavy metal concentrations (parts per million, wet weight) found in surf clams and ocean quahogs by latitude.

Range of lat. N	*n*	Ag		As		Cd		Cu		Zn	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Surf clams											
41 00'-40 30	3	1 63	1 11	2 38	0 146	0 12		3 83	0 786	9 7	0 674
40 30'-40 00'	6	1 42	329	2 63	234	0 13	0 008	2 87	216	18 5	481
40 00'-39 30'	11	1 18	140	2 39	120	0 13	010	2 96	348	18 3	1 14
39 30'-39 00'	11	1 05	130	2 17	200	0 15	015	3 45	226	14 8	1 11
39 00'-38 00'	13	0 94	120	1 91	131	0 13		3 38	211	11 3	485
38 30'-38 00'	13	0 50	082	1 57	082	0 11		2 97	259	10 6	188
38 00'-37 30'	8	0 51	081	2 08	145	0 12		3 54	360	9 1	253
37 30'-37 00'	11	0 44	071	2 22	122	0 12		3 48	478	9 4	228
37 00'-36 30'	14	0 32	046	2 17	233	0 14		3 08	228	9 3	260
36 30'-36 00'	3	0 19	053	1 46	082	0 14		2 88	262	9 6	153
41 00'-36 00'	93	0 76		2 08		0 13		3 23		11 9	
Ocean quahogs											
41 00'-40 30'	8	2 62	0 400	3 90	0 374	0 54	0 069	7 16	0 837	12 6	0 518
40 30'-40 00'	15	2 49	376	3 36	293	0 42	034	5 33	401	14 5	1 04
40 00'-39 30'	9	1 53	296	2 97	171	0 42	035	4 71	348	13 9	741
39 30'-39 00'	9	1 29	138	2 68	236	0 39	035	4 41	280	12 4	991
39 00'-38 30'	5	1 21	371	2 65	114	0 42	059	5 10	727	13 2	806
38 30'-36 30'	6	0 58	120	2 41	326	0 39	051	2 84	434	10 4	1 38
41 00'-36 30'	52	1 69		3 01		0 43		5 04		13 2	

[1]Average of *n* samples with 4-6 clams per sample

TABLE 2.—Average[1] heavy metal concentrations (parts per million, wet weight) found in surf clams and ocean quahogs by latitude

Range of lat. N	*n*	Cr	Hg	Ni	Pb
Surf clams					
41 00'-40 30'	3	0 62	0 05	—	0 7
40 30'-40 00'	6	0 95	0 07	0 71	0 7
40 00'-39 30'	11	0 70	0 08	0 39	0 7
39 30'-39 00'	11	0 69	0 08	0 80	0 7
39 00'-38 30'	13	0 65	0 08	0 60	0 7
38 30'-38 00'	13	0 61	0 08	0 50	0 6
38 00'-37 30'	8	0 53	0 08	—	0 7
37 30'-37 00'	11	0 49	0 07	—	0 7
37 00'-36 30'	14	0 48	0 06	—	0 7
36 30'-36 00'	3	0 48	0 05	—	0 7
41 00'-36 00'	93	0 61	0 07	0 59	0 7
Ocean quahogs					
41 00'-40 30'	8	1 03	0 09	0 91	1 8
40 30'-40 00'	15	1 23	0 06	0 62	1 0
40 00'-39 30'	9	0 70	0 06	0 50	1 2
39 30'-39 00'	9	0 80	0 07	0 50	0 9
39 00'-38 30'	5	1 0	0 08	0 55	1 2
38 30'-36 30'	6	1 1	0 06	0 59	0 9
40 00'-36 30'	52	1 0	0 06	0 61	1 1

[1]Average of *n* samples with 4-6 clams per sample

has not set standards for heavy metals in U.S. fishery products (except mercury), the National Health and Medical Research Council (NHMRC) of Australia has recommended maximum concentrations for a number of metals in seafoods (Mackay et al. 1975). Concentrations of cadmium, copper, lead, and zinc found in surf clams and ocean quahogs were well under these limits (2.0, 30, 2.0, 1,000 ppm, wet weight, respectively) and far below levels found in American oysters harvested from Atlantic coastal waters (Pringle et al. 1968). The NHMRC recommendation of 1.14 ppm (wet weight) arsenic (1.5 ppm as As_2O_3), however, was exceeded at all but a few sampling stations. Mean arsenic concentrations for all stations were 2.1 ppm in surf clams and 3.0 ppm in ocean quahogs. The distribution of arsenic concentrations did not vary greatly with latitude and may indicate that background levels along the mid-Atlantic coast are higher than those in Australian waters. Concentrations of mercury were found to be well below the action limit set by the FDA (0.50 ppm, wet weight).

Major fishing grounds for the surf clam industry are located off the New Jersey and Virginia coasts. Since data for mercury presented in this study are well within the existing guideline set by the FDA for U.S. fishery products and, with a single exception, within the more extensive NHMRC recommendations for Australia, there should be little concern to consumers for surf clams or ocean quahogs harvested from these areas at present.

The latitudinal cline demonstrated in this study should, however, stimulate further interest in heavy metal inputs along the mid-Atlantic coast of the United States. Data indicate that a large area of our eastern coast may be affected by the presence of heavy metals. The effect on clams is important, particularly since surf clams and ocean quahogs are representative of the important shellfisheries located in this area.

Literature Cited

ANONYMOUS.
1971 Ocean quahog becomes more important as surf and bay clams dwindle. Commer. Fish. Rev. 33(4): 17-19.

BELL, T. I., AND D. S. FITZ GIBBON (editors).
1977. Fishery statistics of the United States 1974. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Stat. Dig. 68, 424 p.

BOWEN, H. J. M.
1966. Trace elements in biochemistry. Academic Press, N.Y., 241 p.

BOYDEN, C. R.
1973. Accumulation of heavy metals by shellfish. Proc. Shellfish Assoc. G.B., 4th Shellfish Conf., p. 38-48.

BROOKS, R. R., AND M. G. RUMSBY.
1965. The biogeochemistry of trace element uptake by some New Zealand bivalves. Limnol. Oceanogr. 10:521-527.

CALABRESE, A., R. S. COLLIER, D. A. NELSON, AND J. R. MACINNES.
1973. The toxicity of heavy metals to embryos of the American oyster *Crassostrea virginica*. Mar. Biol. (Berl.) 18:162-166.

CALABRESE, A., AND D. A. NELSON.
1974. Inhibition of embryonic development of the hard clam, *Mercenaria mercenaria*, by heavy metals. Bull. Environ. Contam. Toxicol. 11:92-97.

GOLDBERG, E. G. (convener).
1972. Marine pollution monitoring: strategies for a national program. Deliberations of a workshop held at Santa Catalina Marine Biology Laboratory, Univ. Southern Calif., Allan Hancock Found., Los Ang., Calif., 203 p.

GREIG, R. A., D. WENZLOFF, AND C. SHELPUK.
1975. Mercury concentrations in fish, North Atlantic offshore waters—1971. Pestic. Monit. J. 9:15-20.

LEAR, D. W., AND G. G. PESCH (editors).
1975. Effects of ocean disposal activities on mid-continental shelf environment off Delaware and Maryland. Environmental Protection Agency, Region III, Phila., Pa., 204 p.

MACKAY, N. J., R. J. WILLIAMS, J. L. KACPRZAC, M. N. KAZACOS, A. J. COLLINS, AND E. H. AUTY.
1975. Heavy metals in cultivated oysters (*Crassostrea commercialis* = *Saccostrea cucullata*) from the estuaries of New South Wales. Aust. J. Mar. Freshwater Res. 26:31-46.

MIDDLETON, G., AND R. E. STUCKEY.
1954. The preparation of biological material for the determination of trace metals. Part II. A method for the destruction of organic matter in biological material. Analyst 79:138-142.

PRINGLE, B. H., D. E. HISSONG, E. L. KATZ, AND S. T. MULAWKA.
1968. Trace metal accumulation by estuarine mollusks. Proc. Am. Soc. Civil Eng., J. Sanit. Eng. Div. 94:455-475.

THURBERG, F. P., W. D. CABLE, J. R. MACINNES, AND D. R. WENZLOFF.
1975. Respiratory response of larval, juvenile, and adult surf clams, *Spisula solidissima*, to silver. *In* J. J. Cech, Jr., D. W. Bridges, and D. B. Horton (editors), Respiration of marine organisms, p. 41-52. TRIGOM Publ., South Portland, Maine.

THURBERG, F. P., A. CALABRESE, AND M. A. DAWSON.
1974. Effects of silver on oxygen consumption of bivalves at various salinities. *In* F. J. Vernberg and W. B. Vernberg (editors), Pollution and physiology of marine organisms, p. 67-78. Academic Press, N.Y.

WALDICHUK, M.
1974. Some biological concerns in heavy metals pollution. *In* F. J. Vernberg and W. B. Vernberg (editors), Pollution and physiology of marine organisms, p. 1-57. Academic Press, N.Y.

D. R. WENZLOFF
R. A. GREIG

Northeast Fisheries Center Milford Laboratory
National Marine Fisheries Service, NOAA
Milford, CT 06460

A. S. MERRILL
J. W. ROPES

Northeast Fisheries Center Woods Hole Laboratory
National Marine Fisheries Service, NOAA
Woods Hole, MA 02543

APPARENT FEEDING BY THE FIN WHALE, *BALAENOPTERA PHYSALUS*, AND HUMPBACK WHALE, *MEGAPTERA NOVAENGLIAE*, ON THE AMERICAN SAND LANCE, *AMMODYTES AMERICANUS*, IN THE NORTHWEST ATLANTIC

On 18 May 1977 a large group of fin, *Balaenoptera physalus*, and humpback, *Megaptera novaengliae*, whales was observed on Stellwagen Bank north of Cape Cod (lat. 42°26′N, long. 70°26′W) by Northeast Fisheries Center (NEFC) personnel conducting an annual spring bottom-trawl survey aboard the National Oceanic and Atmospheric Administration RV *Albatross IV*. Nine fin and 14 humpback whales were identified and observed near the vessel. More whales were sighted in the vicinity, but were too far away to identify positively or to observe conveniently. Many great black-back, *Larus marinus*, and herring, *Larus argentatus*, gulls were seen feeding at the surface and circling around the whales. The whales displayed a characteristic feeding behavior described by Gunther (1949) and mentioned in Katona et al. (1975). The animals we observed were circling, spouting often, making short shallow dives, and not moving in any set direction. They behaved in a leisurely manner and were seemingly undisturbed by our presence as noted by Gunther (1949). Echo sounding traces indicated a depth of 40 m in this area and large patches of densely concentrated small fishes throughout the water column, but particularly near the surface. During several 30-min bottom-trawl tows in the area, up to 400 kg of adult American sand lance, *Ammo-*

dytes americanus, were netted per tow (Northeast Fisheries Center[1]) with Atlantic cod, *Gadus morhua*, and spiny dogfish, *Squalus acanthias*, the only other abundant fish species. An examination of several cod stomachs showed them to be packed with sand lance while a similar inspection of sand lance showed them to be feeding on copepods. It is our contention that the abundance and behavior of whales in this area indicates that they were feeding on a concentration of American sand lance.

Similar whale feeding behavior had been previously observed on 18 June 1976 with a humpback whale located at lat. 42°09'N, long. 70°10'W, and with a fin whale located at lat. 42°04'N, long. 70°20'W, and on 20 June 1976 with a humpback whale located in the same general area (Northeast Fisheries Center[2]). During these three observations many herring gulls were again seen feeding at the surface and circling around the whales. Large numbers of American sand lance were also visually observed at the surface by NEFC personnel aboard the Alpine Geophysics RV *Atlantic Twin* and in the water column again by NEFC personnel aboard the General Oceanics research submersible *Nekton Gamma*. These latter two vessels were involved in testing the feasibility of using a research submersible to survey marine organisms (Northeast Fisheries Center[3]).

Bigelow and Schroeder (1953) reported that fin whales were observed feeding on American sand lance that were abundant in Cape Cod Bay in 1880. Nemoto (1959) listed American sand lance as one of the food items of baleen whales of the North Pacific, along with a variety of other fishes and euphausids. Fin and humpback whales are reported to feed on capelin, *Mallotus villosus*, a fish similar to the American sand lance in size, summer habitat, and schooling behavior in the continental shelf waters off Nova Scotia and Newfoundland (Mitchell 1974a). Fin whales landed at Blandford, Nova Scotia, from 1967 to 1972 contained sand lance (May-August), and stomachs from Newfoundland fin whales had >1% sand lance (June-July) in 1970-1972 (Mitchell 1974b). There is little stomach analysis data, though, from baleen whales captured in New England waters in the late 1880's when whaling was popular (True 1904), and no such data since the early 1900's when, for all practical purposes, whaling had ceased. Thus, it is difficult to confirm exactly what fin and humpback whales in the Cape Cod region eat.

The feeding observations which we made imply that the rorqual whales off New England, particularly fin and humpback whales, may be utilizing the high standing stock of American sand lance that is currently available (Northeast Fisheries Center[4]). Additionally noteworthy is that the Atlantic herring, *Clupea h. harengus*, a commonly mentioned rorqual whale food (Allen 1916; Ingebrigtsen 1929; Bigelow and Schroeder 1953; Nemoto 1959), is in low abundance at this time (International Commission for the Northwest Atlantic Fisheries 1976).

Literature Cited

ALLEN, G. M.
1916. The whalebone whales of New England. Mem. Boston Soc. Nat. Hist. 8(2), 322 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

GUNTHER, E. R.
1949. The habits of fin whales. Discovery Rep. 25:115-141.

INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES.
1976. Report of standing committee on research and statistics (STACRES), Eighth special commission meeting - January 1976. Appendix II. Report of *ad hoc* working group on herring. Int. Comm. Northwest Atl. Fish., Redb. 1976:35-50.

INGEBRIGTSEN, A.
1929. Whales caught in the North Atlantic and other seas. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 56, 26 p.

KATONA, S., D. RICHARDSON, AND R. HAZARD.
1975. A field guide to the whales and seals of the Gulf of Maine. Maine Coast Printers, Rockland, 97 p.

MITCHELL, E.
1974a. Present status of Northwest Atlantic fin and other whale stocks. *In* W. E. Schevill (editor), The whale problem, a status report, p. 108-169. Harv. Univ. Press, Camb., Mass.
1974b. Trophic relationships and competition for food in Northwest Atlantic whales. *In* M. B. D. Burt (editor), Proceedings of the Canadian Society of Zoologists annual meeting, June 2-5, p. 123-133.

NEMOTO, T.
1959. Food of baleen whales with reference to whale movements. Whales Res. Inst. Sci. Rep. 14:149-290.

[1]Northeast Fisheries Center. 1977. Cruise Results, NOAA R/V ALBATROSS IV Cruise No. 77-02, Spring Bottom Trawl Survey. Part III. Woods Hole, Mass., 6 p.

[2]Northeast Fisheries Center. Gulf of Maine whale sighting network reports. Groundfish Survey Unit. Data on file, Woods Hole, Mass.

[3]Northeast Fisheries Center. 1976. Cruise Results, R/V Atlantic Twin, Cruise 76-01. Woods Hole, Mass., 8 p.

[4]Northeast Fisheries Center. Spring groundfish survey research cruises 1967-1977. Groundfish Survey Unit. Data on file, Woods Hole, Mass.

TRUE, F. W.
1904 The whalebone whales of the western North Atlantic compared with those occurring in European waters, with some observations on the species of the North Pacific. Smithson. Contrib. Knowl. 33, 332 p.

WILLIAM J. OVERHOLTZ
JOHN R. NICOLAS

Northeast Fisheries Center Woods Hole Laboratory
National Marine Fisheries Service, NOAA
Woods Hole, MA 02543

ESTIMATION OF INTERTIDAL HARVEST OF DUNGENESS CRAB, *CANCER MAGISTER*, ON PUGET SOUND, WASHINGTON, BEACHES[1]

There are two major methods employed in the sport fishery for the Dungeness crab, *Cancer magister*, in Puget Sound, Wash. The first is a passive method. A baited pot, trap, or ring net is placed on a subtidal substrate, left for a period of time, and retrieved. The second is an active method. During periods of low minus tides, sport crabbers seek crabs by sight. The crabbers usually wade out into water between knee and waist level, then walk parallel to the beach. A round metal loop, about 1 ft in diameter, covered with wire mesh and attached to a long handle, is generally used to capture crabs. Beginners often bring fish nets, but find it difficult to extricate the crabs caught in the net. When a crab is seen, the crabber maneuvers the hoop quickly under the crab. The crab's legs go through the mesh, making escape difficult, and the hoop is then pulled from the water. Only male crabs may be taken, and they must be a minimum of 152 mm (6 in) in width, as determined by a caliper measurement across the carapace, directly in front of the 10th anterolateral spines. The daily crab catch is limited to six per person.

Knowledge of the size and distribution of the intertidal sport fishery was limited until 1969, when the Washington Department of Fisheries began aerial surveys to estimate low tide usage of Puget Sound beaches for clam digging and crabbing. By summer 1973, enough data had been collected to show which beaches were being used for crabbing. However, the aerial surveys did not reflect the total use of beaches by crabbers over the entire low tide period, since only a single count was made sometime between 90 min before and 90 min after low tide.

This study was initiated in fall 1973 in an effort to determine the availability of crabs and the magnitude of intertidal harvest on one high-use Puget Sound beach. From data collected, an estimate was made of the total use of Puget Sound beaches by sport crabbers for daylight low tides in 1974.

Methods

From preliminary aerial survey data, Mission Beach, located 60 km north of Seattle and just beyond the Port of Everett, was selected as the study site (Figure 1). The beach is 3 km long, shallow, and sandy, with eelgrass beds below the mean lower low water (MLLW) level. This beach had only one public access, cut through a 15-m bluff. This location provided me with a good view of the entire area and made it possible to interview almost all crabbers using the beach.

From October 1973 to October 1974 there were 19 low tide series with tides lower than −0.30 m MLLW. These tidal series occurred in all months of the year except March and September. I visited Mission Beach during all tides lower than −0.30 m, except under adverse weather conditions in the winter months. I arrived 2.25 h before low water and walked to point 'a' (Figure 1), where I entered the water and moved toward the access at a depth of 0.15 to 0.85 m through the area most intensively utilized by the sport crabbers. For all crabs observed, I recorded the size to the nearest millimeter (taken in a horizontal measurement directly in front of the anterolateral spines on the carapace, by means of a caliper) and sex. Sampling was by the method used by most crabbers.

Beginning 2 h before low tide, I made half-hourly counts of the number of crabbers at the beach, but continued beach sampling of crabs until crabbers began to leave the beach, usually about 0.5 h before the low. At this time, I interviewed the crabbers about their success and time spent crabbing. About 90% of all crabbers using Mission Beach, on tides checked, were interviewed. During the interviews, I measured as many crabs as possible. From the interview data, I estimated the number of crabbers on the beach at any time during a period of 14 min before to 15 min after the half-hourly counts. The average time spent crabbing was slightly over 1.5 h; thus, if all crabbers

[1]Based on work submitted in partial fulfillment of the requirements for the degree of Master of Science.

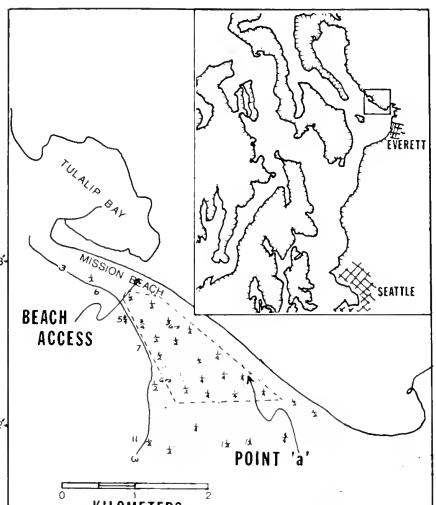


FIGURE 1.—Location of Mission Beach within Puget Sound, Wash. The area most intensively utilized by crabbers at Mission Beach is outlined with dashes.

had been interviewed, the constructed counts would coincide with actual beach use. However, not all crabbers were interviewed, so the half-hourly counts were more accurate for the lowest period of the tide when most people were crabbing.

I then constructed a table for each month which assigned the highest of the two estimates, either the constructed count from the interviews or the half-hourly beach count, to each half-hourly period. The number of crabbers using the beach was computed for each tide by dividing the total crabber hours (the sum of the half-hourly counts) by the average hours spent crabbing (obtained from crabber interviews) and totaled for each month. From the monthly table, the number of crabbers on the beach at any half-hourly interval, divided by the total number of people using the beach for each month during the low tide period, gave a percentage of people using the beach at any half-hourly count. Monthly use curves were then constructed for Mission Beach (Figure 2).

The methods that I employed to develop use curves were similar to those that have been used by researchers who have dealt with other recreational fisheries (Miller and Gotshall 1965; Brown 1969; Tegelberg[2]; Jarman et al.[3]).

In addition to the sampling that I conducted at Mission Beach, personnel from the Washington Department of Fisheries Shellfish Laboratory conducted creel sampling at six other Puget Sound beaches having differing levels of crabber use. From the survey material that they provided, I had insufficient data to construct use curves for

[2]Tegelberg, H. C. 1963. The 1962 razor clam fisheries. State Wash. Dep. Fish., 28 p.

[3]Jarman, R., C. Bennet, C. Collins, and B. Brown. 1970. Angling success and recreational use of twelve state owned lakes in Oklahoma. Paper given at 21st Annu. Meeting South. Div. Am. Fish. Soc., New Orleans, La.

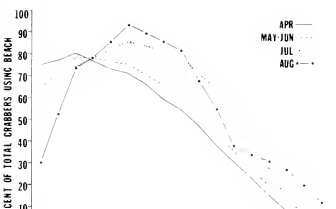


FIGURE 2.—Crabber use curves for Mission Beach based on data gathered April-August 1974

April and August, but I was able to construct use curves for May-June and July, a combined total for those beaches based on 10 and 5 observations, respectively. These use curves, when superimposed over the corresponding Mission Beach use curves, did not vary by more than approximately 10% for the period before, or 20% for the period after, the low tide.

The Washington Department of Fisheries also provided me with data from aerial surveys conducted over Puget Sound beaches on 27 April, 25 May, 22 June, and 20 July 1974. Most of the beaches were surveyed during the hour preceding the low tide, which corresponded to the highest beach use. Thus, the curves derived for Mission Beach were used for estimates for all beaches.

While interviewing crabbers at Mission Beach, it appeared to me that both the tidal height and tidal sequence were important factors in crabbing success. I therefore analyzed the data in two different ways. The various tidal series had from three to eight tides lower than −0.15 m (−0.5 ft). I divided the low tide heights into six levels by 0.15-m increments. The first minus tide of a series to fall into a tidal height category was defined as Tide One in the tidal sequence. Each succeeding tide was consecutively numbered, with the final tide in a series designated as the last minus tide to fall into a tidal height category. Thus, low tides of equal height from different tidal series were not always the same sequence number.

Results and Discussion

The number of crabbers using Mission Beach during the winter nighttime tides was small compared with the number during the summer daytime tides. Of the estimated 762 crabbers using Mission Beach during the year, only 27 (4%) crabbed from October through February, while 735 (96%) crabbed from April through August. Of the estimated 531 crabs taken for the year at Mission Beach, the winter crabbers caught 60 (11%), while the summer crabbers caught 471 (89%).

Stepwise multiple linear regression analysis (Poole 1974) of crabber activity at Mission Beach correlated significantly ($P<0.05$) with tide height, day of week, month, temperature, and wind velocity (Table 1). However, the resultant equation was not strong enough for predictive purposes. The tide height accounted for the largest amount of the variability. The lowest three tide levels had two to four times as many crabbers as the highest three levels (Table 2). The other significant variables indicated the following: weekend use by crabbers per tide was 1.5 times greater than the average weekday use per tide; the average number of crabbers per tide was highest in April, May, and June, with the use dropping off considerably in July and August; there were more crabbers at higher air

TABLE 1.—Summary table of multiple linear regression between total crabbers at Mission Beach and nine independent variables. The resultant equation was significant at $P<0.001$ for all steps.

Step	Variable entered	Significance[1]	Mult R	R^2	R	Overall F
1	Tide height	0.001	0.45	0.20	0.45	12.35
2	Day of week	.003	.59	.34	−.27	12.37
3	Month	.005	.67	.45	−.39	12.61
4	Temperature	.007	.73	.53	0.26	12.92
5	Wind velocity	.027	.76	.58	−.06	12.37
6	Tide sequence	.078	.78	.61	0.08	11.39
7	Previous day's catch/crabber	.698	.78	.61	0.04	9.59
8	Precipitation	.769	.78	.61	−.06	8.21
9	Cloud cover	.825	.78	.61	−.13	7.14

[1]The α level of significance for each variable as it was entered in the equation.

TABLE 2.—Crabber use and catch taken on six different tide heights (mean lower low water) at Mission Beach, Wash., April-August 1974.

Tide height (m)	No. of tides sampled	Mean no. crabbers per tide	Mean no. of crabs caught	Mean catch legal crabs per crabber	Total legal crab catch
−0.15 to −0.29	6	6	1.4	0.2	7
−0.30 to −0.44	14	13	7.9	0.6	110
−0.45 to −0.59	16	9	6.1	0.7	92
−0.60 to −0.74	6	19	24.7	1.3	173
−0.75 to −0.89	4	25	15.0	0.6	62
−0.90 to −1.04	5	27	5.4	0.2	27

temperatures, but this corresponded with the lowest tides in June, which occurred at midday; on days with high winds there were few crabbers. This was probably due to a lowered chance of success because waves on the beach made crabs difficult to see.

The estimated use of the beach by crabbers corresponded with the daily availability of crabs on the beach that I observed by sample crabbing. This availability appeared to be affected by current and tide height. Two hours before low tide, the water level over the eelgrass portion of the beach, where most crabs were found, was generally >1 m. As the tide went out and the water became shallower, I observed few crabs in water <0.15 m deep. The current also appeared to have effects. When the tide approached its lowest level, the current became slack, at which time I observed few crabs. Even on days when a large number of crabs were active an hour before the low, few would be evident at low slack.

The monthly use curves enabled me to take a single aerial survey count of crabbers using a surveyed beach at any time during the low tide period and predict the total crabber use at the beach during the entire low tide period.

I adjusted the total calculated Puget Sound beach use by crabbers during the 1974 aerial surveys by two factors: the number of crabbers excluded because beaches were not surveyed and the improper identification of people as crabbers who were not actually crabbing. Between 1969 and 1973, at least one aerial survey at low tide was conducted over every Puget Sound beach, and all important crabbing beaches were identified. From this data I estimated that the 1974 aerial surveys included 95% of the crabbers and other recreationists on the beaches at any given low tide. At the same time 1974 aerial surveys were made over Mission Beach, I made actual counts of crabbers on the beach. The average overcount of crabbers by the aerial survey was 15.5%.

Total Puget Sound intertidal crabber use for all low tides from April through August was roughly estimated by dividing the total Mission Beach counts on the days of the aerial surveys, April through July, by the adjusted total Puget Sound beach count. The quotient was designated as the percentage of Mission Beach use relative to the adjusted total beach count (Table 3). Due to poor visibility on the day scheduled, no aerial survey was conducted in August, so I used averaged data from the preceding 4 mo. I estimated the total crabber use on all beaches for each month by dividing the percentage Mission Beach use of the total adjusted beach count into the total crabber use of Mission Beach for each month.

In order to estimate the total crabs caught in Puget Sound by intertidal sport crabbers, I needed to know whether the average catch over a low tide period at other Puget Sound beaches was the same as that at Mission Beach. Six other beaches in Puget Sound that had different levels of crabber utilization were sampled on a random basis by personnel from the Washington Department of Fisheries. Their levels of crabber use ranged from a few to 70 crabbers per tide. Four of the six beaches had three or more surveys, and these were compared with Mission Beach by Wilcoxon Rank Sum Tests (Hollander and Wolfe 1973). The four beaches had W values of 13.5, 9.5, 46.5, and 106, which in all cases were greater than the computed values of 6, 6, 39, and 66. Thus the null hypothesis that there were equal catches per crabber at the different beaches could not be rejected. This implies that the number of crabbers at a beach is self-regulating in that crabbers tend to adjust their level of effort to the rate of return, and that rates of return for all crabbers at different beaches remains fairly constant.

This same pattern of utilization was observed in the recreational trout fisheries in California lakes, where the angling effort adjusted proportionally to the numbers of catchable-size trout (Butler and

TABLE 3.—Estimate of the total monthly crabber use in the intertidal Dungeness crab sport fishery for Puget Sound beaches, April-August 1974

Month	Adjusted total Puget Sound beach count on monthly aerial survey	No. of crabbers at Mission Beach on monthly aerial survey	Percentage Mission Beach use of total adjusted beach count (Col 3 ÷ Col 2)	Total crabbers at Mission Beach	Estimated total intertidal crabber use (Col 5 ÷ Col 4)
April	433	27	6.2	79	1,274
May	829	28	3.4	229	6,735
June	954	33	3.5	279	7,971
July	805	29	3.6	121	3,361
August	No observation		[1]4.18	27	646
Total				735	19,987

[1]Average of four previous months

Borgeson 1965). Since the catches did not differ significantly, all beaches were treated together for predictive purposes. An estimate of the total crabs caught by intertidal sport crabbers for the daylight tides in 1974 was made by multiplying the average catch per effort for April, May, June, July, and August at Mission Beach (Table 4) by the estimated total number of crabbers (Table 3) for each month. The number of crabs caught per month increased throughout the spring, reaching a maximum of 5,099 in June. Few crabs were caught after July (Table 5).

When Spearman rank correlation coefficients were computed between a crabber's catch at Mission Beach and a number of independent variables (Hollander and Wolfe 1973), the most significant positive correlation was with the total time spent crabbing (Table 6). Crabbing was better in April-June than in July and August. The tide height and tide sequence were not significantly correlated with the catch per crabber at $P<0.05$, but were significant at $P<0.10$. The highest average catches were on tides ranging from -0.60 to -0.74 m (Table 2).

The higher tides make crabbing difficult, because crabbers have to wade into deeper water to get to the area where crabs are found. In the deeper water, crabs are less visible and the mobility of crabbers is impaired. The catches and number of crabbers arranged by tide sequence are shown in Table 7. The lowest tides of the year are generally four or five tides into a tidal series. The first low tides in the series have already allowed a fair amount of crabbing pressure on the beach, and many of the available crabs have been removed. Additionally, the combination of crabbers wading and less water over the beach on the previous low tides probably causes crabs to move to deeper water during the last low tides in a series.

The sex and size composition of crabs that I observed while sampling are shown in Figure 3. The numbers of legal males (152 mm and larger) include all crabs measured during crabber interviews.

TABLE 4.—Monthly crabber use and mean daily catch at Mission Beach, Wash., April-August 1974.

Month	Number of tides	Number of crabbers	Mean daily catch per crabber	Range of mean daily catches
April	5	79	1.76	0.4-3.0
May	11	229	.86	0.0-3.4
June	14	279	.64	0.0-2.2
July	14	121	.59	0.0-1.7
August	6	27	.30	0.0-0.5

TABLE 5.—Estimated total Dungeness crab sport catch in Puget Sound on intertidal beaches, April-August 1974.

Month	Mean catch per crabber at Mission Beach	Estimated total Puget Sound crabbers	Estimated total crab catch
April	1.76	1,274	2,242
May	.86	6,735	5,792
June	.64	7,971	5,099
July	.59	3,361	1,983
August	.30	646	194
Total		19,987	15,310

TABLE 6.—Spearman correlation coefficients between number of crabs caught per crabber and nine independent variables.

Variable	Correlation coefficient	Significance
Time spent crabbing	0.738	0.001
Month	0.413	.002
Tide height	0.229	.055
Tide sequence	-0.222	.061
Wind velocity	-0.175	.113
Temperature	-0.105	.238
Precipitation	-0.092	.263
Time of low	0.054	.355
Cloud cover	0.010	.473

TABLE 7.—Crabber use and catch taken on different tide heights arranged according to the sequence in which they occurred in a low tide series at Mission Beach, Wash., April-August 1974.

Tide sequence	No. of tides sampled	Mean no. crabbers per tide	Mean no. of crabs caught	Mean catch legal crabs per crabber	Total legal crab catch
1	6	15	7.6	0.5	46
2	9	23	10.3	0.9	163
3	8	13	9.4	0.7	85
4	8	13	6.5	0.5	52
5	8	9	8.9	1.0	71
6	7	18	6.3	0.4	44
7	3	14	2.7	0.2	8
8	1	20	2.0	0.1	2

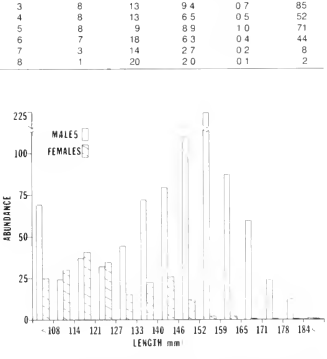


FIGURE 3.—Size composition and sex of crabs observed during sample crabbing at Mission Beach from October 1973 through August 1974. Male crabs >150 mm include those measured during crabber interviews.

In summary, the use of Mission Beach by intertidal crabbers is greatest 1 to 2 h before the low tide. This corresponds to the period when crabs are most readily observable. From the data collected at Mission Beach and aerial survey counts of other Puget Sound beaches, I estimated that about 20,000 crabbers utilized intertidal beaches from April through August 1974. The intertidal Dungeness crab sport fishery is, however, fairly small compared with other marine sport fisheries in Puget Sound.

Acknowledgments

I wish to thank G. Pauley, J. Congleton, C. Woelke, K. Chew, and T. Walker for discussion and critical readings of various stages of the manuscript. Reviewers for the *Fishery Bulletin* helped improve the readability. R. Whitney, as Leader of the Washington Cooperative Fishery Research Unit at the University of Washington, provided encouragement, support, and facilities from the outset of the study. Appreciation is extended to A. Scholz and other members of the Sport Shellfish Section of the Washington State Department of Fisheries, without whose cooperation this study would not have been possible. The study was partially supported by funds from the Washington Department of Fisheries.

Literature Cited

BROWN, B. E.
1969. An analysis of the Oklahoma State lake creel survey to improve creel survey design. Ph.D. Thesis, Oklahoma State Univ., 164 p.

BUTLER, R. L., AND D. P. BORGESON.
1965. California "catchable" trout fisheries. Calif. Dep. Fish Game, Fish Bull. 127, 47 p.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. John Wiley and Sons, N.Y., 503 p.

MILLER, D. J., AND D. GOTSHALL.
1965. Ocean sportfish catch and effort from Oregon to Point Arguello, California, July 1, 1957 to June 30, 1961. Calif. Dep. Fish Game, Fish Bull. 130, 135 p.

POOLE, R. W.
1974. An introduction to quantitative ecology. McGraw-Hill, Inc., N.Y., 532 p.

JOHN G. WILLIAMS

Washington Cooperative Fishery Research Unit
College of Fisheries, University of Washington
Seattle, WA 98195

A CONTRIBUTION TO THE BIOLOGY OF THE PUFFERS *SPHOEROIDES TESTUDINEUS* AND *SPHOEROIDES SPENGLERI* FROM BISCAYNE BAY, FLORIDA

The general biology of the checkered puffer, *Sphoeroides testudineus*, and bandtail puffer, *S. spengleri*, is not as well known as that of the northern puffer, *S. maculatus*. For example, Chesapeake Bay populations of the northern puffer have been examined for length-weight relationships by Isaacson (1963) and Laroche and Davis (1973), for age, growth, and reproductive biology by Laroche and Davis (1973), and for fecundity by Merriner and Laroche (1977). None of this information is available on the checkered or bandtail puffer.

Checkered and bandtail puffers have greater geographic ranges and are more southern in distribution than the northern puffer. The checkered puffer is abundant from the Atlantic coast of southern Florida, throughout the Caribbean Islands, Campeche Bay, and along the coasts of Central and South America to Santos, Brazil (Shipp 1974). The bandtail puffer is common in the Caribbean Sea and along the coasts of peninsular Florida, the Bahamas, and Bermuda (Shipp 1974). I report here on growth, reproduction, and the pharyngeal dentition of these two species gathered during a study of their feeding biology (Targett 1978).

The sampling habitat was a shallow seagrass bed along the southwestern shore of Virginia Key in northern Biscayne Bay, Fla. Turtle grass, *Thalassia testudinum*, was the dominant seagrass with small amounts of shoal grass, *Halodule wrightii*, and manatee grass, *Syringodium filiforme*, also present. Monthly collections from September 1973 to December 1974 yielded 414 checkered puffers (15-215 mm SL; 56% females) and 548 bandtail puffers (16-133 mm SL; 49% females). Seawater temperatures ranged from 16.5° to 32.0°C and salinities from 30.5 to 38.5‰.

Standard length-weight relationships (Figures 1, 2) were calculated using functional regressions (Ricker 1973). Checkered puffers grow to a larger size and are heavier than bandtail puffers at a given length. Comparisons of these results with those for northern puffers from Chesapeake Bay (Isaacson 1963; Laroche and Davis 1973) was made possible by the conversion of total length to standard length using the factor: caudal fin length = 20.2% SL (Shipp 1974). Northern puffers grow

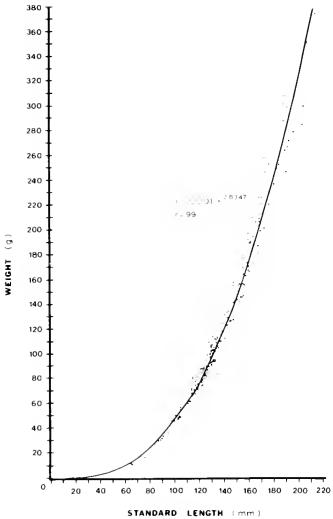


FIGURE 1.—Standard length-weight relationship for 250 checkered puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0014$.

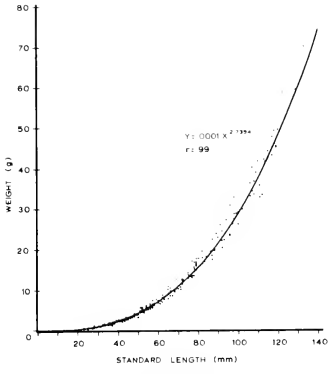


FIGURE 2.—Standard length-weight relationship for 250 bandtail puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0018$.

to a greater maximum size than either checkered or bandtail puffers and are approximately the same weight at a given length as checkered puffers.

Checkered puffers decreased in abundance in June and July due to a drop in numbers of 120-169 mm SL fish (Figure 3). (Some individuals may have left the seagrass bed as early as April and May, since a greater effort was needed to catch checkered puffers at that time.) Males and females decreased equally in abundance. The group leaving the seagrass bed may have been going elsewhere to spawn since their departure corresponded with the time of capture of ripe individuals. Some ripe checkered puffers were captured in April and May; and by August, September, and the beginning of October the few adults caught

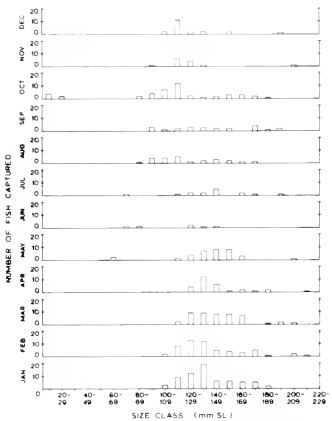


FIGURE 3.—Monthly standard length-frequency distributions for checkered puffers from Biscayne Bay, Fla., during 1974.

were all ripe. Furthermore, Christensen (1965) found evidence that checkered puffers from Jupiter Inlet, Fla., spawned in low salinity waters during the fall. He found young fish (≤10 mm SL) from early November through December in waters having salinities generally <20‰. He also observed that young and juveniles were abundant in the upper reaches of the Loxahatchee River (which flows into Jupiter Inlet) during winter and spring, rarely being found elsewhere. Thus, the checkered puffers leaving the seagrass bed in the present study may have been going to spawn in lower salinity waters found along portions of western Biscayne Bay or in the Miami River. This would explain why no checkered puffers <25 mm SL were captured, except for six in October. Most young likely remain in brackish water areas and move into higher salinity habitats only at larger sizes the following year. The 80-119 mm SL group appearing in August probably composed the 1-yr-old fish moving into the seagrass bed.

The checkered puffer spawning season, beginning in the spring and concentrated during summer and early fall in Biscayne Bay, occurs slightly later than the spring and summer spawning of the southern puffer, *S. nephelus*, at Cedar Key, Fla. (Reid 1954). The northern puffer in Chesapeake Bay has been reported to spawn during May by Hildebrand and Schroeder (1928) and during late May, June, and July by Laroche and Davis (1973).

Fecundity analysis, using the gravimetric technique, was done on nine checkered puffer females ranging from 127 to 178 mm SL (99-256 g). Only yolky eggs, with nuclei obscured, were counted. Regression analyses of fecundity-standard length and fecundity-body weight were done using functional regressions (Ricker 1973). Total fecundity increased exponentially as a function of body length (Figure 4) and linearly as a function of body weight (Fecundity = 1,431.81 [Body wt in grams] − 45,704.97; $r = 0.96$). Over the size range examined, relative fecundity averaged 1,146 eggs/g body wt. These fecundity values are greater than those found by Merriner and Laroche (1977) for northern puffers in Chesapeake Bay. Of the six checkered puffers <25 mm SL, two (15 and 23 mm SL) were males and the sex of the rest (17, 17, 18, and 21 mm SL) was undeterminable. Thus, it was not possible to estimate the body size at which eggs become discernible.

The age structure of the checkered puffer population can be inferred from the monthly length-frequency distributions (Figure 3). The 80-119 mm SL group appearing in August is likely 1-yr-old fish which grow to 120-189 mm SL by the end of their second year. A comparison of the growth of checkered puffers in this population with results from the work of Laroche and Davis (1973) on northern puffers from Chesapeake Bay shows that the checkered puffers reach a smaller size at the end of each year of life and are shorter lived than the northern puffers.

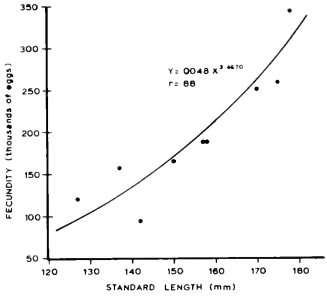


FIGURE 4.—Total fecundity-standard length relationship for nine checkered puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0078$

Eggs became discernible, by microscope, in bandtail puffers at 25-30 mm SL. Spawning season, however, was not easily determined. No ripe or nearly ripe bandtail puffers were caught despite the fact that this species was abundant throughout the year and the full size range (to approximately 160 mm TL (Shipp 1974)) was captured. At least one fish <30 mm SL was collected every month except September, November, and December, although most were captured during March through June. This implies that bandtail puffers have a long spawning season, concentrated in the late fall and early winter, and spawn elsewhere with the young moving into the seagrass bed shortly after hatching.

Both checkered and bandtail puffers feed mainly on crabs, bivalves, and gastropods (Targett 1978). They use their beaklike jaws (paired premaxillary and dentary bones) to break the shelled prey. Two specimens of both species were cleared and stained, revealing that they have similar

pharyngeal dentition. Three pairs of dorsal pharyngeal tooth plates are present, associated with the pharyngobranchial elements of branchial arches I, II, and III, with one tooth plate of each pair being located on either side of the dorsal midline. Each tooth plate is slightly curved with a posteriorly directed dentigerous surface. In the 126- and 137-mm SL checkered puffers, the four tooth plates in the anterior two pairs were each 4 mm long and those in the posterior pair were each 3 mm long. In the 108- and 118-mm SL bandtail puffers, the four tooth plates in the anterior two pairs were each 3 mm long and those in the posterior pair were each 2 mm long. The dorsal pharyngeal tooth plates of both puffer species bear upon the pair of ventrally located, and nondentigerous, fifth ceratobranchial (lower pharyngeal) bones. The pharyngeal tooth apparatuses likely function to pull flesh from and to further grind and break crab and mollusc shells. The smooth puffer, *Lagocephalus laevigatus*, also has strong beaklike jaw teeth but has dentigerous tooth plates associated with the pharyngobranchial elements of only the II and III branchial arches (Tyler 1962). In general, fishes in the Order Plectognathi have very strong jaw teeth and comparatively weak pharyngeal dentition (Al-Hussaini 1947).

Acknowledgments

I thank the many people who helped with the seining of fishes. I also thank Hugh H. DeWitt, Jon G. Stanley, and Nancy M. Targett for their helpful comments on the manuscript.

Literature Cited

AL-HUSSAINI, A. H.
1947. The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighbourhood of the Marine Biological Station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Ghardaqa (Red Sea) 5:1-61.

CHRISTENSEN, R. F.
1965. An ichthyological survey of Jupiter Inlet and Loxahatchee River, Florida. M.S. Thesis, Florida State Univ., Tallahassee, 318 p.

HILDEBRAND, S. F., AND W. C. SCHROEDER
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, 366 p.

ISAACSON, P. A.
1963. Length-weight relationship and stomach contents of the swellfish (*Spheroides maculatus*) in the York River, Virginia. Commer. Fish. Rev. 25(9):5-7.

LAROCHE, J. L., AND J. DAVIS
1973. Age, growth, and reproduction of the northern puffer, *Sphoeroides maculatus*. Fish. Bull., U.S. 71:955-963.

MERRINER, J. V., AND J. L. LAROCHE
1977. Fecundity of the northern puffer, *Sphoeroides maculatus*, from Chesapeake Bay. Chesapeake Sci. 18:81-83.

REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1-94.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SHIPP, R. L.
1974. The pufferfishes (Tetraodontidae) of the Atlantic Ocean. Publ. Gulf Coast Res. Lab. Mus. 4, 163 p.

TARGETT, T. E.
1978. Food resource partitioning by the pufferfishes *Sphoeroides spengleri* and *S. testudineus* from Biscayne Bay, Florida. Mar. Biol. (Berl.) 49:83-91.

TYLER, J. C.
1962. The general osteology of representative fishes of the Order Plectognathi. Ph.D. Thesis, Stanford Univ., Palo Alto, Calif., 388 p.

TIMOTHY E. TARGETT

Department of Zoology
University of Maine
Orono, ME 04473

CORRELATES OF MATURITY IN THE COMMON DOLPHIN, *DELPHINUS DELPHIS*

Maturity of the gonads in mammals is closely related to other aspects of physical development. Therefore, a simple method for estimating an individual's proximity to sexual maturity would be to evaluate appropriate morphometric data. However, the morphometrics traditionally collected on cetaceans are less than ideal for this task.

Studies on cetacean growth patterns have typically used data collected in a cross-sectional manner and have used large samples which included all age-classes. Unfortunately, individual rates and patterns are indistinct when values are averaged using this method (Sinclair 1973). If a large change in growth or development takes place over a short period of time and the beginning of this change does not occur at exactly the same age in each individual, the data acquired from a group of individuals will imply that the change takes place at a slower rate and over a greater period of time than is actually the case for an individual.

The present study used parameters which indicated the proximity of an individual to its own mature condition, not the average mature condi-

tion of the population. In *Delphinus delphis*, an individual's proximity to sexual maturity can be accurately assessed using appropriate morphometric data.

Materials and Methods

I used 35 male and 52 female *Delphinus delphis* specimens collected in southern California waters from 1971 to 1974.

The body weight in kilograms, body length in a straight line to the nearest centimeter from tip of the snout to the anterior portion of the fluke notch, dentine layers, bone development in the flippers, testes weights, and the numbers of scars on the ovaries were recorded.

Teeth were usually from the posterior one-third of the left mandibles; otherwise the largest teeth available were used. A longitudinal section 0.368 mm thick was cut from the center of each tooth, and samples were cleaned in a weak solution of ammonia. After rinsing with water, the sections were etched in 1-2% formic acid at room temperature until the dentine growth layers were distinct, usually 6-12 h. Sections were mounted on microscope slides in an ethanol solution and examined with transmitted light.

One light and one dark band were considered as one dentine layer. The interval for dentine laminar deposition is unknown for the *D. delphis* in the present study but I assume that the bands were laid down at regular intervals. *Delphinus delphis ponticus* Barabash of the Black Sea are reported to have two sets of alternating layers each year (Kleinenberg and Klevezal 1962).

Because different bones fuse at different times in the spotted, *Stenella attenuata*, and the spinner *S. longirostris*, porpoises (Perrin 1972), I used the development of the epiphyses and their fusion to the diaphyses of the flipper bones as the indicator for physical maturity of the specimens. Each flipper was assigned an index by scoring the degree of epiphyseal fusion visible in radiographs: 0 when no epiphysis had been formed; 1 when the epiphysis had been formed but had not started its fusion to the diaphysis; 2 when the epiphysis and diaphysis were in the process of fusing; and 3 when the epiphysis and diaphysis were fused. The distal ends of the radius, ulna, metacarpals, and phalanges of each flipper were scored (Figure 1). The

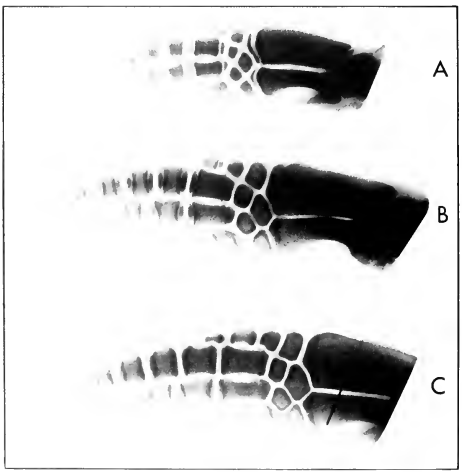


FIGURE 1.—Process of fusion of the epiphyses to the diaphyses in the flipper of *Delphinus delphis*. The flipper labeled A has a score (see text) of 18; B, 49; and C, 72.

sum of the individual epiphyseal fusion scores for both flippers composed the Flipper Index (FI) for that animal. When one of the flippers was damaged, the score for the undamaged flipper was doubled.

The combined weights of the testes with the epididymus removed were used as a measure of sexual maturity in males. In this study, a pair of testes was considered mature at 350 g.

Just as menarche in human females does not mean ovulation but the final developmental stages for the ability to ovulate, delphinid ovarian scars are here inferred to indicate ovulatory capacity. The presence on the surface of at least one corpus albicans or a corpus luteum indicated sexual maturity. However, each ovary also was sliced into sections 1 mm thick and examined for internal corpora.

All statistical tests are described in Sokal and Rohlf (1969).

Results

Development of right and left flippers did not differ significantly in 27 males and 55 females ($P \geq 0.05$, t-test for paired comparisons).

There was no significant difference ($P \geq 0.05$) in weight between the left and right testes of 34 specimens (t-test for paired comparisons).

In all but 2 of 25 mature cases, the left ovary had more scars.

Dentine layers are a poor indicator of sexual development in *D. delphis*. The numbers of dentine layers and ovarian corpora are not significantly related ($P > 0.10$, Kendall's rank correlation test). Both sexually mature and immature females occur with 7-14 dentine layers (Figure 2). Testes weights are so variable in the range of 7-12 dentine layers that they cannot be estimated (Figure 3), although significantly correlated over the entire range of data ($P \leq 0.001$, Kendall's rank correlation).

Body length is a poor indicator of sexual development. Over body lengths 175-190 cm, testes apparently undergo a transitional stage of growth. Gonad weight cannot be accurately estimated from body length over this range (Figure 4) although the two are significantly correlated over the entire range of data ($P \leq 0.001$, Kendall's rank correlation). Body length and ovarian scarring are poorly correlated ($P > 0.10$, Kendall's rank correlation). Body lengths 165-182 cm include both sexually mature and immature females (Figure 5).

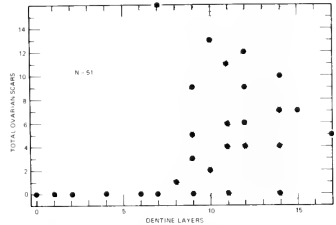


FIGURE 2.—Ovarian corpora in relation to dentine layers in *Delphinus delphis*. The stippled region indicates the range of dentine layers over which sexually mature animals are indistinguishable from immature.

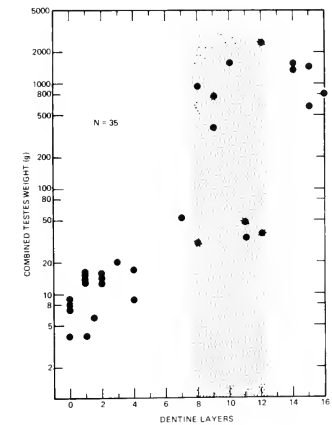


FIGURE 3.—Testis weight in relation to dentine layers in *Delphinus delphis*. The stippled region indicates the range of dentine layers over which testes of mature and immature weights overlap

The FI is significantly correlated with testes weights ($P \leq 0.001$, Kendall's rank correlation) although data are missing in a narrow range (Figure 6). However, inactive ovaries occur in a wide

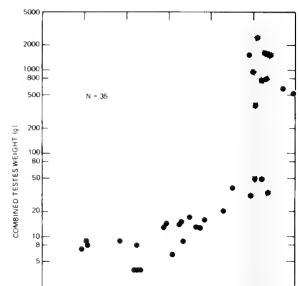


FIGURE 4.—Testes weights in relation to body length. The stippled area indicates the region of overlap for mature and immature testes weights.

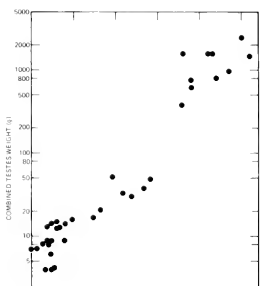


FIGURE 6.—Development of testes related to epiphyseal development of the pectoral appendages in *Delphinus delphis* as indicated by the Flipper Index. The best interpretation of the present data is that two linear phases are separated by a stage of rapid change.

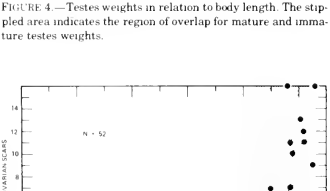


FIGURE 5.—Ovarian corpora related to body length in *Delphinus delphis*. The range of body lengths in which sexually mature and immature animals cannot be distinguished is indicated by the stripped area

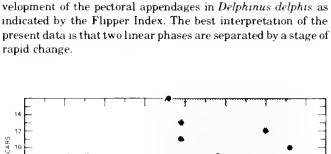


FIGURE 7.—Ovarian corpora related to pectoral epiphyseal development (Flipper Index) in *Delphinus delphis*. The shaded area indicates the range in Flipper Index over which sexually mature and immature animals overlap.

range of FI scores (Figure 7) and there is no significant relationship between the number of ovarian scars and the FI ($P > 0.10$, Kendall's rank correlation).

Robustness is here defined as the body length in centimeters divided by body weight in kilograms. Regardless of body length, only the most robust individuals are sexually mature. Sexual maturity occurs when the male's length/weight ratio declines to about 2.6 (Figure 8). Mature females had length/weight ratios lower than about 3.0 (Figure 9). Of the 24 females with ovarian scars in this study, 16 were pregnant. Assuming the weight of the amniotic sack is nearly equal to that of the fetus, twice the weight of the fetus was subtracted from the gross weight of the mother, leaving the weight of the nonpregnant female for calculations of robustness. The robustness of the pregnant females is not separable from the sexually mature nonpregnant females.

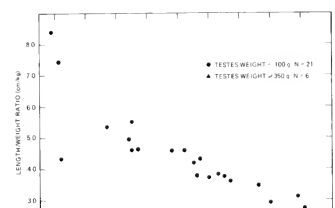


FIGURE 8.—The body length/weight ratio as related to body length in male *Delphinus delphis*. Individuals with combined testes weights of 350 g are considered to be undergoing spermatogenesis. The shading designates the weight/length ratio in which males apparently are sexually mature.

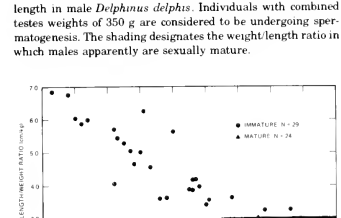


FIGURE 9.—Relationship of the body length/weight ratio to body length in female *Delphinus delphis*. Triangles represent individuals with at least one ovarian corpus. The shaded area denotes length/weight ratios in which sexually mature dolphins predominate.

Discussion

The data indicate that sexual development is better correlated with parameters which indicate the individual's proximity to physical maturity than with fixed morphometric values. A large increase in combined testes weight from <80 g to almost 400 g corresponds with rapid skeletal growth in the individual dolphin (Figure 6). Consequently, the FI is better correlated with sexual maturity in males than dentine layers or body length. Robustness is also highly correlated with sexual development in males but the sample size is small.

For unknown reasons, ovulation is better correlated with the length/weight ratio than with body length, dentine layers, or flipper bone development. Similarly, in studies of humans, it was found that girls who attained early menarche also had greater weight for height than their chronological peers who attained maturity at a later time (Simons and Greulich 1943). Data from *S. attenuata* (Perrin et al. 1976) also show ovarian corpora to be poorly correlated with age and length.

Induced ovulation is a distinct possibility for *D. delphis*. Harrison and Ridgway (1971) concluded that ovulation in *Tursiops truncatus* is induced but the mechanism is unknown. The present data imply that some *D. delphis* females never ovulate, supporting the findings of Harrison et al. (1972).

Oliver's[3] examination of *Delphinus* from the eastern tropical Pacific showed that the smallest testes with spermatogenesis weighed 140 g. For the present study, specimens with combined testes weights >350 g were collected in March, April, July, September, October, November, and December. The large testes weights throughout the year indicate that there is no seasonal rut, supporting the findings of Harrison et al. (1969).

Gaps in the data occur immediately prior to male *D. delphis* sexual maturity: FI scores 85-105 (Figure 6), body lengths 158-177 cm (Figure 4), 4-8 dentine layers (Figure 2). These gaps appear to be the prepuberty ranges for those indicators. Behavior patterns may account for the absence of data in these regions. Young males of *Physeter catodon* (Ohsumi 1971) and *Tursiops truncatus* (Evans and Bastian 1969) frequently herd separately from the rest of the population. Alternatively, these animals may have a greater capacity to escape nets. Female specimens also are lacking in the length, age, and FI ranges just prior to the demonstration of ovarian scars. Preadolescent females, like the males, may easily escape nets, or have a social structure separate from the main herd.

Acknowledgments

Mary F. P. Rieger and Linda J. Harrington provided assistance with the statistics and ovary examination, respectively. G. A. Bartholomew, F. G. Wood, W. E. Evans, W. F. Perrin, and J. C. Quast offered helpful suggestions on the manuscript.

[3]C. W. Oliver, Inter-American Tropical Tuna Commission, La Jolla, CA 92037. Unpubl. data

Literature Cited

EVANS, W. E., AND J. BASTIAN.
1969 Marine mammal communications: social and ecological factors. *In* H. T. Andersen (editor), Biology of marine mammals, p. 425-475. Academic Press, N.Y.

HARRISON, R. J., R. C. BOICE, AND R. L. BROWNELL, JR.
1969 Reproduction in wild and captive dolphins. Nature (Lond.) 222:1143-1147.

HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE.
1972. Reproduction and gonadal appearances in some odontocetes. *In* R. J. Harrison (editor), Functional anatomy of marine mammals, Vol. 1, p. 361-429. Academic Press, N.Y.

HARRISON, R. J., AND S. H. RIDGWAY.
1971. Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). J. Zool. (Lond.) 165:355-366.

KLEINENBERG, S. E., AND G. A. KLEVEZAL.
1962. Towards a method for determining the age of toothed whales. [*In* Russ.] Dokl. Akad. Nauk. SSR Inst. Morfol. Zhivotn.

OHSUMI, S.
1971. Some investigations on the school structure of sperm whale. Sci. Rep. Whales Res. Inst. Tokyo 23:1-25.

PERRIN, W. F.
1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. Univ. Calif. 21, 206 p.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

SIMMONS, K., AND W. W. GREULICH.
1943. Menarcheal age and the height, weight, and skeletal age of girls age 7 to 17 years. J. Pediatr. 22:518-548.

SINCLAIR, D.
1973. Human growth after birth. Oxford Univ. Press, N.Y., 212 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

CLIFFORD A. HUI

Biomedical Branch
Naval Ocean Systems Center
San Diego, CA 92152

LARVAL DEVELOPMENT OF *GOBIESOX RHESSODON* (GOBIESOCIDAE) WITH NOTES ON THE LARVA OF *RIMICOLA MUSCARUM*

Seven species of clingfishes of the genera *Gobiesox* and *Rimicola* occupy the rocky inter- and subtidal areas along the California coast. Extreme modification of the pelvic fins into a suction disc enables them to cling to rock and algal substrates. Although all clingfish species are listed as being uncommon to rare in California by Miller and Lea (1972), clingfish larvae are collected on a regular basis (although in low numbers) by monitoring programs dealing with fish larvae (Brewer,[1] McGowen,[2] and White[3]). Of the seven species recorded in southern California, adults of only two, *G. rhessodon* and *R. muscarum*, are usually encountered (pers. obs.).

Knowledge of larval stages of eastern Pacific (especially Californian) fishes is largely limited to pelagic species of those coastal species with protracted pelagic larval periods (Ahlstrom 1965; Moser et al. 1977). Larvae of many nearshore, coastal fishes are undescribed. Recent concern over the affects of harbor development and thermal discharge and entrainment from power plants on fish populations has intensified the need for proper identification of fish eggs and larvae.

The principal systematic work to date on the adults of eastern Pacific clingfishes was carried out by Briggs (1955). No previous works on the larvae of eastern Pacific clingfishes have been carried out, although the eggs and larvae of an Atlantic clingfish, *G. strumosus*, are well known (Runyan 1961; Dovel 1963).

Descriptions of a larval series of *G. rhessodon* and early larvae of *R. muscarum* are presented here as taxonomic aids to larval fish investigators working in the California coastal region.

Methods and Materials

Eggs and adults of *G. rhessodon* and *R. muscarum* were collected in June 1977 from the intertidal zone at low tide at Catalina Harbor and Little Harbor, Santa Catalina Island, Calif. Adults with their eggs were transported to the Catalina Marine Science Center (CMSC) operated by the University of Southern California and maintained in tanks with running seawater. The failure of hatched larvae to feed (probably due to lack of suitable food) precluded culturing past 2 days (4.0 mm). Additional specimens of *G. rhessodon* utilized in the series were obtained by vertical plankton tow under a night-light at the CMSC dock in Big Fisherman's Cove (4.7 mm) in June 1977; by horizontal tow in King Harbor, Redondo

[1]Gary D. Brewer, Institute for Marine and Coastal Studies, University of Southern California, Los Angeles, CA 90007. Pers. commun. June 1977.
[2]Gerald E. McGowen, Southern California Edison (Occidental College), Redondo Beach, Calif. Pers. commun. June 1977.
[3]Wayne S. White, U.S. Fish and Wildlife Service, Laguna Niguel, Calif. Pers. commun. August 1977.

Beach, Calif. (7.5 mm), in 1977; by otter trawl in Marina del Ray, Calif. (12.0 mm), in June 1977; and from the larval fish collection of the Harbors Environmental Projects (University of Southern California) taken by horizontal plankton tows in Los Angeles Harbor (specimens collected in 1972-73). A total of 32 larvae from 2.6 to 7.5 mm of *G. rhessodon* were examined for larval characteristics. An additional 311 larvae of *G. rhessodon* (2.9-7.5 mm) from King Harbor were checked specifically for the presence of melanophores on the head. Larvae were examined and drawn using a Wild[4] stereomicroscope fitted with a camera lucida. Standard length (SL) was measured from the tip of the snout to the tip of the notochord until completion of notochord flexion and then to the posterior margin of the hypural plate.

Results and Discussion

Gobiesox rhessodon

The most distinctive character of *G. rhessodon* larvae was the presence of 8-17 (mean 12) stellate melanophores, which ran laterally in two or three rows from the pectoral fin region to just posterior to the anus (Table 1, Figures 1-3). The dorsum of the gut was also heavily pigmented with stellate melanophores (not included in the lateral melanophore counts). The gut pigmentation often obscured the well-developed swim bladder. Myomere counts ranged from 24 to 29 (mean 27) but were difficult to count, especially in early stages. All specimens up to 6.9 mm had four to seven regularly spaced melanophores along the ventral portion of the tail region. The length of the gut averaged approximately 35% of body length in all specimens examined. Head length ranged from 19 to 25% SL in most specimens <6.5 mm. Individuals ≥6.5 mm had a much larger head of about 33% of SL. All specimens had a stellate melanophore at the base of each pectoral fin which was covered by the opercular flap in later stages (>6.9 mm). The larvae from Catalina and Los Angeles Harbor possessed from zero to four spots on the dorsal portion of the head. Forty-two percent (mean 24, range 2.6-6.9 mm) of the larvae had head pigmentation in the form of spots. Of the larvae examined from King Harbor, 79% (mean 311) lacked this head pigmentation. The larvae with and without head spots were very similar in every other respect.

The larvae of *G. rhessodon* hatched at about 4.0 mm (three specimens ranged from 3.9 to 4.1 mm) from attached, monolayered eggs laid under rocks and cobble in the intertidal zone at Catalina Island. Nest guarding adults have been found from spring to early summer by Lavenberg.[5] The relatively advanced larvae possessed well-developed jaws and pectoral fins at hatching and a laterally bilobed yolk, which was absorbed within the first 24 h. The gut had two or three constrictions giving it the appearance of being looped. The constrictions were characteristic of the larvae up to 6.9 mm. Notochord flexion occurred between 5.5 and 6.9 mm, and caudal fin rays started to develop just prior to flexion. Dorsal and anal fin ray development began around 6.2 mm and the fins were developed sufficiently for positive identification at about 6.9 mm. The development of the pelvic fins began at 5.5 mm and the characteristic suction disc was formed at about 7.0 mm. Transformation and settling probably occur between 8 and 12 mm as evidenced by an 8-mm planktonic specimen from King Harbor that possessed juvenile pigmentation (McGowen see footnote 2) and the 12-mm juvenile (Figure 3) which was collected by benthic otter trawl. This latter specimen exhibited the ability to cling to surfaces after capture.

Larvae of *G. rhessodon* appear to be the most common *Gobiesox* encountered in several nearshore plankton sampling programs in southern California (Brewer see footnote 1; McGowen see footnote 2; White see footnote 3). This is to be expected in that previous species lists of adult

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

TABLE 1.—Summary of larval measurements and adult counts for *Gobiesox rhessodon* and *Rimicola muscarum* (Miller and Lea 1972 and present study).

Item	*Gobiesox rhessodon*	*Rimicola muscarum*
Larvae		
No. lateral melanophores	8-17 ($\bar{x}$ = 12) in 2-3 rows	40-50 in 4 rows
Myomere count	24-29 ($\bar{x}$ = 27)	(1)
No. ventral tail melanophores	4-7	Absent
Size (mm) at onset of pelvic fin development	5.5	?
Adults		
No. visible dorsal fin rays	10-12	6-8
No. visible anal fin rays	9-10	6-8
No. pectoral fin rays	19-21	14-17
No. vertebrae	[2]28-29	[3]35-36

[1]Lateral melanophores obscurred myomeres so that accurate counts could not be taken.
[2]Counts from Los Angeles County Museum specimen X-rays—*G. rhessodon* (LACM 1998), four specimens; *R. muscarum* (LACM W70-16), six specimens.

[5]Robert J. Lavenberg, Curator of Fishes, Los Angeles County Museum of Natural History, Los Angeles, CA 90007. Pers. commun. June 1977

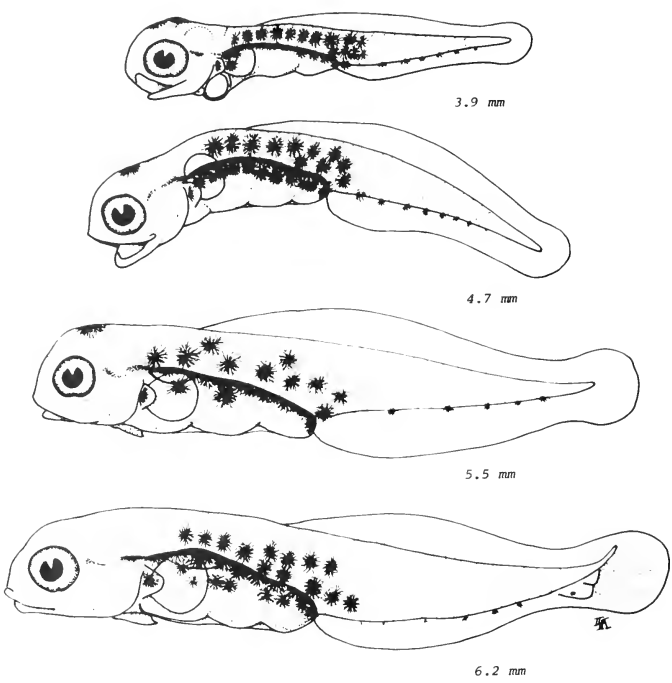


FIGURE 1.—Developmental stages of *Gobiesox rhessodon*. The 3.9-mm larva was reared in the laboratory (<24 h). The remainder are from plankton collections.

juvenile fishes in southern California coastal areas have included *G. rhessodon* exclusively (Horn and Allen 1976).

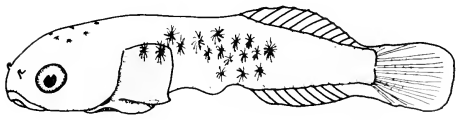
Rimicola muscarum

Yolk-sac larvae of *R. muscarum* (Figure 4), shortly after hatching, can be distinguished from *G. rhessodon* larvae at this stage by the greater number of lateral, stellate melanophores (40-50) in four rows that continue to the sixth or seventh postanal myomere, and the absence of pigmentation on the ventral tail region (Table 1). Yolk-sac larvae do not have head pigment. Adult counts are also markedly different from *G. rhessodon* (Table 1).

Comparison

Three species of *Gobiesox*, in addition to *G. rhessodon*, have been reported in southern California: *G. maeandricus*, *G. papillifer*, and *G. eugrammus*.

FIGURE 2.—Pelagic larvae of *Gobiesox rhessodon*.



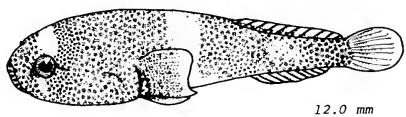


FIGURE 3.—Late pelagic larva (upper) and benthic juvenile (lower) of *Gobiesox rhessodon*.

The larval stages of *G. maeandricus* have recently been described by Marliave (1976). Based on Marliave's description and data from Richardson,[6] *G. maeandricus* larvae differ from *G. rhessodon* mainly in that *G. maeandricus* lack lateral melanophores and possess more myomeres (31-33). In addition, adults of *G. maeandricus* are rare south of Point Conception, Calif. (Miller and Lea 1972). *Gobiesox papillifer* and *G. eugrammus* are also rare in southern California. *Gobiesox papillifer* has been reported only once in southern California, and *G. eugrammus* only ranges as far north as San Diego County (Miller and Lea 1972). The larvae of these two species of *Gobiesox* have not been described, however, it is unlikely that any of these forms were among the specimens examined considering the distributions of the adults.

The Atlantic species of *Gobiesox*, *G. strumosus*, studied by Runyan (1961) and Dovel (1963) was similar in appearance to *G. rhessodon*, but does differ in that the Atlantic species had 10-15 saddle melanophores (as opposed to lateral) and displayed no ventral midline pigment in the early stages (<3.9 mm). Later larvae of *G. strumosus* also appeared to be more heavily pigmented on the trunk portion of the body (4.73-8.78 mm).

The presence or absence of head pigmentation has been used by some investigators to separate *Gobiesox* larvae collected in southern California into two types. This character is variable in *G.*

[6]Sally L. Richardson, School of Oceanography, Oregon State University, Corvallis, OR 97331. Pers. commun. May 1978.

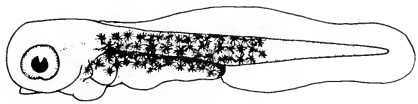


FIGURE 4.—Yolk stage larva of *Rimicola muscarum*.

rhessodon and, therefore, is not useful in distinguishing it from other species.

Acknowledgments

For their advice and instruction, I thank Robert J. Lavenberg and H. Geoffrey Moser. Gary D. Brewer and Gerald E. McGowen gave advice and field and laboratory assistance, and provided specimens. Brian White, Marty Meisler, Marianne Ninos, Layne Nordgren, A. Kubo, Delaine Winkler, Sarah Swank, Scott Ralston, and Tina Behrents assisted in the field collection of eggs, larvae, and adult clingfishes. Michael H. Horn, Robert J. Lavenberg, H. Geoffrey Moser, and Sally L. Richardson greatly enhanced the manuscript through their critical reviews.

Literature Cited

AHLSTROM, E. H.
1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop Oceanic Fish. Invest. Rep 10:31-52.

BRIGGS, J. C.
1955. A monograph of the clingfishes (order Xenopterygii). Stanford Ichthyol Bull. 6.1-224

DOVEL, W. L.
1963. Larval development of clingfish, *Gobiesox strumosus*, 4.0 to 12.0 millimeters in total length. Chesapeake Sci. 4:161-166

HORN, M. H., AND L. G. ALLEN
1976. Numbers of species and faunal resemblance of marine fishes in California bays and estuaries. Bull. South. Calif. Acad. Sci. 75:159-170.

MARLIAVE, J. B.
1976. The behavioral transformation from the planktonic larval stage of some marine fishes reared in the laboratory. Ph.D. Thesis, Univ. British Columbia, Vancouver, 231 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish, Game, Fish Bull. 157, 235 p.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.

RUNYAN, S.
1961. Early development of the clingfish, *Gobiesox strumosus* Cope. Chesapeake Sci. 2:113-141

LARRY G. ALLEN

Department of Biological Sciences
University of Southern California
Los Angeles, CA 90007

SPRING AND SUMMER FOODS OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN THE EASTERN BERING SEA

The walleye (Alaska) pollock, *Theragra chalcogramma* (Pallas 1811), is the most abundant commercial fish species in the eastern Bering Sea (Pereyra et al.[1]) and plays an important role in ecosystem trophodynamics of the region. To obtain better knowledge of the role of the pollock as a predator, we have studied the stomach contents of pollock from the eastern Bering Sea collected on U.S. research vessels in the summer of 1974 and on Soviet and Japanese fishing vessels in the spring of 1977.

Results from this study contribute to our understanding of feeding habits; information on seasonal and size-dependent changes in feeding behavior are used to model interactions between species (trophodynamics), and to predict the influence of commercial fisheries on the abundance of populations in the eastern Bering Sea (Laevastu and Favorite[2,3]).

Methods

Pollock stomachs were collected by U.S. fisheries observers, on an opportunistic basis, aboard Soviet and Japanese motherships in the eastern Bering Sea. Samples were collected in the region of the continental shelf break in April and May 1977 (Figure 1, Table 1). The stomachs were removed, tied in cheesecloth, and preserved in dilute Formalin[4] (ca. 5%) and sent to the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash., for analysis. Identifiable matter was separated by major taxa. Wet weight for each taxa was determined after blotting with paper towels. Uniden-

[1]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Unpubl. manuscr., vol. 1, 619 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2]Laevastu, T., and F. Favorite. 1976. Evaluation of standing stocks of marine resources in the eastern Bering Sea. Unpubl. manuscr., 35 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[3]Laevastu, T., and F. Favorite. 1976. Dynamics of pollock and herring biomasses in the eastern Bering Sea. Unpubl. manuscr., 50 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

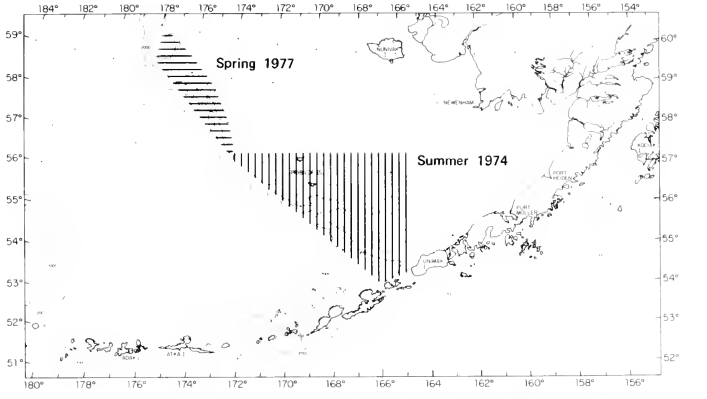


FIGURE 1.—Location sites where walleye pollock stomach samples were collected in the eastern Bering Sea.

TABLE 1.—Summary of walleye pollock stomach samples collected in the eastern Bering Sea.

Vessel	Sampling period	No. of stomachs collected	Depth range (m) of bottom	Average depth (m)
Oregon (U.S.)	July 1974	352	71-132	99
Chikubu Maru (Jpn.)	Apr. 1977	180	124-210	194
Tiraspol (U.S.S.R.)	Apr. 1977	225	128-256	167
Tenyo Maru #3 (Jpn.)	Apr.-May 1977	92	110-165	132
	Total	849		

tifiable matter was classed as "digested material" and also weighed. Percentage of food weight for each major food category, by fish-length group, was calculated as was the weight for each major food category per fish for each length group. Empty stomachs were not included in the analysis.

Detailed length data from foreign fishing vessels were available only from the Japanese fishing vessel *Tenyo Maru*. These data were analyzed by 10-cm fork length classes. Fish lengths from the Japanese fishing vessel *Chikubu Maru* and the Soviet fishing vessel *Tiraspol* were recorded only as greater or less than 35 cm (the approximate length at sexual maturity). This is also the size at which pollock become markedly cannibalistic (Takahashi and Yamaguchi 1972). Data from all three observer cruises were combined using these two major size categories to obtain sufficient sample sizes for comparison with the data collected in 1974.

Data collected in 1974 (RV *Oregon*) were examined by 5-cm length classes. The larger number of stomach samples collected during this cruise allowed a finer analysis of size-related changes in feeding habits. The methods used for processing samples from this cruise were approximately the same as for samples from the foreign vessels.

Results

An examination of stomach content weight by fish-length group provided evidence of related shifts in principal food categories in the diet of pollock (Figures 2, 3). In both spring 1977 and summer 1974, the percentage of copepods as food biomass tended to decrease with increasing size of pollock. The percentage of fish in pollock stomachs tended to increase with the size of pollock. Euphausiids were important food components in most length classes in both sampling periods. Amphipods, however, were only abundant in

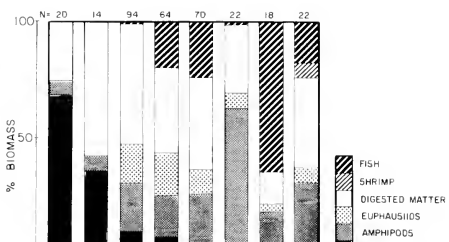


FIGURE 2.—Percent biomass of stomach contents by taxa per 5-cm length group of Bering Sea walleye pollock, summer 1974

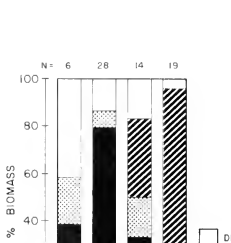


FIGURE 3.—Percent biomass of stomach contents by taxa per 10-cm length group of Bering Sea walleye pollock, spring 1977.

TABLE 2.—Proportion of taxa observed in walleye pollock stomachs in the eastern Bering Sea.

	Observer cruises, spring 1977		*Oregon* cruise, summer 1977	
Taxa	Weight (g)	% biomass	Weight (g)	% biomass
Fish	277 07	28 53	223 21	25 94
Copepods	349 81	36 02	44 60	5 18
Euphausiids	210 02	21 62	81 70	9 49
Amphipods	2 15	0 22	235 63	27 38
Chaetognaths	0 47	0 05	17 77	2 07
Cephalopods	0 30	0 03	—	—
Mollusks	0 15	0 02	0 89	0 10
Ostracods	0 02	—	—	—
Larvaceans	0 08	0 01	0 08	0 01
Annelids	3 99	0 42	3 40	0 40
Shrimp	12 91	1 33	9 79	1 14
Cumacean	—	—	0 01	—
Nemerteans	—	—	0 92	0 11
Mysids	—	—	0 55	0 06
Crab	—	—	4 56	0 53
Unidentified	—	—	1 64	0 19
Digested	114 09	11 75	235 83	27 40
Total	971 06	100 00	860 58	100 00

TABLE 3.—Grams of food organisms per fish (not including fish with empty stomachs) in each size class, *Tenyo Maru*, spring 1977.

	Fork length (cm) of pollock			
Item	15-24	25-34	35-44	≥45
Grams copepods/fish	0 08	0 97	0 66	0 14
Grams euphausiids/fish	0 04	0 09	0 35	0 82
Grams fish/fish	—	—	0 69	5 28
Grams total food/fish	0 20	1 22	2 04	6 50
No. of fish with food	6	28	14	19
Percentage of fish with empty stomachs	57	26	18	17

stomachs collected in summer 1974, and the percentage of amphods as food biomass tended to increase with increasing pollock size. Other food organisms that appeared in the diet are listed in Table 2.

The analysis of stomach contents by weight-percentage masks the behavioral aspects of pollock feeding due to size differences in food organisms. More information can be obtained from the data when analyzed as grams of food organisms per fish for each length class (Tables 3, 4). From this analysis it appears that larger pollock tended to exclude smaller food items from their diet. As the pollock grew larger they fed more on euphausiids, amphipods, and fish.

Data on the species composition of fish in pollock stomachs were available from the summer cruise of 1974 (*Oregon*). Fish ingested were identified from the stomachs of 27 pollock ranging in fork length from 26 to 57 cm (mean = 40 cm). Of the fish ingested, 89% by weight and 39% by number were

TABLE 4.—Grams of food organisms per fish (not including fish with empty stomachs) in each size class, *Oregon*, summer 1974.

Item	Fork length (cm) of pollock							
	20	20-24	25-29	30-34	35-39	40-44	45-49	49
Grams copepods/fish	0 42	0 26	0 14	0 16	0 13	0 02	—	—
Grams amphipods/fish	0 04	0 04	0 27	0 33	0 80	2 90	2 20	1 23
Grams euphausiids/fish	—	—	0 20	0 38	0 30	0 25	0 31	0 31
Grams shrimp/fish	—	—	—	—	0 01	—	—	0 40
Grams fish/fish	—	—	0 01	0 40	0 73	0 02	7 18	0 71
Grams total food/fish	0 62	0 70	1 27	1 97	2 91	4 57	11 24	4 00
No. of fish with food	20	14	94	64	70	22	18	22
Percentage of fish with empty stomachs	35	0	7	2	4	8	14	4

pollock. Other fishes identified included gadids, cottids, hexagrammids, and zoarcids.

Pollock food composition in summer 1974 and spring 1977 can be compared although geographic locations of stomachs collected varied (Figure 4). Pollock were observed with more copepods as a percentage of food biomass in spring 1974 than in summer 1977. Amphipods were nearly absent from stomachs collected in spring 1974 but were an important food component in summer 1977.

Discussion

Previous studies on the food of the walleye pollock in the eastern Bering Sea indicated that in winter 1972, juvenile pollock fed mainly on euphausiids, while adult pollock fed on euphausiids, small pollock, and other fish (Mito 1974). In summer 1970, juvenile pollock fed on copepods and euphausiids, while adult pollock fed on euphausiids, small pollock, and other fish (Takahashi and Yamaguchi 1972). Our study indicates that in summer 1974 juveniles fed mostly on copepods, euphausiids, and amphipods, while adults fed on euphausiids, amphipods, and fish. In spring 1977, juvenile pollock fed mostly on copepods and euphausiids, while adult pollock fed on copepods, euphausiids, and fish. The results of these studies indicated that euphausiids are an important year-round food source of both juvenile and adult pollock. Fish appear to be an important year-round resource to adult pollock. The relative importance of other prey organisms in the diet of pollock seems to fluctuate between the studies.

Adult pollock tend to obtain a greater percentage of their food biomass from larger prey organisms than juvenile pollock, by ingesting more fish, euphausiids, and amphipods as they grow larger (Figures 2, 3). Additionally, larger pollock tend to exclude copepods from their diet (Tables 3, 4). These observations could result from an active process, based on preference or capture efficiency,

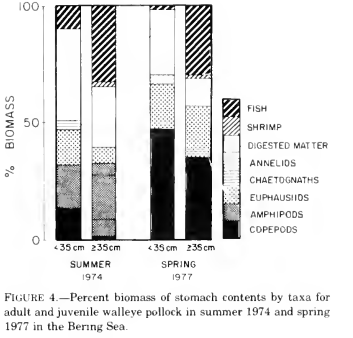


FIGURE 4.—Percent biomass of stomach contents by taxa for adult and juvenile walleye pollock in summer 1974 and spring 1977 in the Bering Sea.

or a passive process, resulting from spatial distribution.

Additional information is needed to understand the complexities of pollock feeding behavior, including: 1) seasonal variations in feeding behavior, 2) geographical variations, and 3) effects of alternate prey on cannibalism and grazing on other fish. This information would be useful in ecosystem modelling to understand the natural competitive and predatory interactions between fish populations and the potential effects of heavy exploitation.

Acknowledgments

We thank the following persons at the Northwest and Alaska Fisheries Center: Donald Day for collecting and making preliminary analysis of 1974 data, Robert French for arranging the collection, and Beverly Vinter and Jay Clark for iden-

tifying the contents of fish stomachs collected in 1977.

Literature Cited

MITO, K.
1974. Food relationships among benthic fish populations in the Bering Sea on the *Theragra chalcogramma* fishing ground in October and November of 1972. [In Jpn.] M.S. Thesis, Hokkaido Univ., Hokkaido, Jpn., 135 p.

TAKAHASHI, Y., AND H. YAMAGUCHI.
1972. II—2. Stock of the Alaska pollock in the Bering Sea. [In Jpn., Engl. summ. on p. 418-419.] *In* Symposium on the Alaska pollock fishery and its resources, p. 389-399. Bull. Jpn. Soc. Sci. Fish. 38

KEVIN BAILEY
JEAN DUNN

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, WA 98112

FECUNDITY OF THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

Although some work has been done to determine the time and place of spawning, age of spawning, and fecundity of Atlantic menhaden, *Brevoortia tyrannus* (Higham and Nicholson 1964), no attempt has been made to relate fecundity and age. In this study, 1) examined the ovaries of fish 1 to 5 yr old collected during autumn 1970, in the vicinity of Beaufort, N.C.; 2) estimated the number of ripening ova in sexually mature fish; 3) calculated the mean number of ova spawned by fish of each age; and 4) determined the reproductive potential and the net reproductive rates for the 1954-63 year classes.

Atlantic menahden, family Clupeidae, constitute a single biological population (Nicholson 1972, 1978; Dryfoos et al. 1973) inhabitating coastal waters from Florida to the Gulf of Maine. It is subjected to an intensive purse seine fishery from Florida to New England. Fish are landed daily at reduction plants and processed into meal, oil, and solubles. Fishing begins in Florida and North Carolina in late April, in New Jersey coastal waters in early June, and in New England waters in late June. Fishing usually ends in mid to late November, except in the vicinity of Beaufort where schools of migrating fish of all ages from northern areas provide an intensive fishery from November to late December or early January.

Atlantic menhaden make extensive coastal movements and during the fishing season are stratified along the coast by age and size. In autumn most fish north of Virginia move southward and by January are concentrated in offshore waters from Cape Hatteras to northern Florida. About mid-March they begin a northward movement and by mid-June are stratified in coastal waters by age and size, the younger and smaller farther south and the older and larger farther north (Nicholson 1971). South of Cape Hatteras and in Chesapeake Bay most fish are ages 1 and 2. Age-2 fish dominate in coastal waters off New Jersey, ages 3 and 4 in Long Island Sound, and age 4 and older north of Cape Cod. Although they may live to age 9, few older than age 6 are caught.

Menhaden spawn in offshore coastal waters where the eggs hatch in 36 to 48 h (Reintjes 1962). Larvae, carried inshore by ocean currents, enter estuaries where they metamorphose to the adult form at about 35 mm total length. Although some spawning occurs in summer and early autumn in Long Island Sound and New England waters—the only areas where fish of spawning age are found during that time — most spawning occurs in the South Atlantic area from January to March and in the Middle Atlantic area from October to December and March to May. Although there appears to be only one spawning cycle each year, evidence is uncertain as to whether Atlantic menhaden are fractional spawners (Higham and Nicholson 1964).

As the population size decreased in the 1960's age structure also changed. Fish older than age 3 became extremely scarce, and most plants in the northern areas that were dependent on older fish closed. By 1969 few fish older than age 4 were landed, even in the North Carolina fall fishery, which traditionally had been dependent on older fish (Nicholson 1975).

Collection and Preparation of Ovaries

Ovaries were collected from 17 November to 29 December 1970 during the North Carolina fall fishery at the same time catches were being sampled routinely for age and size (June and Reintjes 1959). Sampling personnel measured and weighed the fish, removed scales for aging, and removed the ovaries. Only ripening ovaries fitting the

Stage III classification of Higham and Nicholson (1964) were retained. They were blotted on paper towels to remove excess moisture, weighed to the nearest 0.1 g, split longitudinally and turned inside out, and placed in individual jars of Gilson's fluid modified by Simpson (Bagenal 1967). The jars were shaken to liberate all eggs. After the Gilson's fluid was poured off, along with most pulverized ovarian tissue, the ova were washed and decanted in water several times and forced through a sieve to remove remaining fragments of ovarian tissue, spread on large trays covered with paper towels, and dried under incandescent lamps.

Higham and Nicholson (1964) described four stages in the maturation of ovaries. Ovaries in the immature and intermediate stages contain only undeveloped ova; ovaries in the maturing and ripe stages contain developing as well as undeveloped ova. They concluded that only maturing ova ripened during each spawning period. Maturing ova were described as being opaque and yellow and between 0.35 and 0.78 mm in diameter. I followed this description to separate immature from maturing ova. I also measured fecundity by estimating the number of maturing ova in both ovaries. Instead of counting ova in sample sections of the wet ovary, however, I counted ova in two replicate samples of the dried ova that had been separated from connective tissues. Before being weighed, eggs were allowed to equilibrate with air humidity. Each sample was weighed to the nearest 0.01 mg. If both ovaries weighed more than 12 g, two samples, each weighing 1/350 of the total weight, were taken. If the ovaries weighed 12 g or less, two replicate samples, each weighing 0.035 g, were taken, since fecundity would have been difficult to estimate in samples smaller than 0.035 g. Proportional sampling tended to minimize the counting error for a fixed amount of counting effort. Ova in each sample were counted under a stereoscope. The number of ova in both ovaries, N, was estimated by multiplying the number of ova in the two samples, N_s, by the ratio of total dry weight of eggs, W_t, to dry weight of eggs in samples, W_s ($N = N_s W_t / W_s$). To minimize counting error between samples, a coefficient of variation of 3.0% or less was maintained.

Preliminary calculations indicated that fecundity could be estimated with a precision of about 15% if 30 fish were selected randomly from each age-class. The ultimate number in each age-group was age 1, 21; age 2, 34; age 3, 33; age 4, 12; and age 5, 1 (Table 1).

TABLE 1.—Mean number of eggs (thousands) and mean ovary weight (grams), by age, for Atlantic menhaden sampled from the North Carolina fall fishery, 1970.

Age	No. of fish	Mean no. of eggs	Range	C.V.[1] (%)	Mean ovary wt.	Range	C.V. (%)
1	21	115.8	26.5-250.7	47	17.9	4.0-43.5	54
2	34	177.4	39.2-368.8	50	30.1	5.0-62.5	55
3	33	302.8	127.7-458.3	30	50.9	21.1-96.9	34
4	12	308.6	142.7-514.0	36	48.5	22.0-74.8	36
5	1	568.4	—	—	90.0	—	—

[1]Coefficient of variation

Fecundity

The regressions of fecundity on ovary weight, $F = 6{,}908(OW) - 17.937(OW)^2$, and fecundity on total fish weight, $F = 293(TW) + 0.214(TW)^2$, were curvilinear, but fecundity on body weight only, $F = 488(BW)$, was linear. The R^2 values were 0.981, 0.675, and 0.916, respectively. Although the relative merits of predicting fecundity from different variables are debatable (Bagenal 1967), these three models seem less useful than fecundity on age, which can be used to determine reproductive potential and calculate life table estimates, and fecundity on fish length, which can be used to predict the number of eggs spawned by different size classes.

A statistical test failed to support the curvilinear relation implied by a plot of fecundity on age, perhaps because of the few fish in older age-groups. Of the two linear models tested for estimating fecundity at age, I selected $F = 92{,}592(\text{Age})$ as the better estimator ($r^2 = 0.879$; SE slope = 3,440; SE regression = 89,110). It had tighter confidence limits and a higher r^2 than the model $F = a + bL$.

A logarithmic model ($\log F = a + bL$) was selected to describe the curvilinear relation between fecundity and length and was fitted to both my data and the data of Higham and Nicholson (1964) (Figure 1). Values predicted by this model fit observed values more closely over the entire range than those predicted by the nonlogarithmic model ($F = b_1 L + b_2 L^2$). The difference in the slope coefficients of the logarithmic model fitted to the two sets of data was significant ($P < 0.001$). Estimated fecundities were in reasonable agreement for fish up to 275 mm, but diverged for large fish. For 350 mm fish the model fitted to Higham and Nicholson data predicted about 1.75 as many ova as the model fitted to my data.

Differences in fish ages or in the time of year fish were collected, or actual changes in fecundity might account for differences in estimates of ova

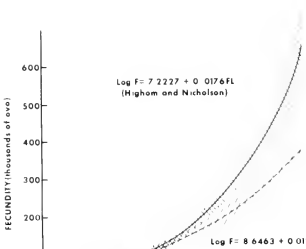


FIGURE 1.—Regression of fecundity on fork length for Atlantic menhaden showing confidence limits on the mean at 95% level. For $\log F = 7.2227 + 0.0176FL$, $N = 38$, SE regression = 0.3069; SE regression coefficient = 0.0011, $r^2 = 0.726$; for $\log F = 8.6463 + 0.0120FL$, $N = 101$, SE regression = 0.3330, SE regression coefficient = 0.0007, $r^2 = 0.871$.

for larger fish. Higham and Nicholson (1964), e.g., had four fish with between 400,000 and 500,000 ova, four with between 500,000 and 600,000, and one with over 600,000, whereas from nearly three times as many fish I had only two with over 500,000 and six with between 400,000 and 500,000. I believe, however, that differences in counting techniques caused the differences in ova estimates. I used proportional sampling, whereas they did not. I separated the eggs from each other and from the connective tissue, dried and weighed the eggs, and then counted those in a sample. They counted the eggs in a sample from the wet ovary. Also, a certain amount of subjectivity is involved in distinguishing between maturing and nonmaturing ova.

Reproductive Potential and Net Reproductive Rate

Since the sex ratio of Atlantic menhaden is about equal (Nicholson and Higham 1964), I was able to calculate the annual numbers of females of each age in the population, 1955-68, by dividing half of the number of fish caught at each age by the exploitation rate for all ages (Schaaf and Huntsman 1972). When I collected my material in 1970, recording the maturing stage of fish in catch samples had been discontinued, but Higham and Nicholson (1964) estimated that about 10% of age-1 fish, 90% of age 2, and 100% of age-3 or older fish examined during the North Carolina fall fishery in October-December from 1955 to 1959 had maturing ovaries. From these figures I calculated the number of females of each age that would spawn each year and multiplied it by the mean number of ova spawned by fish of each age to estimate the number of eggs spawned each year (Table 2).

The net reproductive rate, R_0, of a population is defined as the sum of the products of the age-specific survival rate l_x and the age-specific natality rate m_x, of females (Odum 1971). A value of 1.0 for each generation would indicate that the population is stable and that there is a balance between births and deaths. In fish populations it is nearly impossible to obtain accurate counts or estimates of the number of offspring produced by each age-group. It is possible, however, to estimate the mean number of eggs spawned for fish of each age. If this variable is used for m_x in the formula given by Odum and if $\Sigma l_x m_x$ is called, $R_0{}^*$, then the reciprocal of $R_0{}^*$ should be a rough estimate of the survival rate of female eggs, providing the population is approximately stable. Although the Atlantic menhaden population declined after about 1960, I think in view of the imprecise estimates of other parameters, that it can be assumed stable for the purpose of estimating egg mortality.

$R_0{}^*$ values were calculated for the 1954-63 year classes. I assumed a 0.65 survival rate up to age 1, which I divided into the estimated number of fish that were age 1 (Schaaf and Huntsman 1972) for an estimate of the number of fish at the postlarval stage. Since the sex ratio is equal, this number divided into the estimated number of fish surviving to each age (Schaaf and Huntsman 1972)

TABLE 2.—Estimated number of eggs (multiply by 10^{11}) spawned by Atlantic menhaden, by year and age.

	Age in years							
Year	1	2	3	4	5	6	7-9	Total
1955	83.0	377.6	723.2	119.5	43.6	8.7	3.5	1,359.1
1956	69.7	443.9	103.7	465.1	118.8	31.1	10.7	1,243.0
1957	106.9	136.6	166.7	127.2	144.9	19.7	6.0	708.0
1958	161.1	131.3	51.0	62.8	42.9	28.8	3.0	480.9
1959	73.0	599.2	85.9	40.7	53.0	23.4	10.6	885.8
1960	329.8	205.3	457.9	142.0	59.4	21.1	6.8	1,222.3
1961	44.8	1,938.4	51.2	104.6	12.7	4.3	1.5	2,157.5
1962	57.7	270.2	877.6	85.0	85.0	12.4	3.4	1,391.3
1963	42.2	143.8	88.0	136.6	34.0	13.0	2.6	460.2
1964	38.4	95.3	34.1	19.9	21.0	5.0	1.4	215.1
1965	32.2	108.0	28.2	5.6	4.7	3.4	0.4	182.5
1966	31.2	44.0	9.0	1.1	0.4	0.5	0.2	86.4
1967	20.5	101.1	11.8	1.5	—	—	—	134.9
1968	41.3	91.2	24.7	3.0	0.2	—	—	160.4

yielded age-specific-survival fractions (l_x) for females of each year class. R_0* for each year class ranged from 7,100 to 25,800 (Table 3). The reciprocal of these numbers, 0.000141 and 0.000039, respectively, indicate a survival rate ranging from 39 to 141 females, or 78 to 282 fish of both sexes, for each 1,000,000 eggs spawned.

Any estimate based in turn on a series of rather imprecise and arbitrary estimates must be viewed with caution, and this one is no exception. Yet it is in line with current knowledge that the survival rate of pelagic fish eggs is extremely low.

TABLE 3.—Net reproductive rates (R_0*) and their reciprocals ($1/R_0$*) for the 1954-63 year classes of Atlantic menhaden.

Year class	R_0*	$1/R_0$*	Year class	R_0*	$1/R_0$*
1954	16,546	0.000060	1959	22,297	0.000045
1955	7,109	0.000141	1960	10,120	0.000099
1956	25,932	0.000039	1961	14,073	0.000071
1957	11,850	0.000084	1962	11,024	0.000091
1958	21,856	0.000046	1963	11,181	0.000089

Literature Cited

BAGENAL, T. B.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Blackwell Sci. Publ., Oxf., Engl.

DRYFOOS, R. L., R. P. CHEEK, AND R. L. KROGER
1973. Preliminary analyses of Atlantic menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. Fish. Bull., U.S. 71:719-734.

HIGHAM, J. R., AND W. R. NICHOLSON
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.

JUNE, F. C., AND J. W. REINTJES
1959. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1952-55; with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 317, 65 p.

NICHOLSON, W. R.
1971. Coastal movements of Atlantic menhaden as inferred from changes in age and length distributions. Trans. Am. Fish. Soc. 100:708-716.
1972. Population structure and movements of Atlantic menhaden, *Brevoortia tyrannus*, as inferred from back-calculated length frequencies. Chesapeake Sci. 13:161-174.
1975. Age and size composition of the Atlantic menhaden, *Brevoortia tyrannus*, purse seine catch, 1963-71, with a brief discussion of the fishery. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-684, 28 p.
1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries 1:141-150.

NICHOLSON, W. R., AND J. R. HIGHAM, JR.
1964. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1959, with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 478, 34 p.

ODUM, E. P.
1971. Fundamentals of ecology. 3d ed. W. B. Saunders Co., Phila., Pa., 574 p.

REINTJES, J. W.
1962. Development of eggs and yolk-sac larvae of yellowfin menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 62:93-102.

SCHAAF, W. E., AND G. R. HUNTSMAN
1972. Effects of fishing on the Atlantic menhaden stock, 1955-1969. Trans. Am. Fish. Soc. 101:290-297.

CHARLES S. DIETRICH, JR.

Southeast Fisheries Center Beaufort Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 570, Beaufort, NC 28516

ROLE OF LAND AND OCEAN MORTALITY IN YIELD OF MALE ALASKAN FUR SEAL, *CALLORHINUS URSINUS*

The annual commercial harvest of male fur seals has fluctuated widely and declined since the early 1950's. This has occurred despite a fairly stable harvesting regime and efforts to maintain the population near the level believed to be consistent with maximum sustainable productivity (Chapman 1961, 1964, 1973). Variations in early natural mortality are mainly responsible for these changes in the harvest of males which occurs at ages 2-5 yr (mostly 3-4 yr). Kenyon et al. (1954) and Chapman[1] emphasized that natural mortality between birth and age 3 yr is high and that most of it probably occurs during the first winter just after weaning.

This report gives estimates of male survival from natural mortality of pups on land and from the first 20 mo of life at sea, a total interval of approximately 2 yr. The importance of pup numbers and early survival rates in determining annual variations in abundance at age 3 yr is quantified also.

Methods

Data for survival estimates are in Table 1. The age composition of annual kills before 1950 cannot be determined accurately because an aging technique was not available until then (Scheffer

[1]Chapman, D. G. 1975. Methods of forecasting the kill of male seals on the Pribilof Islands. Background paper for the 19th Annual Meeting of the North Pacific Fur Seal Commission, 10 p. (Unpubl. rep.)

TABLE 1.—Estimated numbers of male pups (born, dead, and living at the time of migration) and age-specific commercial kill of males from the 1950-70 year classes on St. Paul Island, Pribilof Islands, Alaska.[1]

Year class	Number of pups (thousands)			Number killed at age				
	Born	Dead	Living	2	3	4	5	2-5
1950	225.5	26.7	199	855	40,656	15,365	332	57,208
1951	223.5	35.3	188	1,384	32,350	18,083	3,057	54,874
1952	219.0	20.4	199	1,735	30,773	31,410	675	64,553
1953	222.5	39.1	183	839	38,312	8,855	54	48,060
1954	225.0	48.1	177	2,918	23,473	5,599	554	32,544
1955	230.5	37.8	193	1,015	27,863	10,555	115	39,548
1956	226.5	49.4	177	885	10,671	2,762	532	14,850
1957	210.0	30.8	179	2,590	24,283	15,344	773	42,990
1958	193.5	15.6	178	1,977	48,458	14,149	1,587	66,171
1959	167.5	20.0	148	2,820	26,456	14,184	1,764	45,224
1960	160.0	31.4	129	1,619	14,310	10,533	1,240	27,702
1961	168.4	29.0	139	1,098	22,468	12,046	1,270	36,882
1962	139.2	22.6	117	2,539	19,009	12,156	1,287	34,991
1963	132.0	16.3	116	1,264	25,535	11,785	1,542	40,126
1964	142.5	10.8	131	3,143	26,991	13,279	1,469	44,882
1965	133.4	19.6	113	2,200	18,706	10,565	731	32,202
1966	150.0	10.7	138	1,673	17,826	11,548	1,338	32,385
1967	142.0	7.0	135	2,640	22,176	12,503	2,185	39,504
1968	117.5	12.6	105	1,725	12,888	14,932	721	30,266
1969	116.8	6.6	110	323	15,024	10,800	1,631	27,778
1970	115.8	10.3	105	916	16,337	15,533	1,402	34,188

[1]Sources for data in Table 1 and footnotes are given below.
Pups born: 1950-60, table 112 from Chapman (1973); 1961-65 and 1969-70, table 14 from Marine Mammal Biological Laboratory (1971[a]); 1967-68, table 10 from Marine Mammal Division (1976[b]). A 1:1 sex ratio is assumed (Kenyon et al. 1954; H. Kajimura pers. commun.).
Dead pups: 1950-60 (except 1952), appendix table 39 from Marine Mammal Biological Laboratory (1961[c]); 1952, counts (from same source) on sample rookeries only, extrapolated to island total from average contribution of these rookeries to known totals in 1951 and 1953; 1961-69, table A-12 from Marine Mammal Biological Laboratory (1971). A 1:1 sex ratio is assumed (Kenyon et al. 1954; M. C. Keyes pers. commun.).
Living pups: Pups born less dead pups, rounded to nearest thousand.
Kill by age: 1950-56 year classes, table 1 from Marine Mammal Biological Laboratory (1961[c]); 1957-64 year classes, table 1 from Marine Mammal Biological Laboratory (1971); 1965-70 year classes, table 1 from Marine Mammal Division (1976[b]).

[a]Marine Mammal Biological Laboratory. 1971. Fur seal investigation, 1970. Unpubl. manuscr., 155 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[b]Marine Mammal Division. 1976. Fur seal investigations, 1975. Unpubl. manuscr., 115 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[c]Marine Mammal Biological Laboratory. 1961. Fur seal investigation, Pribilof Islands, Alaska. Unpubl. manuscr., 148 p. U.S. Fish. Wildl. Serv., Bur. Commer. Fish.

1950). However, the average numbers of pups migrating from land and of seals harvested at age 3 yr are approximated for the 1920-22 year classes in order to include in the yield-pup relationship a data point for the relatively small pup population then present. It should be mentioned that basic data were not taken during 1925-46 from which to estimate annual pup production.

The 1920-22 averages are based on kill data from Lander and Kajimura[2] and on pup data from Kenyon et al. (1954). The average number of pups born annually on St. Paul Island during 1920-22 was approximately 150,700. Their mean mortality rate on land was 2.2%, so an average of about 74,000 male pups migrated to sea annually. Because the harvest always has been selective for animals the size of 3- and 4-yr-olds, these 1920-22 year classes contributed to the kills mainly in 1923-26. The annual average kill then was 14,300, of which about 9,100 were age 3 yr assuming the same average (64%) as in the kills from the 1950-70 year classes (Table 1).

The kill of 3-yr-olds is used as an index of abundance at that age. The assumption is justified reasonably well by the generally stable harvesting regime and the usual predominance of this age group in the kills.

Annual population monitoring and behavioral data (Bartholomew and Hoel 1953; Peterson 1968) show the median date of birth on St. Paul Island is about 8 July, pup mortality on land is essentially over by mid-August, and the median date when pups migrate to sea is around 1 November. Survival of pups on land is calculated as the ratio of living pups to pups born (Table 1).

Few seals haul out on land until 24 mo of age, and survival is estimated for the first 20 mo at sea. These ocean survival rates are calculated from the data for living pups and age-specific kills (Table 1) and from the model of Lander (1975) with time intervals appropriately modified.

Results

Figure 1 shows wide fluctuations in the kill at age 3 yr around the regression line for pups born. After the effects of pup mortality on land are removed, high variability persists around the line

[2]Lander, R. H., and H. Kajimura. 1976. Status of northern fur seals. Food and Agriculture Organization of the United Nations, Scientific Consultation on Marine Mammals, Bergen, Norway, August 31-September 9, 1976, 50 p. (Unpubl. rep.)

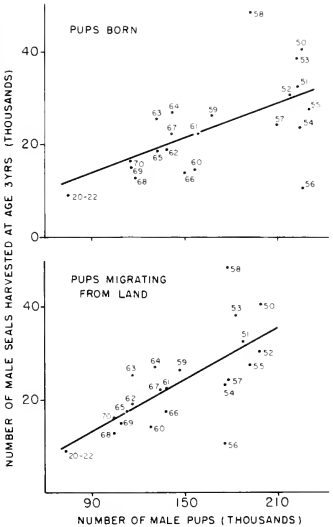


FIGURE 1.—Yield-pup relation for male fur seals of the 1920-22 and 1950-70 year classes from St. Paul Island. Least squares regression lines are shown for pups born ($a = 2.341$, $b = 0.126$) and for pups migrating from land ($a = 3.740$, $b = 0.188$).

for pups migrating from land. Most of the variation in abundance at age 3 yr is evidently due to changes in the ocean survival rate undergone by the different year classes, not to changes in the rate of pup survival on land.

Estimated survival rates for the 1950-70 year classes are in Table 2 (ocean survival could not be estimated for the 1920-22 year classes without age composition data). The means and ranges of survival estimates in Table 2 are 87% (78-95%) for pups on land, 40% (18-49%) for the first 20 mo at sea, and 35% (14-45%) for both stages between birth and 2 yr of age.

Figure 2 shows a statistically significant association between the ocean and land survival estimates ($r = 0.67$, $P < 0.01$). Conditions of weather, feeding, and disease which promote good survival

TABLE 2.—Estimated natural survival rates of male fur seals from St. Paul Island in two stages from birth to age 2 yr, 1950-70 year classes.

Year class	Pups on land	First 20 mo at sea until start of kill at age 2 yr	Birth to age 2 yr
1950	0.88	0.41	0.36
1951	0.84	0.42	0.35
1952	0.91	0.46	0.42
1953	0.82	0.38	0.31
1954	0.79	0.30	0.24
1955	0.84	0.33	0.28
1956	0.78	0.18	0.14
1957	0.85	0.37	0.31
1958	0.92	0.49	0.45
1959	0.88	0.43	0.38
1960	0.81	0.34	0.28
1961	0.83	0.39	0.32
1962	0.84	0.43	0.36
1963	0.88	0.47	0.41
1964	0.92	0.47	0.43
1965	0.85	0.41	0.35
1966	0.92	0.36	0.33
1967	0.95	0.42	0.40
1968	0.89	0.42	0.37
1969	0.94	0.38	0.36
1970	0.91	0.46	0.42
All	0.87	0.40	0.35

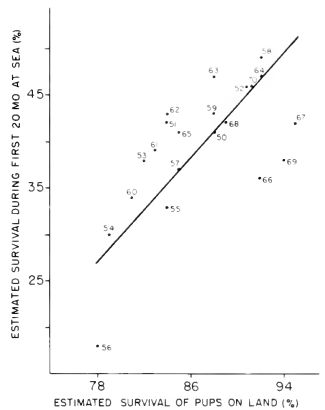


FIGURE 2.—Relation of estimated survival rate during first 20 mo at sea to estimated survival rate of pups on land for male fur seals of the 1950-70 year classes from St. Paul Island. Functional regression line shown (Ricker 1973) has intercept $a = 0.830$ and slope $b = 1.425$.

of pups on land apparently equip them to survive relatively well at sea. As in Figure 1, however, the wide scatter about regression is prominent—emphasizing again that events at sea contribute

heavily to fluctuations in the survival of different year classes.

Values in Tables 1 and 2 were also analyzed under the multiple linear regression model

$$Y = A + B_1X_1 + B_2X_2 + B_3X_3 + E$$

where Y = kill at age 3 yr in thousands, X_1 = male pups born in thousands, X_2 = survival rate pups on land, and X_3 = survival rate during the first 20 mo at sea. E is a random error term; the intercept A and slopes B_i are parameters to be estimated.

Table 3 shows that multiple regression is highly significant ($F = 26.60$, $P < 0.001$). Given that the pup survival rate on land is not significant (deletion of X_2 causes no change in R^2 here), 100 R^2 = 82% of the annual variation in estimated abundance at age 3 yr, as indexed by the kill, is explained by annual changes in pup production and in the survival rates of different year classes during their first 20 mo at sea. The remaining variability, 18%, is due to random sampling errors and possibly to systematic errors.

Discussion

This report helps to quantify the importance of early ocean mortality in determining the average number of males available for harvest at age 3 yr and their pronounced annual fluctuations. Kenyon et al. (1954) speculated that only half the pups survive the attempted transition from a milk diet on the Pribilof Islands to the quest for fishes and squids in a stormy environment after the islands are left behind. The authors stated that starvation during prolonged storms is a direct cause of death and noted that unusually large numbers of young seals from the 1949 year class were washed ashore on the Washington coast in emaciated condition during the severe winter of 1949-50. Ichihara (1974) postulated that the apparently higher mortality of males between birth and age 3 yr (Chapman 1964) was due to the greater proportion of males wintering in stormy northern areas than in calmer waters to the south where females predominate.

TABLE 3.—Statistics and tests for linear regression of male seals killed on St. Paul Island at age 3 yr (thousands) from the 1950-70 year classes (Y) on pups born (X_1, thousands), estimated survival rate of pups on land (X_2), and estimated survival rate during the first 20 mo at sea until age 2 yr (X_3).

Item		Calculated value
Source of sum of squares, degrees of freedom, and mean square		
Multiple regression		1,531 60 3 = 510 53
Deviations		326 26 17 = 19 19
Total		1,857 86 20 = 92 89
Test of multiple regression	F	= 510 53 19 19 = 26 60**
Square of multiple correlation	R^2	= 1,531 60 1,857 86 = 0 82
Parameter estimates and variances		
a, s^2_a		70 355, 533 294
b_1, $s^2_{b_1}$		0 203, 0 001
b_2, $s^2_{b_2}$		21 389, 753 857
b_3, $s^2_{b_3}$		103 012 350 151
Tests of individual regresions		
Pups born	t_1	= 0 203 ÷ 0 001 = 6 42**
Land survival rate	t_2	= 21 389 ÷ 753 857 = 0 78
Ocean survival rate	t_3	= 103 012 ÷ 350 157 = 5 50**

Literature Cited

BARTHOLOMEW, G. A., JR., AND P. G. HOEL.
1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. J. Mammal. 34:417-436.

CHAPMAN, D. G.
1961. Population dynamics of the Alaska fur seal herd. Trans. North Am. Wildl. Nat. Resour. Conf. 26:356-369.
1964. A critical study of Pribilof fur seal population estimates. U.S. Fish Wildl. Serv., Fish. Bull. 63:657-669
1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:325-332.

ICHIHARA, T.
1974. Possible effect of surface wind force on the sex-specific mortality of young fur seals in the eastern Pacific. Bull. Far Seas Fish. Res. Lab. (Shimizu) 11:1-8.

KENYON, K. W., V. B. SCHEFFER, AND D. G. CHAPMAN
1954. A population study of the Alaska fur-seal herd. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl. 12, 77 p.

LANDER, R. H.
1975. Method of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. J. Fish. Res. Board Can. 32:2447-2452.

MARINE MAMMAL BIOLOGICAL LABORATORY.
1971. Fur seal investigations, 1969. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 628, 90 p.

PETERSON, R. S.
1968. Social behavior in pinnipeds with particular reference to the northern fur seal. *In* R. J. Harrison et al. (editors), The behavior and physiology of the pinnipeds, p. 1-53. Appleton-Century-Crofts, N.Y.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SCHEFFER, V. B.
1950. Growth layers on the teeth of Pinnepedia as an indication of age. Science (Wash., D.C.) 112:309-311

ROBERT H. LANDER

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112

NOTICES

NOAA Technical Reports NMFS published during the last 6 mo of 1978.

Circulars

414. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). By Grace Klein-MacPhee. November 1978, iii + 43 p., 21 fig., 28 tables. Also FAO Fisheries Synopsis No. 117.

415. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). By Labbish Ning Chao. September 1978, v + 64 p., 41 fig., 1 table.

416. Ocean variability: Effects on U.S. marine fishery resources - 1975. Julien R. Goulet, Jr. and Elizabeth D. Haynes, editors. December 1978, iii + 350 p.

417. Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the order. By Daniel M. Cohen and Jørgen G. Nielsen. December 1978, vii + 72 p., 103 fig., 2 tables.

418. Annotated bibliography of four Atlantic scombrids: *Scomberomorus brasiliensis*, *S. cavalla*, *S. maculatus*, and *S. regalis*. By Charles S. Manooch III, Eugene L. Nakamura, and Ann Bowman Hall. December 1978, iii + 166 p.

Special Scientific Report—Fisheries

726. The Gulf of Maine temperature structure between Bar Harbor, Maine, and Yarmouth, Nova Scotia, June 1975-November 1976. By Robert J. Pawlowski. December 1978, iii + 10 p., 14 fig., 1 table.

NOAA Technical Reports NMFS are available free in limited numbers to Federal and State government agencies. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies, if available, may be obtained by purchase from the Superintendent of Documents or by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including Zip code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations*. (*Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, °C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Jay C. Quast, Scientific Editor
Fishery Bulletin
Northwest and Alaska Fisheries Center
Auke Bay Laboratory,
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Notes

Notices

GPO 696-364

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Vol. 77, No. 2 April 1979

(Continued on back cover)

Seattle, Washington

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, Room 450, 1107 NE 45th Street, Seattle, WA 98105. Controlled circulation paid to Finance Department, USPS, Washington, DC 20261.

Fishery Bulletin

CONTENTS

Vol. 77, No. 2 April 1979

Notes

(Continued on next page)

Seattle, Washington

1979

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year $12.00 domestic and $15.00 foreign. Cost per single issue $3.00 domestic and $3.75 foreign.

Vol. 77, No. 1 was published on 30 May 1979.

AGGREGATION AND FISHERY DYNAMICS: A THEORETICAL STUDY OF SCHOOLING AND THE PURSE SEINE TUNA FISHERIES[1]

COLIN W. CLARK[2] AND MARC MANGEL[3]

ABSTRACT

This paper describes mathematical models of exploited fish stocks under the assumption that a certain portion of the stock becomes available through a dynamic aggregation process. The surface tuna fishery is used throughout as an example. The effects of aggregation on yield-effort relationships, indices of abundance, and fishery dynamics are discussed. The predictions of the theory are notably different from those obtained from general-production fishery models, particularly in cases where the available substock has a finite saturation level. Possible effects include fishery "catastrophes" and lack of significant correlation between catch-per-unit-effort statistics and stock abundance. Various management implications of the models are also discussed

The relationship between fishing effort, catch rate, and stock abundance is of fundamental importance to the management of commercial fisheries. To a first approximation, it is usually assumed that catch per unit effort (C/E) is proportional to stock abundance (P), with a fixed constant of proportionality (catchability coefficient), q:

$$C = q\,EP, \tag{1}$$

where C denotes catch per unit time and E denotes fishing effort. By combining this relationship with an appropriate model of population dynamics, one obtains a dynamic fishery model which can then be used as a basis for management policy (Schaefer 1957).

The form of Equation (1) is predicated on certain underlying assumptions pertaining to the fishing process, particularly a) that fishing consists of a random search for fish and b) that all fish in the stock are equally likely to be captured. More precisely, by introducing an explicit stochastic model of the fishery based upon such assumptions, one can deduce Equation (1) for the expected catch rate C. But such models can also be employed to investigate the consequences of alternative, and possibly more realistic, assumptions. For example, stochastic models of purse seine fisheries, incorporating detailed descriptions of the operation of fishing vessels, have been discussed by Neyman (1949), Pella (1969), and Pella and Psaropulos (1975). On the other hand, the effects of concentration of fish and of fishing effort have been studied by Calkins (1961), Gulland (1956), and others.

In this paper we discuss fishery models in which the assumption of equal availability of all portions of the stock is relaxed. Specifically, we are concerned with fisheries that exploit aggregations of fish; these aggregations are assumed to constitute a dynamically changing substock of the entire population. Although a general class of such models could be developed, we shall restrict the discussion here to the case of the tuna purse seine fisheries, in which aggregation apparently occurs through the process of surface school formation. Several alternative models of the interchange process between surface and subsurface tuna subpopulations will be presented, and the effects of the surface fishery will be investigated for each model. Evidence arising from studies carried out at the Inter-American Tropical Tuna Commission (Sharp 1978), and at the Southwest Fisheries Center, National Marine Fisheries Service, shows that yellowfin tuna, *Thunnus albacares*, captured in surface schools in the eastern tropical Pacific Ocean do in fact spend part of their time below the surface. Little seems to be known, however, about the dynamics of the interchange process; our analysis of alternative models indicates that such knowledge could become crucial to the management of the fishery.

[1]Research performed under contract to NOAA, National Marine Fisheries Service, Contract No. 03-6-208-35341

[2]Department of Mathematics, University of British Columbia, Vancouver, B.C., Canada V6T 1W5.

[3]Center for Naval Analyses, 1401 Wilson Boulevard, Arlington, VA 22209

Manuscript accepted October 1978.
FISHERY BULLETIN VOL. 77, NO. 2, 1979

Fisheries for various other pelagic, schooling species, such as anchoveta, herring, and mackerel, also appear to involve aggregative processes. Several of these fisheries have in fact experienced collapses which are qualitatively similar to those predicted by our aggregation models.[4] Other mechanisms, however, may be involved in these fisheries, including: predation (Clark 1974); competitive exclusion (Murphy 1966); increased catchability (Fox[5]); depensation in stock-recruitment relationships (Clark 1976). In some cases, stocks have failed to recover following a collapse, even when fishing has been greatly curtailed (Murphy 1977). Dynamic behavior of this kind is not consistent with any of the traditional models employed in fishery management.

On the other hand, discontinuous behavior of continuous nonlinear systems is a well-known phenomenon in applied mathematics. Thus the term "bifurcation" refers to such discontinuous changes induced by continuous parameter shifts in explicit mathematical models. More recently the subject "catastrophe theory" has been developed as an abstract approach to these phenomena (Thom 1975; Zeeman 1975; see also the report in *Science* by Kolata (1977)).

A discussion of catastrophe theory as it applies in the fishery setting appears in Jones and Walters (1976). Indeed these authors assert that ". . . the tropical tuna fisheries have almost certainly moved into a cusp region, . . . where small changes in investment policy or failure to rapidly adjust catch quotas could lead to fishery collapse." (Jones and Walters 1976:2832). Since no specific biological (or technological) catastrophe-inducing mechanism has been suggested by Jones and Walters, their assertion stands only as a plausible conjecture—a warning that possible nonlinear system effects ought to be investigated more fully.

In this paper we shall investigate in some detail the interactions between the schooling behaviour of tuna and the operation of the purse seine fishery. Since current knowledge about the schooling strategy of tuna is limited, we shall construct a variety of models in order to investigate the possible effects of and interactions with the fishery. In particular, we shall discuss the following topics:

1. yield-effort relationships,
2. indices of stock abundance,
3. fishery dynamics,
4. management implications.

The results turn out to be highly, perhaps surprisingly, sensitive to the assumptions and parameters of our models. Of particular importance is the way in which the size of surface tuna schools depends upon the overall abundance of tuna. If it is the case that school size (as unaffected by the fishery) is relatively independent of total tuna abundance, then our models indicate the possibility (under certain additional conditions) of a catastrophic collapse of the tuna fishery as the intensity of fishing passes some critical level. That such a prediction could arise from a potentially biologically realistic tuna model was completely unexpected at the beginning of the study, in spite of the theoretical investigations mentioned above.

Another significant result of our analysis is that, under our model assumptions, the catch-per-unit-effort (CPUE) statistic may constitute an extremely unreliable index of stock abundance. The bias may be in either direction depending on the model adopted—CPUE may severely either underestimate or overestimate the decline in abundance as the fishery develops, while in other cases CPUE may quite accurately represent abundance.

Following the description and analysis of our various models, we shall present some simple simulated development paths for the tuna purse seine fishery, based upon the models. The first simulation that we performed utilized our best guesses as to realistic parameter values. In this simulation the fishery experiences a catastrophic collapse when effort is increased to 18,000 standardized vessel days per annum. The decline of the tuna population itself occurs quite gradually, but is not reflected by any significant decline in catch or in CPUE, until the fishery is virtually destroyed. In other words, the collapse of the fishery involves not an abrupt change in the stock, but rather an abrupt change in the input-output relationship.

TUNA PURSE SEINE FISHERY

The commercial fishery for tuna in the eastern tropical Pacific Ocean began in the years following World War I, the two main species taken being yellowfin tuna and skipjack tuna, *Katsuwonus*

[4]Similar collapses have not occurred in tuna stocks, perhaps because of their relative diffuseness.

[5]Fox, W. W., Jr. 1974. An overview of production modelling. Unpubl. manuscr. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

pelamis. Annual catches in the between-war period rose to a total of about 70,000 short tons. Following World War II "there was a great upsurge in the fishery" (Schaefer 1967:89), which has continued to the present time, see Figure 1. The entire period has also seen a progressive expansion of the fishery into the offshore waters, concomitant with progressive developments in technology. Of particular significance is the switchover from bait boats to purse seiners, which occurred in the early 1960's and has resulted in substantial continuing increases in the catch of yellowfin tuna. Much of this increase has resulted from the offshore fishery on porpoise-associated tuna schools.

The purse seine tuna fishery operates by locating schools of tuna at or near the surface of the sea. The main types of schools encountered are: a) nonporpoise associated schools (pure yellowfin tuna, pure skipjack tuna, or mixed schools) and b) porpoise schools (yellowfin tuna only). Schools of tuna that are not associated with porpoise are sometimes associated instead with concentrations of floating debris ("log schools"). Management of the yellowfin tuna fishery has been complicated by the controversial problem of limiting the incidental kill of porpoise, but this question will not concern us here.

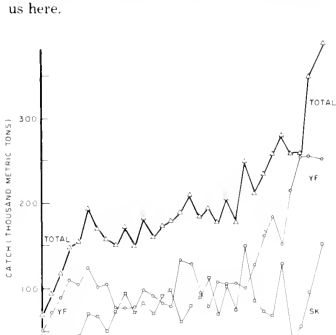


FIGURE 1.—Annual catches of yellowfin (YF) and skipjack (SK) tuna in the eastern tropical Pacific Ocean, 1945-75.

Schools of tuna are normally located by visual search, often by noting the presence of flocks of sea birds. After sighting and approaching a school, the vessel attempts to capture tuna by setting its purse seine net about the school. During a set on porpoise schools, speedboats may be lowered into the water to assist in concentrating the porpoise so that the school can be encircled by the net. Of the daylight hours spent on the fishing grounds, perhaps 70% are spent in searching for schools and 30% on setting of nets.

According to biological observations (Sharp 1978), only a portion of the total tuna population is available to the fishery, as schooled fish, at any given time. It appears that the magnitude of this available portion may be related to environmental conditions, particularly the depth in the ocean of certain thermal isoclines. Furthermore, it seems evident that there must exist a dynamics of school formation and exchange. The fishery interacts with this dynamic process by removing some of the schools. To our knowledge, the implications of such a dynamic availability phenomenon have not been previously investigated in detail.

Since present knowledge about the schooling strategy of tuna is limited, we shall discuss a coterie of submodels for the formation of schools. The models have been chosen in an attempt to "bracket" the possible range of schooling strategies; a wide variety of alternative models could obviously also be set up (see Appendix B).

We next describe a submodel for the purse seine fishery. In order to keep the length of this paper within bounds we discuss only a single fishery submodel, in which vessels search at random for randomly distributed surface schools. Finally we introduce our submodel of tuna population dynamics, which will be the standard Schaefer model. In the main body of the paper we employ the continuous-time version of the Schaefer model, but a discrete-time version will be discussed in Appendix A.

In Appendix B we describe several more detailed models pertaining to the schooling strategy of tuna, using techniques known from chemical kinetics. This approach yields as special cases the two submodels described in the text proper and also gives rise to a number of interesting new details.

Although the background of our schooling and fishery models is stochastic, we concern ourselves only with expected values, so that the analysis remains essentially deterministic. (Explicit

stochastic considerations are taken up in a forthcoming paper by Mangel.[6]) Two important omissions from our models are: a) age structure and b) spatial distribution of the tuna population; the multispecies aspect is also not covered. These omissions were dictated by our desire to concentrate on the novel features of our work, viz the schooling strategy and its implications. Further research will be required (probably based primarily on simulation techniques) if more sophisticated, disaggregated models are to be studied.

SCHOOL FORMATION SUBMODELS

We imagine a given number, K, of school "attractors," such as porpoise schools, or collections of floating debris. (Our models also apply to nonporpoise and nonlog schools provided that the exchange process between subsurface and surface schools satisfies the appropriate hypotheses, see Equations (10).) Tuna from an underlying, or "background," population associate with these attractors according to one of the submodels A or B below; the attractors are independent of one another and do not interchange associated tuna. Let N denote the number of tuna present in the background (subsurface) population. The number of tuna in an individual generic school is denoted by $Q = Q(t)$. (A full list of variables and parameters is given in Table 1.)

TABLE 1.—Basic parameters and variables of the models. Symbols endemic to the appendices are given below.

Item	Meaning	Units of measurement
Parameters		
α	schooling rate per attractor	day $^{-1}$
β	deschooling rate	day $^{-1}$
Q^*	maximum equilibrium school size	tons
b	catchability of attractors	(standard vessel day) $^{-1}$
K	number of attractors	—
χ_0	capture ratio	—
r	intrinsic growth rate	day $^{-1}$
N	carrying capacity	tons
Variables		
Q	school size	tons
t	time	days
N	subsurface tuna population	tons
E	fishing effort	standardized vessels
Y	catch rate	tons × (day $^{-1}$)
S	surface tuna population	tons
S^*	carrying capacity of S	tons
π	net rate of transfer	tons × (day $^{-1}$)
G	growth rate	tons × (day $^{-1}$)
Appendix A Parameters		
T	length of fishing season	days
$\bar{P}$	carrying capacity	tons
g	growth parameter	(day $^{-1}$)
Variables		
R	recruitment	tons
P	escapement	tons
Appendix B Parameters		
γ	number of core schools per complex	—
S_0	weight of core schools	tons
Variables		
T	number of core schools	—
C	number of complexes	—

Model A

Tuna associate with a given attractor at a rate αN proportional to the background population, and dissociate at a rate βQ proportional to the current school size:

$$\frac{dQ}{dt} = \alpha N - \beta Q. \tag{2}$$

(The dissociated tuna return to the background population, see Equation (15).) For fixed N the resulting equilibrium school size Q^* is given by

$$Q^* = \frac{\alpha N}{\beta}. \tag{3}$$

If $Q(0) = Q_0$, Equation (2) has the solution (for fixed N):

$$Q(t) = Q^*\,(1 - c_0 e^{-\beta t}), \tag{4}$$

where $c_0 = 1 - Q_0/Q^*$.

Thus in model A, the equilibrium size of schools is directly proportional to the background tuna population. (Since we treat the number of attractors, K, as fixed, we do not discuss the possibility that school size could also depend on K.)

Model B

In this alternative submodel, we assume that the maximum school size is a constant, Q^*, which is independent of the background tuna population. Equation (2) is replaced by

$$\frac{dQ}{dt} = \alpha N\left(1 - \frac{Q}{Q^*}\right) \tag{5}$$

where Q^* = fixed maximum school size.

Thus we now have (for fixed N)

[6]Mangel, M. 1978. Aggregation, bifurcation, and extinction in exploited animal populations. Cent. Nav. Prof. Pap. 224. Center for Naval Analyses, 1401 Wilson Boulevard, Arlington, VA 22209.

$$Q(t) = Q^* - (Q^* - Q_0)e^{-\alpha Nt/Q^*}. \qquad (6)$$

As will be seen in the sequel, the characteristics of our purse seine fishery model are severely inflenced by the choice of the schooling submodel A or B. Which of these submodels more accurately reflects the actual schooling strategy of tuna is a question we are not qualified to answer.[7] It may be the case that neither extreme (school size Q^* strictly proportional to tuna abundance N in submodel A, and Q^* strictly independent of N in submodel B) is realistic. For example, school size may saturate for large N, but exhibit density dependence at low N, giving rise to a combination of models A and B. Submodels involving more general links between Q^* and N could easily be constructed, but we will not attempt to work through the details here. A more general class of schooling submodels is discussed in detail in Appendix B.

Let us remark here that models A and B assume in effect a uniformly distributed "background" tuna population. The models discussed in Appendix B assume instead that the background population consists of "core" schools; according to Sharp (1978) the latter assumption is more realistic. In certain cases the core-school models reduce to the models A and B described above.

MODEL OF THE PURSE SEINE FISHERY

We shall use a simple Poisson model to describe the process whereby the fishing fleet searches for schools of tuna. The hypotheses underlying this model are well known (see, e.g., Ludwig 1974) and will not be specified here. Let us note, however, that our model pertains to a single type of school (e.g., porpoise school, log school); a more refined model might allow for a random intermingling of school types. A nonrandom distribution of school types, on the other hand, would lead to the as yet unsolved problem of attributing allocation of effort by fishing vessels.

The probability that the fishing fleet locates exactly K school attractors with the expenditure of t days of searching effort, is given by

$$P_k(t) = \frac{(\lambda t)^k}{k!} e^{-\lambda t} \qquad (7)$$

where $\lambda = (a/A)K$

a = area searched per day

A = total area of fishing ground

K = number of school attractors.

If searching effort is properly standardized, we will have

$$a/A = bE,$$

where E = effort

b = a constant.

Hence

$$\lambda = b\,E\,K. \qquad (8)$$

The average number of attractors located by the fleet in time t is

$$\bar{k} = \lambda t = bEKt.$$

Thus the total catch rate of tuna, Y, is given by

$$Y = bEK\chi_0 Q \qquad (9)$$

where χ_0 = capture ratio (average fraction captured when a school is encountered).

Let $S(t)$ denote the total number of tuna present at time t in surface schools: $S = KQ$. Our model then implies that

$$\frac{dS}{dt} = \begin{cases} \alpha KN - \beta S - b\chi_0 ES & \text{(Model A)} \\ \alpha KN(1 - S/S^*) - b\chi_0 ES & \text{(Model B)} \end{cases} \qquad (10)$$

where $S^* = KQ^*$ represents the total "carrying capacity" of the surface school attractors. (Note that, replacing αKN by ρN = flow rate from subsurface to surface populations, we could simply adopt Equation (10) as the basic hypothesis of our model, eliminating any particular assumption regarding the attractive mechanism for surface schools.)

Let us assume for the moment that an equilibrium is achieved rapidly in the surface fishery, relative to adjustments in the underlying population N. (The dynamics of the underlying popula-

[7] Broadhead and Orange (1960) imply that Q^* is nearly constant, although it may in some cases be slightly density dependent. However, for skipjack tuna, in the eastern Pacific, school size and population size as indexed by CPUE are highly correlated (but the two estimates are not independent). J. Joseph, Director of Investigations, Inter-American Tropical Tuna Commission, La Jolla, CA 94720, pers. commun. July 1978.

tion will be modeled below.) Setting $dS/dt = 0$, we obtain the following "catch equations":

$$Y = \begin{cases} \dfrac{b\chi_0 \alpha KEN}{\beta + b\chi_0 E} & \text{(Model A)} \\ \dfrac{b\chi_0 \alpha KQ^*EN}{\alpha N + b\chi_0 Q^* E} & \text{(Model B)} . \end{cases} \quad (11)$$

These equations appear not to be of a standard form, as encountered either in ecology (where Y/N would be termed the "functional response," see Fujii et al.), or in economics (where Y would be termed the "production function" of the fishery, see Clark 1976, sec. 7.6), or in the fisheries literature (Paloheimo and Dickie 1964; Rothschild 1977). This unfamiliarity is perhaps to be expected since, as far as we know, the peculiar "skimming" process of the purse seine fishery has not previously been modeled. Equations (10) are however closely analogous to the Michaelis-Menten equation of enzyme kinetics (White et al. 1973) as might be expected from the observation that the attractors serve to "catalyze" the purse seine fishery, see Appendix B.

Regarding the catch Equations (11), let us observe that both submodels exhibit a saturation effect with respect to fishing effort E, whereas only submodel B exhibits a saturation effect with respect to tuna abundance N. For a fixed background population level N, the catch rate Y bears an asymptotic relationship with fishing effort E. For small E we have, from Equations (11):

$$Y \approx \begin{cases} \dfrac{b\chi_0 \alpha NK}{\beta} E & \text{(Model A)} \\ b\chi_0 Q^* KE & \text{(Model B)} . \end{cases} \quad (12)$$

Since $Q^* = \alpha N/\beta$ in Model A, these expressions are in fact the same for the two submodels, and concur with the standard Schaefer fishery production function. For large E we have

$$\lim_{E \to \infty} Y = \alpha NK = Y_\infty \quad (13)$$

for both submodels. For submodel B we also have (for fixed E)

$$\lim_{N \to \infty} Y = b\chi_0 KQ^*E \quad \text{(Model B)}. \quad (14)$$

FISHERY DYNAMICS

As our submodel of population dynamics of the subsurface tuna population, we adopt the familiar Schaefer logistic model (Schaefer 1957):

$$\frac{dN}{dt} = rN(1 - N/\bar{N}) - \theta \quad (15)$$

where r = intrinsic growth rate
$\bar{N}$ = environmental carrying capacity
θ = net rate of transfer to the surface population.

The net rate of transfer, θ, is obtained from Equations (2) and (5):

$$\theta = \begin{cases} \alpha NK - \beta S & \text{(Model A)} \\ \alpha NK(1 - S/S^*) & \text{(Model B)}. \end{cases} \quad (16)$$

Our dynamic models of the surface tuna fishery then consist of the simultaneous system of Equations (10) and (15). For convenience we rewrite the two systems as follows:

$$\text{Model A:} \quad \left.\begin{aligned} \frac{dS}{dt} &= \alpha KN - \beta S - b\chi_0 ES \\ \frac{dN}{dt} &= G(N) - (\alpha KN - \beta S) \end{aligned}\right\} \quad (17)$$

$$\text{Model B:} \quad \left.\begin{aligned} \frac{dS}{dt} &= \alpha KN(1 - S/S^*) - b\chi_0 ES \\ \frac{dN}{dt} &= G(N) - \alpha KN(1 - S/S^*) \end{aligned}\right\} \quad (18)$$

where $G(N) = rN(1 - N/\bar{N})$. (19)

Although the difference between these two models may appear minor, their qualitative behavior turns out to be quite dissimilar. Their behavior is also quite different from the standard Schaefer model (Schaefer 1957). As indicated by results discussed in the appendices, however, the qualitative behavior of the above models seems to be characteristic of a wide variety of alternative

*Fujii, K., P. M. Mace, and C. S. Holling. 1978. A simple generalized model of attack by predator. Unpubl. manuscr., 39 p. University of British Columbia, Institute of Animal Resource Ecology, Vancouver, B.C., Canada V6T 1W5.

models of both population dynamics and the school-formation process. We next discuss the behavior of our models in detail.

Model A

Figure 2(a) and (b) show the system of solution trajectories $(N(t), S(t))$ for the Equation system (17), for the two cases

$$\alpha K < r \text{ and } \alpha K > r$$

respectively. The system has a unique stable equilibrium at the point (N_∞, S_∞); the corresponding sustained yield from the fishery is given by

$$Y = b\chi_0 E S_\infty.$$

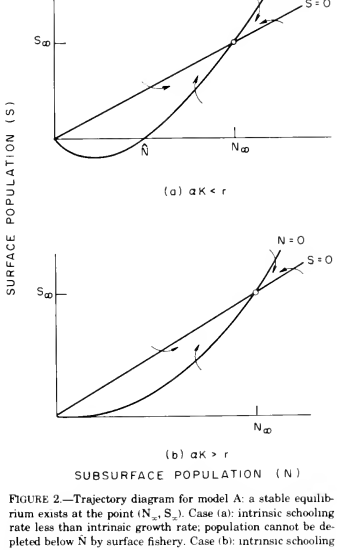


FIGURE 2.—Trajectory diagram for model A: a stable equilibrium exists at the point (N_∞, S_∞). Case (a): intrinsic schooling rate less than intrinsic growth rate; population cannot be depleted below $\hat{N}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate; population can theoretically be fished to arbitrarily low levels (see also Figure 3).

In these Figures, the effect of an increase in the effort parameter E is to rotate the isocline $\dot{S} = 0$ in a clockwise direction, thus decreasing both population levels N_∞ and S_∞. The corresponding yield-effort curves are shown in Figure 3(a) and (b) respectively.

The shape of these yield curves is easily explained. Note from Equations (16) that the constant

$$\rho = \alpha K$$

represents the maximum net rate at which the subsurface population N aggregates to the surface; this may be referred to as the "intrinsic aggregation rate" (or "intrinsic schooling rate" in the present model). If the intrinsic aggregation rate ρ is less than the intrinsic growth rate r (see Figures 2(a), 3(a)), then the population cannot be exhausted by the surface fishery; in this case $N \to \hat{N} > 0$ and $Y \to \hat{Y} > 0$ as effort $E \to \infty$. (Figure 3(a) shows yield increasing to a maximum level and then declining as effort increases. This situation arises if $\hat{N} < \bar{N}/2$, i.e., if $\rho > r/2$; otherwise, Y simply increases to an asymptotic value $\hat{Y}$.)

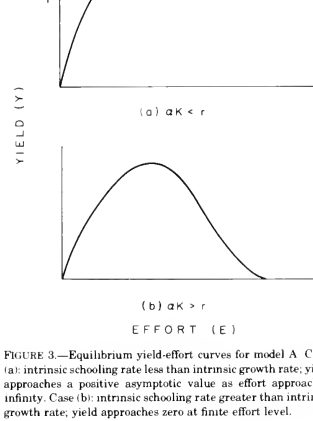


FIGURE 3.—Equilibrium yield-effort curves for model A. Case (a): intrinsic schooling rate less than intrinsic growth rate; yield approaches a positive asymptotic value as effort approaches infinity. Case (b): intrinsic schooling rate greater than intrinsic growth rate; yield approaches zero at finite effort level.

On the other hand, if $\rho > r$ (Figures 2(b), 3(b)) then exhaustion is possible at sufficiently high levels of effort. This case is similar to the Schaefer model.

For model A, CPUE is a seriously biased index of total stock abundance. The instantaneous CPUE is, of course, simply an index of abundance for the surface population. Sustained CPUE progressively overestimates the decline in abundance at high levels of effort. Conversely, particularly if the aggregation rate is large, CPUE may underestimate the decline in abundance at intermediate levels of effort. It is clear in general that no simple transformation of the CPUE index can provide an unbiased estimator of abundance, for this model. Any fishery exploiting a substock of a biological population necessarily provides only partial information concerning total abundance; in the event that the fishery itself affects the relationship between the substocks, the interpretation of a time series of catch-effort data becomes extremely difficult.

To summarize, if the present model realistically represents the process of aggregation (via surface schooling) of tuna, then CPUE data may ultimately overestimate the decline in abundance of tuna. Management policy based on such data may then be unduly restrictive. The situation may be very different, however, if model B is the more realistic representation. We now turn to this case.

Model B

The solution trajectories of Equations (18) are illustrated in Figure 4(a) and (b), again corresponding to the cases $\alpha K < r$ and $\alpha K > r$ respectively. The corresponding yield-effort curves are shown in Figure 5.

In case (a), $\alpha K < r$, the system has a unique stable equilibrium (N_∞, S_∞). As in model A, we have $N_\infty \to \bar{N} > 0$ as $E \to +\infty$. The yield-effort curve for this case has the same shape as for model A.

A new phenomenon arises, however, in the case that $\alpha K > r$. For small E (see Figure 4(b)) there now exist two stable equilibria, at (N_∞, S_∞) and at (0,0), separated by a point of unstable equilibrium. As E increases, the stable and unstable equilibria coalesce and then disappear, leaving only the stable equilibrium at (0,0). In mathematical terminology, the Equation system (18) undergoes a "bifurcation" at the critical effort level $E = E_c$ where the two equilibria coalesce. The graph of systainable yield vs. effort (Figure 5(b)) becomes

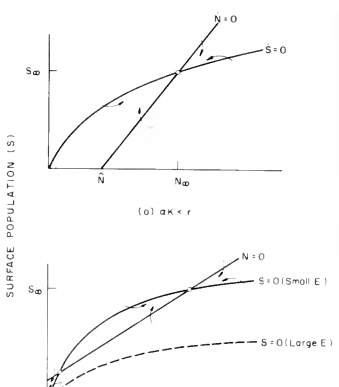


FIGURE 4.—Trajectory diagrams for model B: a stable equilibrium exists at point (N_∞, S_∞); in diagram (b) an unstable equilibrium also exists for small E, but both equilibria disappear for large E. Case (a): intrinsic schooling rate less than intrinsic growth rate; population cannot be depleted below $\bar{N}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate population can theoretecally be shed to arbitrarily low levels; the transition from $N = \bar{N}$ to $N = 0$ is "catastrophic"; see also text and Figure 5(b).

multivalued for this case. Model B exhibits an explicit mathematical "catastrophe."

The significance of multivalued yield-effort curves for fishery management has been discussed by Clark (1974, 1976); see also Anderson (1977). As effort E expands from a low level, the catch follows the upper stable branch (Figure 5(b)), possibly with some lag. But once E exceeds the critical level E_c, sustainable yield drops discontinuously to zero and the fish population goes into a steady decline. Subsequent decreases in effort do not necessarily result in recovery of the fishery, which may become "trapped" at a position of low abundance. This behavior is characteristic of the "catastrophe" situation (here the so-called "fold" catastrophe (Zeeman 1975)). In general, once a catastrophic jump has occurred, a large-scale change in the control variable (effort) is required

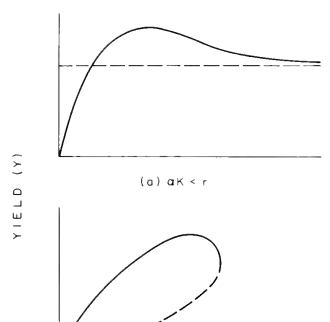


FIGURE 5.—Equilibrium yield-effort curves for model B. Case (a): intrinsic schooling rate less than intrinsic growth rate; yield approaches a positive asymptotic value as effort approaches infinity. Case (b): intrinsic schooling rate greater than intrinsic growth rate; yield undergoes a catastrophic transition when effort exceeds critical level E_c.

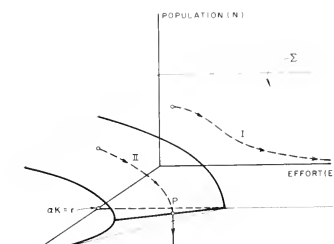


FIGURE 6.—Catastrophic surface (Σ) corresponding to model B. This surface describes the equilibrium population level (N) as a function of effort (E) and intrinsic schooling rate (αK). Path I represents the development of the fishery, as effort increases, in the case that $\alpha K < r$, while Path II corresponds to the case $\alpha K > r$. In the latter case the fishery experiences a catastrophic collapse at point P.

in order to return the system to the original stable equilibrium.

The behavior of our model (submodel B) can be described in terms of Figure 6, in which the horizontal plane represents the "control space," with effort E as the basic control and intrinsic schooling rate αK as a parameter (which in some cases might also be subject to manipulation, or to stochastic variation). The vertical axis represents subsurface stock size N. The surface Σ is the locus of equilibrium solutions for our model.

Two possible paths for the development of the fishery are also shown in Figure 6. (Simulated versions of these paths will be presented below.) Path I, corresponding to Figure 5(a), occurs if $\alpha K < r$; here there is a steady decline in the equilibrium population level $N = \hat{N}$ as the effort parameter increases. (If E varies rapidly over time, then equilibrium conditions will not prevail, and the actual development path will diverge from Path I lying on Σ. Figure 6 is still useful for understanding the dynamics in this case, however.)

Path II, with $\alpha K > r$, behaves similarly to Path I for small levels of effort, but then suddenly falls over the "edge" of the catastrophe surface Σ, at point P. (Notice that for $\alpha K > r$ the surface Σ folds under itself, the upper sheet $N = \hat{N}$ and the lower sheet $N = 0$ being stable equilibria, while the middle sheet $N = N^{\dagger}$ is unstable. This surface shape is the typical "cusp" catastrophe of Thom 1975.)

The management implications of the theory will be discussed later; the question of robustness of the models will be taken up in the appendices.

Figure 6 stresses the significance of the parameter $\rho = \alpha K$ for the interactive dynamics of aggregation and fishing. For tuna, ρ may be age-dependent, as suggested by the differences in age distribution between longline and purse seine catches. Also, as noted previously, ρ may vary over time and space as a result of environmental gradients. The theoretical consequences of such complexities have yet to be investigated (Mangel see footnote 6).

A "cusp" catastrophe surface similar to that depicted in Figure 6 can also be used to describe the response of the tuna fishery to simultaneous exploitation of the surface schools and the subsurface (background) population. If a given level of fishing mortality f_s is applied to the subsurface population, the effect will be to replace our dynamic Equation (15) by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - f_s N - \theta$$

$$= (r - f_s) N \left(1 - \frac{r}{r - f_s}\frac{N}{K}\right) - \theta.$$

Thus the net biological growth rate becomes $r - f_s$ and the condition for catastrophic behavior in submodel B becomes

$$\alpha K > r - f_s.$$

If we now consider effort E in the surface fishery and mortality f_s in the subsurface fishery as control variables (now assuming αK = constant), it is clear that the surface of equilibrium N-values has the same nature as shown in Figure 6. Thus while the surface fishery might be "subcatastrophic" in the absence of any subsurface fishery, the development of the latter might transform the system into a catastrophic region.

One further possibility is worth noting. As remarked earlier, the schooling behavior of tuna may be influenced by environmental factors, particularly the depth of certain thermal isoclines. If so, the system might switch randomly between catastrophic and noncatastrophic states. Under these circumstances the fishery might exist for sometime at a level of stable sustained yield, but could suffer a catastrophic collapse induced by unusual, or unusually protracted environmental conditions.

The practical importance of these possibilities is increased by the fact that CPUE is likely severely to misrepresent the decline in abundance of the tuna population. In the first simulation reported below, for example (Figure 7), CPUE falls by only 20% even though the tuna population declines by over 99%.

A SIMULATED CATASTROPHE

Figures 7 and 8 show the outcome of two simulations based on submodel B. (These simulations employed the discrete-time version of the population-dynamics submodel, as described in Appendix A. Qualitatively the results are the same as for the continuous-time model.) The following parameter values were utilized:

K = 5,000 attractors
χ_0 = 0.5

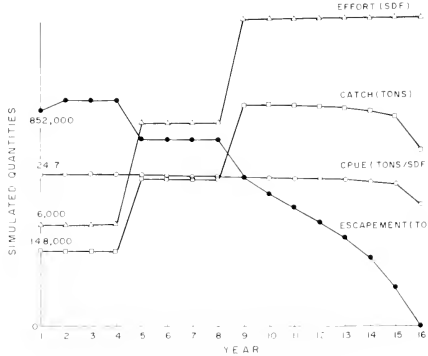


FIGURE 7.—Simulation results—model B, "catastrophic" case. Effort (measured in standardized days fishing (SDF)) is increased at years 1, 5, and 9. The final effort level produces a catastrophic but gradual decline in the tuna population, which is not "picked up" by the catch-per-unit-effort (CPUE) index until the population has been essentially eliminated. (Scales for the four curves are linear but not related, see initial values shown.)

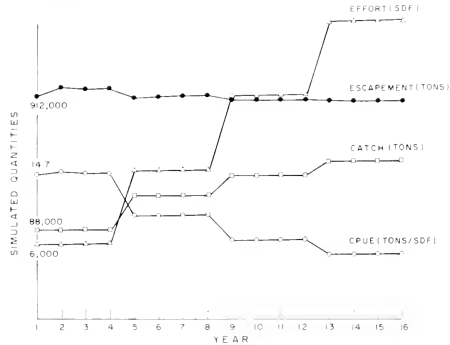


FIGURE 8.—Simulation results: Model B, noncatastrophic case. In this case, CPUE (catch per unit effort) seriously overestimates the decline in tuna abundance. SDF = standardized days fishing.

$$Q = 50 \text{ tons}$$
$$b = 2 \times 10^{-4} \text{ per vessel day}$$
$$r_0 = 1.5 \text{ per annum}$$
$$N = 10^6 \text{ tons.}$$

In the first simulation (Figure 7) we set $\alpha = 10^{-5}$, implying an intrinsic schooling rate of 5% per day. Since this is well in excess of the intrinsic growth rate of 0.1% per day, a catastrophe is observed. In the second simulation (Figure 8) we set $\alpha = 1.5 \cdot 10^{-7}$, implying an intrinsic schooling rate of 0.075% per day, which is below the intrinsic growth rate.

In Figure 7, effort is fixed at 6,000 vessel days for years 1-4, then 12,000 vessel days for years 5-8, and finally 18,000 vessel days for all later years. The escapement population stabilizes at about 890,000 tons by year 4, and stabilizes again at about 735,000 tons by year 8. However in years 9-17 the effort level is above $E_s \cong 15{,}000$ vessel days, and the population is steadily reduced, ultimately to a level $\cdot$ 100 tons. Although the population decline itself occurs gradually, neither catch nor CPUE shows any marked decline until the tuna population has crashed. For example, the decline in catch (and CPUE) in year 14 is 2.5% relative to the level for year 1, and in year 15 is 5.4% relative to the same level. Even in year 16, when the tuna population is virtually destroyed, the catch (and CPUE) falls by only 20%.

The same effort profile was used in the simulation shown in Figure 8, except for an additional increase in effort at year 12. In this simulation, CPUE declines significantly, but the population level is only slightly reduced. The biological explanation lies in the low rate of schooling in comparison with the first simulation. Because of this low schooling rate, increased effort mainly has the effect of reducing the surface population, and (at the levels shown here) has little effect on the subsurface population. This also explains why CPUE is much lower, at any fixed E, than in the first simulation.

Finally, Figure 9 shows the results of a simulation based on submodel A, using the same parameter values as for Figure 7. This simulation indicates that, as expected, submodel A behaves quite similarly to traditional fishery models.

MANAGEMENT IMPLICATIONS

The models described above, and in the appendices, indicate that traditional methods of fishery management may be inappropriate in cases where aggregation processes significantly affect the fishery. On the one hand, such processes may be the source of bias in CPUE indices of stock abundance. On the other hand, these processes may also lead to a catastrophic relationship between fishing effort and sustainable yield. The latter situation will be especially serious in the event that CPUE underestimates declines in abundance.

In addressing the management implications of

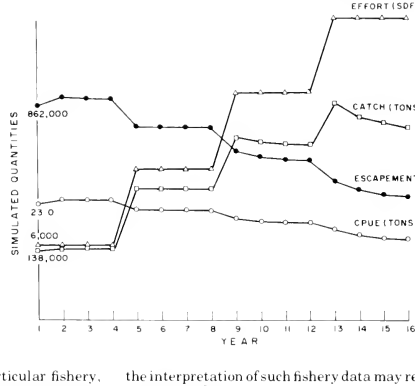


FIGURE 9.—Simulation results. Model A. The behavior of the model is similar to that of traditional fishery models. SDF = standardized days fishing, CPUE = catch per unit effort.

these theoretical results, for a particular fishery, we face two main problems. First, what is the likelihood that the fishery in question does involve an aggregation process, and if so, that catastrophic conditions may prevail? (We remark again that catastrophic conditions may be the result of processes other than aggregation.) Secondly, given that such conditions may exist, what are the implications for management policy?

If an aggregation process is known to exist, our models suggest that the next question that ought to be addressed is whether aggregation is density dependent, and if so, to what extent it depends on population abundance? Also, the rate parameters of the process should be determined. Unfortunately this information may be extremely difficult to obtain, and the question arises whether inferences can be drawn from data supplied by the fishery, such as catch-effort data, school size, density of schools, size composition of catches, and so on.

For example, if aggregation is density dependent, then the size of the aggregated (surface) population will decrease with the size of the residual (subsurface) population. For the case of tuna, either the number or the size of schools (or both) should decrease as the fishery develops. But the converse implication cannot be made: school size and/or number may decrease merely because the surface population is reduced by fishing pressure. Unless a direct, independent abundance estimate of the subsurface population is available, the interpretation of such fishery data may remain ambiguous.[9]

The possibility that aggregation may lead to catastrophic yield-effort relationships lends a sense of urgency to the question of achieving a fuller understanding of the dynamics of the aggregation process. But whenever such catastrophic relationships seem possible, for whatever reason, a conservative approach to management appears appropriate. In view of the uncertainties involved, quotas should probably be established at a level lower than the estimated maximum sustainable yield. Furthermore, since depletion may nevertheless occur unexpectedly, emphasis should be placed on achieving a high degree of controllability of the fishery. To a certain extent this necessity has been recognized by the Inter-American Tropical Tuna Commission, the Director of Investigations now being empowered to close the yellowfin tuna fishery in the event of a sharp decline in CPUE. However, if the decline were truly "catastrophic," more drastic measures, such as a moratorium of some duration, might become necessary. Although the possibility may seem remote at present, we feel that further attention

[9]Various alternative indicators of depletion, involving size composition of the catch and the results of cohort analysis, are in fact employed by the Tuna Commission and have demonstrated no severe change that can be attributed to the fishery. The validity of such indicators should not be affected by the presence of an aggregation process, but we have not attempted to extend our model to include cohort structure.

needs to be given to these problems. Experience gained from other fishery failures suggests that control may be extremely difficult to achieve unless expansion of the fishing industry is kept under control. For domestic fisheries operating within 200-mi zones, such control is now a possibility. For international pelagic fisheries, such as the tropical tuna fisheries, however, the problem of entry limitation remains unresolved.

ACKNOWLEDGMENTS

This research was performed under contract to Southwest Fisheries Center, National Marine Fisheries Service, under contract number 03-6-208-35341.

For valuable discussions and correspondence about the tuna fisheries we are indebted to many people, including particularly Robin Allen, William Fox, Robert Francis, Paul Greenblatt, John Gulland, Daniel Huppert, James Joseph, Peter Larkin, William Perrin, Gary Sakagawa, Gary Sharp, Carl Walters, and Norman Wilimovsky. Responsibility for errors and expressed opinions, however, lies solely with the authors.

LITERATURE CITED

ANDERSON, L. G.
1977. The economics of fisheries management. The Johns Hopkins Univ. Press, Baltimore, Md., 214 p.

ARONSON, D., AND H. WEINBERGER.
1975. Nonlinear diffusion in population genetics, combustion and nerve pulse propagation. *In* J. A. Goldstein (editor), Partial differential equations and related topics, p. 5-49. Lecture notes in mathematics 466. Springer-Verlag, N.Y.

BROADHEAD, G. C., AND C. J. ORANGE.
1960. Species and size relationships within schools of yellowfin and skipjack tuna, as indicated by catches in the Eastern Tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 4:447-492.

CALKINS, T. P.
1961. Measures of population density and concentration of fishing effort for yellowfin and skipjack tuna in the Eastern Tropical Pacific Ocean, 1951-1959. Inter-Am. Trop. Tuna Comm., Bull. 6:69-152.

CLARK, C. W.
1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. 36:7-14.
1976. Mathematical bioeconomics: The optimal management of renewable resources. Wiley-Interscience, N.Y., 352 p.

GULLAND, J. A.
1956. The study of fish populations by the analysis of commercial catches. Cons. Perm. Int. Explor. Mer Rapp. P.-V. 140:21-27.

JONES, D. D., AND C. J. WALTERS.
1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33:2829-2833.

KOLATA, G. B.
1977. Catastrophe theory: the emperor has no clothes. Science (Wash., D.C.) 196:287, 350-351.

LUDWIG, D.
1974. Stochastic population theories. Lecture notes in biomathematics 3. Springer-Verlag, N.Y., 108 p.

MAY, R. M.
1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science (Wash., D.C.) 186:645-647.

MOORE, W.
1972. Physical chemistry. Prentice-Hall, Englewood Cliffs, N.J., 977 p.

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci., Ser. 4, 34:1-84.
1977. Clupeoids. *In* J. A. Gulland (editor), Fish population dynamics, p. 283-308. Wiley, N.Y.

NEYMAN, J.
1949. On the problem of estimating the number of schools of fish. Univ. Calif. Publ. Stat. 1:21-36.

PALOHEIMO, J. E., AND L. M. DICKIE.
1964. Abundance and fishing success. Cons. Perm. Int. Explor. Mer Rapp. P.-V. 155:152-163.

PELLA, J. J.
1969. A stochastic model for purse seining in a two-species fishery. J. Theoret. Biol. 22:209-226.

PELLA, J. J., AND C. T. PSAROPULOS.
1975. Measures of tuna abundance from purse-seine operations in the eastern Pacific Ocean, adjusted for fleet-wide evolution of increased fishing power, 1960-1971. Inter-Am. Trop. Tuna Comm., Bull. 16:281-400.

ROTHSCHILD, B. J.
1977. Fishing effort. *In* J. A. Gulland (editor), Fish population dynamics, p. 96-115. Wiley, N.Y.

SCHAEFER, M. B.
1957. A study of the dynamics of the fishery for yellowfin tuna in the Eastern Tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 2:245-285.
1967. Fishery dynamics and present status of the yellowfin tuna population of the Eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 12:87-137.

SHARP, G. D.
1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas. Academic Press, N.Y.

THOM, R.
1975. Structural stability and morphogenesis. Benjamin, Inc. Reading, Mass., 348 p.

WHITE, A., P. HANDLER, AND E. L. SMITH.
1973. Principles of biochemistry. McGraw-Hill, N.Y., 1296 p.

ZEEMAN, E. C.
1975. Levels of structure in catastrophe theory illustrated by applications in the social and biological sciences. Proc. Int. Congr. Math., Vancouver, B.C., p. 533-546.

APPENDIX A

The purpose of these appendices is to test the robustness of our models, by introducing alternative submodels for population dynamics (Appendix A) and for the schooling process (Appendix B). In this appendix we replace the continuous-time Schaefer model by a discrete-time stock-recruitment model. We postulate a fishing season of given length, during which the stock is fished down, followed by an interim season which results in the replenishment of the stock. The purpose of this exercise is not particularly to provide a more realistic model of tuna population dynamics, but simply to enquire whether our main results are independent of the type of model employed. (See Clark 1976, chapter 7, for a general discussion of models of the sort considered here.)

Our alternative Model A is governed by the equations

$$\left.\begin{aligned}\frac{dS}{dt} &= \alpha KN - \beta S - bY_0 ES\\ \frac{dN}{dt} &= -(\alpha KN - \beta S)\end{aligned}\right\} \quad 0 \le t \le T \qquad \text{(A1)}$$

$$N(0) = R,\ S(0) = \alpha KR/\beta \qquad \text{(A2)}$$

where R denotes recruitment prior to the fishing season, and T denotes the length of the fishing season. In Equation (A2) we also assume, for simplicity, that the surface population S reaches equilibrium with N before the fishing season begins.

Let $P = N(T)$ denote escapement at the close of the fishing season. From the linearity of Equations (A1) it follows that P is a linear function of $R = N(0)$:

$$P = C_E \cdot R \qquad (C_E = \text{constant} < 1). \qquad \text{(A3)}$$

Clearly C_E is a decreasing function of E; it is easily seen that

$$\lim_{E \to \infty} C_E = \exp(-\alpha KT). \qquad \text{(A4)}$$

If $G(P)$ now denotes the stock-recruitment function, the coupling between successive years is given by the equations

$$\left.\begin{aligned}R_{t+1} &= G(P_t)\\ P_t &= C_E R_t\end{aligned}\right\}. \qquad \text{(A5)}$$

If, for example, $G(P)$ is quadratic:

$$G(P) = gP(1 - P/\bar{P}), \qquad \text{(A6)}$$

the equilibrium escapement level P_* is easily calculated:

$$P_* = \begin{cases} \bar{P}(1 - 1/gC_E) & \text{if } gC_E > 1\\ 0 & \text{if } gC_E \le 1.\end{cases}$$

Exhaustion of the stock by the surface fishery is thus possible if and only if

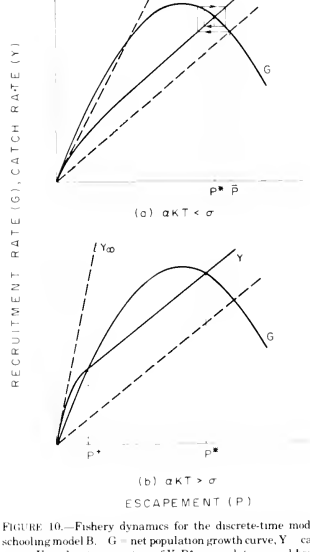


FIGURE 10.—Fishery dynamics for the discrete-time models; schooling model B. G = net population growth curve, Y = catch curve, Y_∞ = limiting position of Y, P^* = population equilibrium for given Y. Case (a): intrinsic schooling rate less than intrinsic growth rate, escapement population cannot be reduced below level $\bar{P}$ by surface fishery. Case (b): intrinsic schooling rate greater than intrinsic growth rate; population can be fished to arbitrarily low levels; P^* denotes an unstable equilibrium. (The corresponding yield-effort curve is similar to Figure 5(b).)

$$\exp(\alpha KT) > g,$$

i.e., if and only if the intrinsic schooling rate (over the duration of the fishing season) exceeds the intrinsic growth rate.

It is also clear that the yield-effort curves for this model have the same appearance as in Figure 3. Hence the behavior of the two models is closely analogous; bifurcations do not arise.

The discrete-time version of model B is obtained by replacing the expression $(\alpha KN - \beta S)$ in Equation (A1) by $\alpha KN(1 - S/S_0)$. This gives rise to a nonlinear escapement-recruitment relationship

$$P = \Psi_E(R).$$

It can be shown (we omit details) that

$$\lim_{R \to 0} \Psi_E'(R) = \exp(-\alpha KT)$$

$$\lim_{E \to \infty} \Psi_E(R) = \exp(-\alpha KT) \cdot R$$

$$\lim_{R \to \infty} (R - \Psi_E(R)) = b\Omega_0 S^* TE.$$

The resulting dynamics can be described in terms of Figure 10. If $\alpha KT - \sigma = \ln g$ the model is noncatastrophic (Figure 10(a)), having a single equilibrium P^* (escapement) which approaches $P^* = 0$ as $E \to +\infty$. (If $g = 2$ the equilibrium at P^* may be unstable, even "chaotic," for small E (May 1974), but this possibility will not concern us here.) But if $\alpha KT - \sigma$ a second, unstable, equilibrium P^* emerges, and a bifurcation occurs at some critical effort level $E = E_c$.

To summarize, this appendix has demonstrated that the qualitative predictions of our schooling strategy models are independent of the basic population dynamics of the tuna population. Although we have explicitly established this fact only for two specific models, it should be clear that the theory will remain valid for a large variety of other models, including alternative forms of the growth and stock-recruitment functions and including delayed-recruitment models as well as cohort models. In all cases, the nature of yield-effort curves will depend critically upon a) the relationship between intrinsic schooling rate and biotic potential and b) the schooling strategy of tuna to the extent that school size is sensitive to the total tuna population.

APPENDIX B

In this appendix, we present two detailed, kinetic models of the schooling behavior of tuna and tuna-porpoise complex formation. The models are more general that either model A or model B, which are in fact special cases of the models developed in this appendix. Since our basic assumptions are quite different from those used in the body of the paper, it is interesting that equivalent results can be obtained, at least in special cases.

The models are based on the following assumption: in some large area of ocean, Ω, there are $T(t)$ core tuna schools and $K(t)$ "attractors" (porpoise schools or logs) at time t. We assume that the core schools move independently of each other and that the motion is random.

We first assume that when an attractor and γ ($\gamma \geq 1$) tuna schools "collide" (i.e., come within some critical distance), a tuna-attractor complex is formed. Let $C(t)$ denote the number of tuna-attractor complexes at time t. The fishery is assumed to fish only on these complexes. We shall postulate different mechanisms of complex formation and analyze the resulting kinetic equations. The kinetic equations are derived assuming a law of "mass action" similar to the one used in chemical kinetics (Moore 1972).

We shall not consider the mechanism by which the core tuna schools are formed. Whenever it is necessary for the analysis, we shall assume that the number of core schools has a logistic growth function. This assumption is derived by firstly assuming that the biomass of tuna, $N(t)$, has a logistic growth function. Namely, if no fishing occurred and no complexes formed:

$$\frac{dN}{dt} = rN(1 - N/N_0) \tag{B1}$$

where N_0 is the carrying capacity of Ω, in terms of biomass of tuna. Let S_0 denote the weight of a core school. Then we have

$$\frac{dT}{dt} = rT(1 - T/T_0) \tag{B2}$$

where $T(t) = N(t)/S_0$ is the number of core schools at time t.

A model in which the tuna-attractor complex is formed by one collision between γ tuna schools and one attractor is first analyzed. Submodel A of the paper is a special case of this model. We show that

the harvest rate is a nonlinear function of effort and saturates as $E \to \infty$. Consequently Y/E is not a valid biomass estimate. We discuss other possible biomass indices, the behavior of $T(t, E)$ as a function of effort and the sensitivity of the results to the parameters which appear in the kinetic equations.

Next, a multistep complex formation process is considered. A two-step model is analyzed in full detail. Submodel B is contained as a special case. In addition to exhibiting all of the features of the one-step model a multistep mechanism may lead to "catastrophic" behavior. The catastrophic behavior was not built into the model but arises naturally from the dynamics.

The models presented in this appendix (particularly the multistep model) are based on what appear to be reasonable assumptions about the schooling behavior of tuna and formation of the complexes.

The ultimate behavior of the system (fishery + tuna + porpoises) does not appear to be an artifact of the models, but a result of the basic assumptions that the tuna form into schools and that the fishery seeks tuna schools associated with attractors. In fact, Thom's (1975) theorem on the structural stability (robustness) of unfoldings asserts that small modifications of our models will not alter the qualitative behavior.

The analysis of discrete-time versions of our models is relatively intractable. Numerical studies are underway. We do not expect the results will be qualitatively different from the continuous-time results. The analysis presented in Appendix A supports this expectation.

We have not included spatial effects (e.g., diffusion) in our kinetic equations. The addition of diffusion greatly complicates the analysis of the kinetic equations. However, preliminary work based on the recent theory of Aronson and Weinberger (1975) has been carried out, treating the kinetic equations with spatial dependence. We expect that if diffusion is added to the models in this appendix, the transitions between high and low tuna steady states may occur at effort levels lower than those predicted by the models without diffusion.

Single-Step Collision Model

In this model we assume that γ tuna schools collide, at once, with one attractor to form a complex:

$$K + \gamma T \underset{\beta}{\overset{\alpha}{\rightleftharpoons}} C, \tag{B3}$$

The rate constants α, β measure the association and dissociation rates of the complex. The complexes are fished at a rate bE with capture ratio χ_0:

$$C \xrightarrow{\chi_0 bE} K + \text{harvest of } \gamma \text{ schools}. \tag{B4}$$

Equation (B3) indicates that γ schools must be present for a complex to form. In particular, if $\gamma = 1$ this model does not allow for the formation of "partial" complexes, with fewer than γ tuna schools in the complex. It is clear that this assumption is restrictive; later we relax it and allow for complexes with $1, 2, \ldots, \gamma$ tuna schools.

The kinetic equations corresponding to Equations (B3) and (B4) are

$$\dot{T} = g_T - \alpha K T^{\gamma} + \beta \gamma C \tag{B5}$$

$$\dot{K} = g_K - \alpha K T^{\gamma} + \beta C + bE\chi_0 C \tag{B6}$$

$$\dot{C} = \alpha K T^{\gamma} - \beta C - bE\chi_0 C; \tag{B7}$$

in Equations (B5) and (B6) g_T and g_K are the tuna and attractor growth functions, respectively ($g_K = 0$ for logs).

The term proportional to T^{γ} arises in the following way. Consider a small area of ocean, a. The probability, p, that a tuna school is in a should be proportional to a/Ω and to T:

$$p = k\frac{a}{\Omega} \cdot T = \tilde{k}T. \tag{B8}$$

If a complex containing γ tuna schools is to form, γ schools must be in a. Since the tuna schools move independently and randomly, the probability of finding γ schools in a is proportional to $p^{\gamma} = k^{\gamma}T^{\gamma}$. (A more precise analysis would lead to $\tilde{k}T(T-1)(T-2)\ldots(T-\gamma+1)$ instead of $\tilde{k}T^{\gamma}$, since once a school is in a specified area of ocean, there remain $T-1$ schools to be distributed over the ocean. Once the location of two schools has been specified, there remain $T-2$ schools, etc. When T is large, as we are assuming, $\tilde{k}T^{\gamma}$ is a good approximation to the exact expression.)

The steady-state number of complexes is determined by setting $\dot{C} = 0$. We obtain

$$C = \frac{\alpha K T^{\gamma}}{\beta + bE\chi_0}. \tag{B9}$$

The instantaneous rate of harvest, Y, is the product of (the number of complexes) × (the encounter rate bE) × (the capture ratio χ_0) × (the number of schools per complex). Thus

$$Y = \frac{bE\chi_0\alpha KT^{\gamma}S_0}{\beta + bE\chi_0}. \qquad \text{(B10)}$$

If $\gamma = 1$, Equation (B10) becomes

$$Y = \frac{bE\chi_0\alpha KTS_0}{\beta + bE\chi_0} \qquad \text{(B11)}$$

which is, with the exception of S_0, identical to Equation (11A). The additional factor S_0 arises here because we are considering numbers of tuna schools, whereas model A of the main part works directly with tuna biomass.

Model A is thus a subcase of the model in this section. Hence, we have provided a second physical picture for the mechanism which generates model A used in the paper.

Equation (B11) exhibits a saturation as E increases and is similar to results obtained in the Michaelis-Menten approach to enzyme kinetics (White et al. 1973). This is not unexpected, since our models are based on the assumption that the attractors "catalyze" the fishery.

The tuna and attractor steady states are determined from the steady-state versions of Equations (B5) and (B6). Adding Equations (B6) and (B7) gives

$$g_K = 0, \qquad \text{(B12)}$$

which we assume has a solution $K = K_*$. (Note that this model does not allow for the loss of attractors due to fishing.) The steady-state tuna population satisfies

$$0 = g_T - \alpha KT^{\gamma} + \beta\gamma\left[\frac{\alpha KT^{\gamma}}{\beta + bE\chi_0}\right] \qquad \text{(B13)}$$

or

$$g_T = \alpha KT^{\gamma}\left[\frac{bE\chi_0 - \beta(\gamma - 1)}{\beta + bE\chi_0}\right]$$

$$= \alpha KT^{\gamma} f(E,\gamma). \qquad \text{(B14)}$$

Since the case in which $\gamma = 1$ was analyzed in the body of the paper, we shall not consider that case here. We shall briefly consider the case of $\gamma \geq 2$. This case may be of little interest in the actual tuna fishery, but there may be other instances where $\gamma \geq 2$ is interesting (e.g., animal populations).

When E is small, so that $bE\chi_0 < \beta(\gamma - 1)$, the coefficient $f(E,\gamma)$ is negative. Equation (B14) has a graphical solution sketched in Figure 11. The steady-state tuna level, T_s, is greater than the "natural level" T_0, but this is explained as follows. At any time there are a certain number of tuna schools bound in the complexes. The remaining, uncomplexed, tuna achieve the steady state level T_0. The total number of tuna, however, is T_0 plus the number in the complexes.

As E increases, a level of effort is reached so that $f(E,\gamma) = 0$. At this point, Equation (B14) becomes

$$g_T = 0. \qquad \text{(B15)}$$

The tuna level is at the natural steady state, because tuna are removed from the complexes as quickly as they enter the complexes.

As E increases further, $f(E,\gamma) \to f_\infty$, where $f_\infty = 1$ is the limit as $E \to \infty$ of $f(E,\gamma)$. Equation (B14) becomes

$$g_T = \alpha KT^{\gamma}. \qquad \text{(B16)}$$

The graphical solution of Equation (B16) is

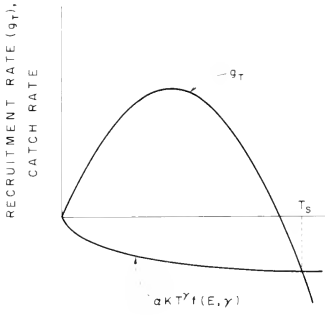


FIGURE 11.—Graphical determination of the steady-state tuna population (T_S) for the one-step kinetic model, when the natural dissociation rate is greater than fishing mortality (see text).

sketched in Figure 12. When $\gamma > 2$, it is impossible to overfish the tuna into extinction (compare Figure 12 with Figure 2, which corresponds to the case $\gamma = 1$). The reason for this behavior is that, as the tuna level decreases, the rate of formation of complexes, αKT^{γ}, decreases much more rapidly since $\gamma > 2$. When T is small, it is unlikely that a complex will form. This result should be contrasted with the case of $\gamma = 1$, in which is it possible to overfish the tuna to extinction.

From Equation (B10) we have

$$Y/E = \frac{b\lambda_0\gamma\alpha KT^{\gamma} S_0}{\beta + bE\lambda_0} . \qquad \text{(B17)}$$

Thus, if $\beta \gg bE\lambda_0$ we obtain

$$T^{\gamma} \propto Y/E \qquad \text{(B18)}$$

so that

$$T \propto (Y/E)^{1/\gamma}. \qquad \text{(B19)}$$

Thus $(Y/E)^{1/\gamma}$ is a possible biomass index, if $\beta \gg bE\lambda_0$.

If $bE\lambda_0 \gg \beta$, then

$$Y/E \approx \frac{\gamma\alpha KT^{\gamma}}{E} S_0. \qquad \text{(B20)}$$

In this limit a possible biomass index is $(Y)^{1/\gamma}$. Thus, the catch itself is a biomass index.

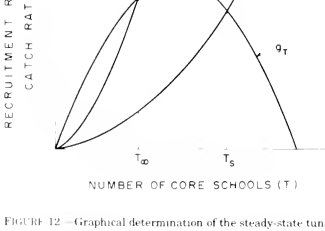


FIGURE 12.—Graphical determination of the steady-state tuna population (T_s) for the one-step kinetic model, when fishing mortality is greater than the natural dissociation rate (see text).

In the intermediate region $\beta \approx bE\lambda_0$ it appears that no simple biomass index is available.

The determination of the appropriate biomass index depends upon the size of $bE\lambda_0/\beta$. This is a natural measure since it compares the rate at which complexes are dissociated due to fishing with the natural dissociation rate β.

Multistep Collision Model

The model in the last section is somewhat unrealistic in that the complex with γ tuna schools is formed only if the γ schools collide simultaneously with an attractor. Hence, the model did not allow for complexes with $\gamma - 1, \gamma - 2, \ldots, 1$ tuna school per complex. A more realistic model is one in which the tuna-attractor complexes form by a multistep mechanism:

$$\begin{aligned}
&\gamma_1 T + K \underset{\beta_1}{\overset{\alpha_1}{\rightleftharpoons}} C_1 \\
&\gamma_2 T + C_1 \rightleftharpoons C_2 \\
&\gamma_3 T + C_2 \rightleftharpoons C_3 \\
&\qquad \vdots \\
&\gamma_n T + C_{n-1} \rightleftharpoons C_n \\
&C_l \xrightarrow{bE\lambda_0} K + \text{harvest of } \sum_{j=1}^{l} \gamma_j \text{ schools}
\end{aligned} \qquad \text{(B21)}$$

where $l = 1, \ldots, n$.

More detail could be added, e.g., when a complex C_i is fished, $j = 1, \ldots, l$ tuna schools might be removed with probabilities p_j. When all $\gamma_j = 1$, Equation (B21) is undoubtedly the most realistic model presented here. (Since the probability that two core schools are added at the same instant is essentially zero, the idea of stepwise addition of schools seems justified.) The kinetic equations corresponding to the reactions in Equation (B21) are (for $\gamma_j = 1$ for all j)

$$\dot{T} = -T\left\{\alpha_1 K + \sum_{j=2}^{n-1} \alpha_j C_{j-1}\right\} + \sum_{j=1}^{n} \beta_j C_j + g_T(T)$$

$$\dot{C}_1 = \alpha_1 KT - (\beta_1 C_1 + bE\lambda_0 C_1 + \alpha_2 C_1 T) + \beta_2 C_2$$

$$\dot{C}_n = \alpha_n C_{n-1} T - (\beta_n C_n + bE\lambda_0 C_n + \alpha_{n+1} C_n T) + \beta_{n+1} C_{n+1} \qquad (n \geq 2) \qquad \text{(B22)}$$

$$\dot{K} = -\alpha_1 KT + bE\lambda_0 \left\{ \sum_{j=1}^{n} C_j \right\} + \beta_1 C_1 + g_K(K).$$

Steady-states of the system are obtained if we set the left-hand sides in Equation (B22) equal to zero. We then find that the steady states are determined by:

$$C_1 = \frac{\alpha_1 KT + \beta_2 C_2}{\beta_1 + bE\lambda_0 + \alpha_2 T}$$

$$C_n = \frac{\alpha_n C_{n-1} T + \beta_{n+1} C_{n+1}}{\beta_n + bE\lambda_0 + \alpha_{n+1} T} \quad (n \geqslant 2) \qquad \text{(B23)}$$

$$g_K(K) = 0$$

$$0 = -T\left\{\alpha_1 K + \sum_{j=2}^{n-1} \alpha_j C_{j-1}\right\} + \sum_{j=1}^{n} \beta_j + g_T(T).$$

Equations (B22) and (B23) seem to represent a fairly realistic model of the fishery dynamics. A full analysis of these equations would be quite illuminating. However, as it is, the analysis of this model quickly becomes intractable. In order to illustrate the behavior of this model, we will analyze the case $n = 2$ (for arbitrary γ_1, γ_2):

$$\begin{aligned} &K + \gamma_1 T \underset{\beta_1}{\overset{\alpha_1}{\rightleftharpoons}} C_1 \\ &C_1 + \gamma_2 T \underset{\beta_2}{\overset{\alpha_2}{\rightleftharpoons}} C_2 \\ &C_1 \xrightarrow{bE\lambda_0} K + \text{harvest of } \gamma_1 \text{ tons} \\ &C_2 \xrightarrow{bE\lambda_0} K + \text{harvest of } \gamma_1 + \gamma_2 \text{ tons.} \end{aligned} \qquad \text{(B24)}$$

The results of the analysis of three-(or higher)step mechanisms should be similar to the analysis of the two-step mechanism.

The multistep model provides a picture of the tuna-porpoise bond which appears to be relatively realistic. For example, we may imagine that the first γ_1 schools are bound strongly to the complex (α_1 large, β_1 small) and that the next γ_2 schools are bound less strongly ($\alpha_2 < \alpha_1$, $\beta_2 > \beta_1$). Sharp's (1978) discussion of the effect of the thermocline on the tuna-porpoise association supports this model. In particular, it seems likely that the α_i and β_i depend upon the location of the thermocline.

The kinetic equations corresponding to the multistep model are

$$\dot{T} = g_T - \alpha_1 T^{\gamma_1} K - \alpha_2 T^{\gamma_2} C_1 + \beta_1 C_1 + \beta_2 C_2 + \gamma_1 \beta_1 C_1 + \gamma_2 \beta_2 C_2 \qquad \text{(B25)}$$

$$\dot{K} = g_K - \alpha_1 T^{\gamma_1} K + \beta_1 C_1 + bE\lambda_0 (C_1 + C_2) \qquad \text{(B26)}$$

$$\dot{C}_1 = \alpha_1 T^{\gamma_1} K - \beta_1 C_1 - \alpha_2 C_1 T^{\gamma_2} + \beta_2 C_2 - bE\lambda_0 C_1 \qquad \text{(B27)}$$

$$\dot{C}_2 = \alpha_2 C_1 T^{\gamma_2} - \beta_2 C_2 - bE\lambda_0 C_2 \qquad \text{(B28)}$$

In the steady state, we have

$$C_2 = \frac{\alpha_2 C_1 T^{\gamma_2}}{\beta_2 + bE\lambda_0}. \qquad \text{(B29)}$$

Adding the steady-state version of Equations (B25)–(B28) gives

$$g_K = 0 \qquad \text{(B30)}$$

which we assume has the solution $K = K_0 > 0$. The steady-state version of Equation (B27), using Equation (B29), is:

$$0 = \alpha_1 K T^{\gamma_1} - \beta_1 C_1 - \alpha_2 C_1 T^{\gamma_2} - bE\lambda_0 C_1 + \alpha_2 \beta_2 T^{\gamma_2} C_1 / (\beta_2 + bE\lambda_0)$$

which can be solved to give the steady-state level of C_1 complexes:

$$C_1 = \frac{\alpha_1 K T^{\gamma_1}}{\beta_1 + \alpha_2 T^{\gamma_2} + bE\lambda_0 - \alpha_2 \beta_2 T^{\gamma_2} / (\beta_2 + bE\lambda_0)}. \qquad \text{(B31)}$$

The instantaneous harvest rate is given by:

$$Y = bE\lambda_0 (\gamma_1 C_1 + (\gamma_2 + \gamma_1) C_2) S_0 \qquad \text{(B32)}$$

$$= \frac{bE\lambda_0 S_0 \alpha_1 K T^{\gamma_1}}{\beta_1 + \alpha_2 T^{\gamma_2} + bE\lambda_0 - \alpha_2 \beta_2 T^{\gamma_2} / (\beta_2 + bE\lambda_0)} \times (\gamma_1 + \gamma_2 \alpha_2 T^{\gamma_2} / (\beta_2 + bE\lambda_0)). \qquad \text{(B33)}$$

Note that if we set $\beta_1 = \beta_2 = 0$ and $\gamma_1 = \gamma_2 = 1$, Equation (B33) becomes

$$Y = \frac{bE\chi_0 S_0 \alpha_1 KT}{bE\chi_0 + \alpha_2 T} \times (1 + \alpha_2 T/bE\chi_0). \quad \text{(B34)}$$

With the exception of the multiplicative term $(1 + \alpha_2 T/bE\chi_0)$, Equation (B34) is equivalent to Equation (11) (model B) in the body of the paper. We shall show that the model presented in this section contains model B as a special case and also exhibits "abrupt" transitions, between multiple steady states.

As $E \to \infty$, the harvest rate saturates and

$$Y \to Y_\infty = \alpha_1 \gamma_1 S_0 K_e T^{\gamma_1}. \quad \text{(B35)}$$

Hence, when E is large, $(Y)^{1/\gamma_1}$ is a biomass estimate.

When E is small, Equation (B33) becomes

$$Y \approx \frac{bE\chi_0 S_0 \alpha_1 KT^{\gamma_1}}{\beta_1} \left(\gamma_1 + \frac{\gamma_2 \alpha_2}{\beta_2} T^{\gamma_2}\right), \quad \text{(B36)}$$

which can be written as

$$Y/E \approx h_1 T^{\gamma_1} + h_2 T^{\gamma_1 + \gamma_2} \quad \text{(B37)}$$

where $h_1 = \dfrac{b\chi_0 S_0 \alpha_1 K \gamma_1}{\beta_1}$, $h_2 = \dfrac{h_1 \gamma_2 \alpha_2}{\gamma_2 \beta_2}$. (B38)

Unlike the one-step model, in the multistep model Y/E is not a useful biomass estimate at any level of effort.

The steady-state tuna level is determined from the steady-state version of Equation (B25). After Equations (B29) and (B32) are used for the values of C_1 and C_2 and the resulting expression is simplified, we obtain

$$g_T = \alpha_1 T^{\gamma_1} K \frac{\Delta(\alpha, \beta, E, T)}{\rho(\alpha, \beta, E, T)} \quad \text{(B39)}$$

where $\Delta = (\gamma_1 + 1)[\beta_1\beta_2 + \beta_1 bE\chi_0]$

$$+ (\gamma_2 - 1)\beta_2 T^{\gamma_2}$$

$$+ \beta_2 bE\chi_0 + (bE\chi_0)^2 \quad \text{(B40)}$$

$$\rho = \beta_1\beta_2 \quad \text{(B41)}$$

$$+ bE\chi_0(\beta_1 + \beta_2 + bE\chi_0 + \alpha_2 T^{\gamma_2}).$$

Because Δ and ρ are so complicated, Equation (B39) is difficult to analyze as it stands. To simplify the analysis, we assume that $\beta_1 = \beta_2 = 0$. Physically, this means that the rate of dissociation of complexes due to fishing is much greater than the natural dissociation rate of complexes. Since our major interest is in the qualitative behavior of Equation (B39), this assumption seems acceptable.

If $\beta_1 = \beta_2 = 0$, Equation (B39) becomes

$$g_T = \frac{\alpha_1 T^{\gamma_1} KbE\chi_0}{bE\chi_0 + \alpha_2 T^{\gamma_2}}, \quad \text{(B42)}$$

which can be analyzed. We denote by $f(E, \gamma_1, \gamma_2, T)$ the right-hand side of Equation (B42). The solutions of Equation (B42) will be discussed according to the values of γ_1 and γ_2. A complete analysis of Equation (B42) is very involved. We shall present a partial analysis, in order to illustrate the types of behavior which may occur. We first consider the case in which $\gamma_1 = \gamma_2 = 1$. Equation (B42) becomes

$$g_T = \frac{\alpha_1 KbE\chi_0 T}{bE\chi_0 + \alpha_2 T}, \quad \text{(B43)}$$

which is analogous to Equation (11B) of the body of the paper. Consequently, we shall not pursue the analysis here. In the analysis of Equation (11B), we showed that Equation (B43) may have multiple steady states. As effort increases, a transition between the steady state where the tuna level is high and the steady state where $T = 0$ is possible if $\alpha_1 K > g_T'(0)$ (the "catastrophe" condition).

In the one-step model, a complex containing two tuna schools was formed only if the two schools, at once, came into close contact with an attractor. That model did not exhibit multiple steady states, or even the possibility of overfishing the tuna into extinction.

On the other hand, if the complex that contains two schools is formed by a stepwise process, so that schools are added to an attractor one at a time, "catastrophic" behavior and extinction of the tuna are possible.

Sudden transitions in population (catastrophes) are usually difficult to predict. However, the model presented here leads to a natural measure of overfishing. From Equations (B29) and (B31), when E is large we have

$$C_1 \sim \frac{1}{bE\lambda_0} \qquad C_2 \sim \frac{1}{(bE\lambda_0)^2}. \tag{B44}$$

Consequently, if overfishing is occurring, the number of complexes with two tuna schools is much less than the number of complexes with one school. As effort increases further, the fishery will find more and more attractors without any associated tuna schools. Such observations should act as a warning that the tuna are being overexploited. We note that it is possible that CPUE will not decrease, even though the number of tuna schools per complex is decreasing (see Figure 7).

A host of complex solutions and bifurcations can be determined if the values of γ_1, γ_2 are not 1. Since $\gamma_1 = 1$, $\gamma_2 = 1$ do not have an immediately obvious interpretation for fishery dynamics, we will not consider those cases here.

In this Appendix, we have taken an approach to modelling the fishery that is substantially different from the approach in the main part of the paper. The results obtained here complement the main results, and extend them. We have shown that models A and B presented in the paper arise as special cases of the kinetic models in this Appendix. It is clear that these models could be greatly elaborated and many other details explored.

SHALLOW MARSH HABITATS AS PRIMARY NURSERIES FOR FISHES AND SHELLFISH, CAPE FEAR RIVER, NORTH CAROLINA

MICHAEL P. WEINSTEIN[1]

ABSTRACT

Seine and rotenone collections taken during 1977 from the upper reaches of tidal creeks and along the marsh fringe in the vicinity of the Cape Fear River, N.C., indicated that these areas serve as primary nursery habitats for postlarval and juvenile fishes and shellfish. Average densities (number 400m²) for several ocean-spawned species at the peak of postlarval or early juvenile recruitment were high: spot, *Leiostomus xanthurus*, 3,099; Atlantic menhaden, *Brevoortia tyrannus*, 839; striped mullet, *Mugil cephalus*, 711; white mullet, *Mugil curema*, 525; and brown shrimp, *Penaeus aztecus*, 329. Standing crops for the majority of species studied further indicated that lower productivity per unit area occurred in high salinity marshes closest to the ocean. In addition, distribution patterns for several species were significantly correlated with salinity and substrate characteristics or combinations of them and seasonal effects also were evident so that related and potentially competing species were separated temporally.

Community analyses demonstrated that each marsh complex was unique, however, overall similarity for the most abundant species was high. The differences were related to salinity gradients and to the presence of an "edge effect" where marshes closest to the river mouth were species rich due to seasonal invasion by low densities of reef, nearshore, and shelf marine species. Similarly, freshwater fishes invaded brackish marshes during periods of high river flow.

Patterns of distribution of estuarine species have often been correlated with environmental gradients (Remane 1934; Hedgepeth 1957; Gunter 1961; Khlebovich 1969; Gamey and Greenberg 1977) and have also been described in terms of characteristic estuarine zones: marshes, tidal flats, sounds, bays, and channels. Within these areas, organisms are frequently associated with specific habitats; for example, the marshes can be divided into the high marsh and tidal creeks, the latter characterized by soft muds at their headwaters and by more scoured areas downstream. Several properties of the water column also vary in these creeks, being generally more stable near the creek mouth (Hackney et al. 1976), and the presence of food organisms is often correlated with sediment properties so that predators may frequent one area more than another (de Sylva 1975). On the basis of individual tolerances, some species will frequent habitats under a wide range of conditions, while others will be more restricted in their distribution. These tolerances may change with the age of the individual so that a given species may be a member of several different communities during its life cycle.

When the nursery role of estuaries is considered in this framework, it becomes evident that information is lacking on age-specific utilization of estuarine zones. Few investigators have studied the primary nursery areas where the youngest members of many ocean-spawned species first take up residence (Herke 1971; Parker 1971; Purvis[2]). In one such area, the tidal salt marshes, comprehensive sampling efforts have demonstrated that a temporal succession takes place with many species residing in the upper reaches of tidal creeks during their earliest days and then moving gradually downstream as they grow (Herke 1971; Dunham 1972; Purvis see footnote 2). A similar successional pattern occurs in the upper reaches of the Chesapeake Bay (Haven 1957; McHugh 1967; Chao and Musick 1977) and in open bay waters near the heads of estuaries in South Carolina (Bearden 1964), Louisiana (Thomas and Loesch 1970), and Florida (Hansen 1970).

The present study details the composition of the nekton community of several shallow marsh areas, including tidal creeks and marshes adjacent to the river shoals. Consideration is given to the role of these habitats as primary nurseries, and patterns

[1]Lawler, Matusky & Skelly Engineers, One Blue Hill Plaza, Pearl River, N.Y., present address: Department of Biology, Virginia Commonwealth University, Richmond, VA 23284.

[2]Purvis, C. 1976. Nursery area survey of Northern Pamlico Sound and tributaries. Div. Mar. Fish. Rep. (prepared for U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv.), 62 p.

Manuscript accepted January 1979.
FISHERY BULLETIN: VOL. 77, NO. 2, 1979.

of distribution of individual species are described. An attempt is also made to correlate these distributions with both biotic and abiotic parameters.

STUDY AREA

All sampling stations were situated within the Cape Fear River, N. C., located at approximately lat. 33° N (Figure 1). The estuary is relatively narrow, averaging only 1.6-3.6 km wide and extending 45 km from the general location of the salt boundary at Wilmington, N.C., to the river mouth at Baldhead Island. A 12 m deep ship channel is maintained from Wilmington to the river entrance, and numerous spoil islands are found adjacent to this channel over its entire length. Tidal velocities in the Cape Fear are high, averaging 1.5 m/s at the river mouth during ebb.

Tidal salt marshes cover approximately 8,900 ha and form the largest contiguous system of this type in North Carolina (U.S. Army Corps of Engineers[3]). Dominant plant species include the smooth cordgrass, *Spartina alterniflora*, and black needle rush, *Juncus roemerianus*, with giant reed grass, *Spartina cyanosuroides*, prevalent upstream at lower salinities. Tidal creeks cover an estimated 648 ha, and shallow open water areas (shoals) between the channel and salt marshes contribute an additional 7,285 ha of suitable nursery habitat.

MATERIALS AND METHODS

Nine stations were established within several major marsh systems and along the river shoals (Figure 1; Table 1). Suitable interior marsh sites could not be located in the middle reaches of the estuary, since the few available creek systems were inaccessible or could not be sampled without great difficulty. Salinities at the chosen sites ranged from 0 to 35‰, and a wide variety of substrata were included, ranging from soft organic ooze, approximately 10-20 cm deep, to sandy areas containing little organic material. Stations were sampled on a monthly basis from January through December 1977 with several exceptions (Table 1). Because of ice cover, the Dutchman and Walden Creek rotenone stations were not sampled in January, and new stations were established at Shellbed Island and Hechtic Creek in February and at Barnards Creek in April.

Two collection methods were employed throughout this study: seining, where footing was satisfactory, and rotenone application (5% emulsifiable Fish-Tox[4]), where softer mud or snags predominated. Before either method was attempted, an area of tidal creek was isolated utilizing large blocking seines. Nets were extended from shore to shore and were anchored with U-shaped lengths of concrete reinforcing rods, especially helpful in pinning the leadline along the contours of the banks on each side of the station (at several sites, one shoreline was always bordered by a bar formation). In addition, a length of heavy chain was affixed to the leadline of each block net to ensure direct contact with the substrate. Initially, 6.5 mm mesh block nets were employed; beginning in April 1977 these were replaced with fine mesh (approximately 1.0 mm) nets capable of retaining the smallest ocean-spawned larvae. The enclosed area then was swept repeatedly with a 7.6 m, 6.5 mm mesh, seine or treated with sufficient rotenone to kill all fish present.

To determine the number of seine sweeps required, a study was conducted in October 1976 when nekton diversity remained near a yearly maximum. After the block nets were set at the Dutchman Creek site, a total of 13 sweeps were taken, and the contents of each sweep kept separate. The results were plotted (Figure 2) as the cumulative number of species, the expected number of species (ENS) (Hurlburt 1971) and the cumulative diversity (H', Shannon and Weaver 1949). As seen in the figure, little new information was gained after the eighth sweep, i.e., an asymptote was approached. A separate study at Baldhead Creek in September 1977 confirmed these results, and a procedure requiring eight sweeps was instituted at each seine station.[5] In addition, three overlapping sweeps with a 7.6 m, approximately 1.0 mm mesh, seine were taken at each site. These served to capture the smallest fish present, those capable of passing through the 6.5 mm meshes. A preliminary experiment indicated that these seines were capable of significantly reducing the lower size range of key species studied (Table 2).

[3]U.S. Army Corps of Engineers. 1977. Maintenance of Wilmington Harbor, North Carolina. Final environmental statement. U.S. Army Engineers District, Wilmington, N.C. 97 p.

[4]References to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]A 50-ft (15.2 m) seine was used on the last sweep, this was the original downstream blocknet.

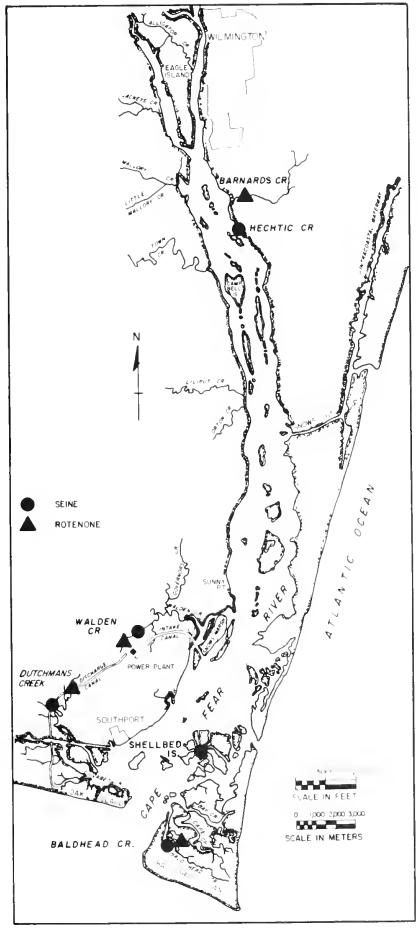


FIGURE 1.—Seine and rotenone sampling sites, Cape Fear River estuary, N C.

TABLE 1.—Sampling localities and dates for collections of fishes and invertebrates, Cape Fear River estuary, N.C., including physicochemical data. D = approximate distance from river mouth to creek entrance; SD = standard deviation, MPS = median particle size, SC = sorting coefficient.

Station	Location	Sampling schedule	D (km)	Average salinity ‰ SD	Average temperature °C SD	Sediment parameters: Sand (%) Medium	Sand (%) Fine	Silt-clay	Organics (%)	MPS (mm)	SC (σ_I)	No. of cores
Baldhead Cr	Tidal											
seine	creek	Jan.-Dec.	0.9	25.7 ± 7.0	21.1 ± 7.6	13	86	1	1.88	0.23	0.65	7
rotenone		Jan.-Dec.	0.9	25.9 ± 6.7	21.3 ± 7.8	34	65	1	1.13	0.34	0.80	6
Sheltbed Is.	River											
seine	shoal	Feb.-Dec.	4.6	26.6 ± 5.9	23.1 ± 6.8	7	92	1	0.77	0.23	0.60	3
Dutchman Cr.	Tidal											
seine	creek	Jan.-Dec.	6.6	25.1 ± 6.9	19.9 ± 8.3	10	86	4	2.67	0.21	0.79	7
rotenone		Feb.-Dec.	6.6	18.1 ± 8.7	20.4 ± 8.9	20	66	14	10.42	0.20	1.31	4
Walden Cr.	Tidal											
seine	creek	Jan.-Dec.	9.7	8.6 ± 4.8	21.4 ± 8.1	12	87	1	0.80	0.21	0.59	6
rotenone		Feb.-Dec.	9.7	9.2 ± 5.4	21.2 ± 7.7	12	87	1	0.43	0.25	0.56	3
Hechtic Cr.	River											
seine	shoal	Feb.-Dec.	33.6	6.0 ± 5.5	21.4 ± 9.8	27	66	7	2.30	0.28	1.13	6
Barnards Cr.	Brackish											
rotenone	stream	Apr.-Dec.	33.9	6.1 ± 5.6	22.3 ± 7.6	8	86	6	33.17	0.24	0.72	3

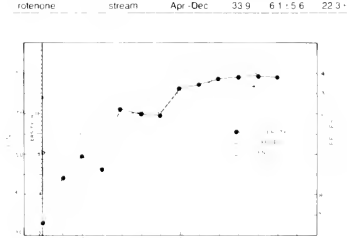


FIGURE 2.—Dutchman Creek, N.C., survey (October 1976) designed to determine the number of seine sweeps required to produce a representative sample. Cumulative number of species (ENS) and Shannon-Weaver diversity (H') are plotted on separate axes.

At rotenone sites, sufficient toxin was introduced to kill all fishes present; this quantity was determined by the presence of certain "indicator" species in the collections, especially killifish (*Fundulus* spp.) and eels (e.g., speckled worm eel, *Myrophis punctatus*; American eel, *Anguilla rostrata*) which are resistant to rotenone and may also burrow in the substrate. Stricken fishes were dipnetted as long as they were visible on the surface, and the downstream block nets were also picked at the end of the survey. During winter, additional rotenone was added to ensure that toxicity remained uniform, and in all months, potassium permanganate ($KMnO_4$) was added downstream to detoxify rotenone carried below the sites. During this study, no attempt was made to account for rotenone losses due to settling.

All collections were initiated near low tide to reduce the effects of current and to sample postlarval fishes that were not swept downstream by tidal flows. To ensure uniformity of water volume between the block nets, staff gauges and landmarks were used to standardize the volume/area sampled. Throughout this paper, all catches will be reported as the number of individuals per 400 m^2, the average surface area of the stations.

Temperature was recorded prior to each collection with a calibrated stick thermometer or temperature mode on a Beckman (model RS 5-3) salinometer; surface salinity was measured with the same instrument. The salinometer was calibrated prior to each monthly sampling trip with a

TABLE 2.—Comparison of length-frequency distributions from 6.5 and 10 mm mesh, seine collections, Cape Fear River estuary, N.C. A = 6.5 mm mesh seine, seven sweeps; B = 10 mm mesh seine, three sweeps. Lower one-tailed *t*-test, ** = $P < 0.01$, ns = not significant. Specimens < 28 mm are not included in mean values.

Species		Length (mm) 9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	28	Total	Mean
Mugil cephalus	A										4	36	37	62	41	20	15	13	7	18	253	21.4
	B											2	5	9	10	1				3	30	21.1 ns
Leiostomus xanthurus	A					1			2	4	20	42	49	24	19	5	2	1		1	170	19.9
	B						1	1	1	7	5	9	6	3							33	18.4 **
Paralichthys spp.	A				1	2		2	2			1									8	14.9
	B	1	1	4	10	9	4	7	3												39	13.0 **

known resistor and periodically checked against salinity standards. Fishes and shellfish were preserved in 10% Formalin and lengths (standard length for fishes, carapace width for crabs, and total length for shrimp) recorded for selected species. Subsampling for lengths was employed when sorted collections contained more than 100 individuals of a given species.

Sediments were collected with a 0.01 m^2 plug sampler. Three to seven cores, 5 cm deep, were taken at each site, with the actual number at any one location governed by the expected homogeneity of the substratum. Where the bottom was uniform, three evenly spaced cores were taken along a diagonal across the site; where bar formations formed a border of the site, six or seven evenly spaced cores were collected along two transects located parallel to each shore. Cores were processed according to prescribed methods of the American Society for Testing and Materials (American Society for Testing and Materials 1963). Hydrometer analysis was used for the fine fraction, and particle size descriptions were based on the unified scale (U.S. Corps of Engineers 1953).

The degree of similarity among sites was compared with the percent similarity index (PSI) (Whittaker and Fairbanks 1958):

$$PSI = 100 \sum (p_{ia}, p_{ib})$$

where p_{ia} and p_{ib} are the proportion of species i in samples a and b, respectively. Since species with single occurrences (singletons) and taxa not identified to species contributed little to similarity among sites or to an understanding of their role in the community, they were omitted from the analyses. Separate matrices were constructed for pooled monthly data at each site on the basis of station and species affinities (recurring species groups) and clustered by the unweighted pair group-average method (Sneath and Sokal 1973). Data were $\log_{10}$ transformed prior to these analyses to give added emphasis to less common species and decrease the effect of extreme values (Clifford and Stephenson 1975). Three separate dendrograms were constructed—a station association dendrogram in which all nine stations were compared, and a pair of dendrograms which reflected station and species associations for seine sites. Results for the latter comparisons were then cross-referenced by construction of a two-way coincidence table (Clifford and Stephenson 1975).

Partial correlations were calculated with physicochemical data and monthly abundances for selected species (Fisher 1973). The latter were based on sufficient sampling densities (taken as at least 10 individuals collected among all sites in any given month) and served to reduce the effect of zero catches in the data. Prior to the analyses, abundance data were $\log_{10}$ transformed in order to stabilize variances (Winsor and Clark 1940).

RESULTS

Physicochemical Parameters

Among the seine sites, two distinct salinity patterns were observed (Table 1); high salinity stations (Baldhead and Dutchman Creeks and Shellbed Island) generally ranged above 15‰, while Hechtic Creek (well upriver) and Walden Creek (part of a fairly extensive freshwater drainage basin) ranged downwards from this value. Seasonal patterns also were evident, with salinity depressions occurring in the spring, especially in March and April, and again during the fall. Although the pattern for rotenone stations was not as distinct as that for seine sites, results were similar, with the exception of the Dutchman Creek station (located at the headwaters of this creek system) which reflected local runoff.

Sediment characteristics (Table 1) represent means for all cores taken at each site. Fine sands (1.25-3.75 ϕ) were the major component of the sediment at all stations averaging 80%, with slightly coarser material (−1.0 to 1.25 ϕ) contributing 20% or more of the bottom particle composition at the Dutchman and Baldhead Creek rotenone sites and at the Hechtic Creek seine site. In general, silts and clays (> 3.75 ϕ) were minor components of the substratum at stations located in the Baldhead Island complex, although this percentage increased in Dutchman Creek, with a maximum (14%) at the rotenone site. Both upriver stations, Hechtic and Barnards Creeks, also contained more silts and clay. Organic fractions were similarly distributed, with the lowest station mean recorded for the well-scoured Walden Creek system. Dutchman Creek and upriver sites generally had sediments with high organic content, with a maximum at Barnards Creek of 33.17%.

Sorting coefficients (σ_f) were calculated (Table 1) for each site according to the methods of Folk (1974). Sediments were poorly sorted at the Dutchman Creek rotenone station, located at the

headwaters of the marsh creek where flows were minimal throughout the tidal cycle, and at Hechtic Creek which also "dead-ends" a short distance upstream. Median particle size, computed as the geometric mean for all core samples collected at the site, generally fell within a narrow range, with the exception of the Baldhead Creek rotenone station where larger particles were associated with the medium sand fraction. The percentage of this fraction was considerably greater (34%) than at other localities.

Interstation Comparisons

Species richness was greatest at the Baldhead Creek stations, closest to the ocean entrance, while the total number of individuals captured varied among sites (Table 3). The low catch at Barnards Creek is reflected in the reduced sampling effort at this station which was first sampled in April. Catches at Walden Creek were similar to those at Baldhead Island, although fewer taxa were collected. On a seasonal basis, peak total abundance occurred mainly in the winter and early spring, coincident with the presence of winter-spawned species, primarily spot, *Leiostomus xanthurus*; Atlantic menhaden, *Brevoortia tyrannus*; mullets, *Mugil* spp.; and flounders, *Paralichthys* spp.

Differences in relative numbers of species in monthly collections were tested with the Wilcoxon signed rank test (Table 4). Seine and rotenone stations were treated separately, and in comparisons involving Barnards Creek, only the months April to December were used. Among seine stations, Baldhead Creek yielded greater numbers of species than all sites except Hechtic Creek, while the Baldhead Creek rotenone site produced significantly more species than other rotenone stations. The upriver sites, Hechtic and Barnards Creeks, were also richer in species than either Dutchman or Walden Creek, but did not yield more species than the station at Shellbed Island.

The most abundant species (collectively composing 0.5% or more of the total number of individuals) were essentially similar among stations (Table 5), differing only in their order of abundance. For example, *Leiostomus xanthurus*; mummichog, *Fundulus heteroclitus*; and striped mullet, *Mugil cephalus*, were ubiquitous, and *Brevoortia tyrannus*; white mullet, *M. curema*; and Atlantic silverside, *Menidia menidia*, nearly so. Other abundant species seemed more closely associated with specific habitats; the striped killifish, *F. majalis*, for example, was restricted mainly to high salinity areas, while the Atlantic croaker, *Micropogonias undulatus*, and hogchoker, *Trinectes maculatus*, were collected more frequently in brackish water with bottoms high in organic matter. It should be emphasized that seine and rotenone methods used here differed somewhat with respect to gear efficiency and selectivity (Weinstein and Davis in prep.) and, in addition, invertebrates such as brown shrimp, *Penaeus aztecus*, and blue crab, *Callinectes sapidus*, were not considered to be sampled quantitatively with rotenone. These species, however, were common at all seine sites except Shellbed Island.

The effects of the extreme cold in January and February 1977 along the eastern seaboard were reflected in the data with severely reduced catches of organisms in these months. Although catches might have been expected to be higher at this time of year, ice covered the headwaters of several marsh creeks, and water temperatures in the shallows hovered between 0° and 2° C. These tempera-

TABLE 3.—Total number of individuals and species collected at seine and rotenone sampling sites, Cape Fear River estuary, N C

Sampling site	No. of individuals	No. of species	Sample size
Baldhead Creek			
Seine	15,320	52	12
Rotenone	12,259	58	11
Shellbed Island			
Seine	23,611	43	11
Dutchman Creek			
Seine	25,964	36	12
Rotenone	36,750	30	11
Walden Creek			
Seine	14,929	35	12
Rotenone	18,183	37	11
Hechtic Creek			
Seine	23,113	44	11
Barnards Creek			
Rotenone	8,063	39	9

TABLE 4.—Species richness comparisons among seine and rotenone stations, Cape Fear River estuary, N C. The test statistic is the Wilcoxon signed rank test. * = significant at $\alpha = 0.05$; ns = not significant.

Seine station	Baldhead Creek	Shellbed Island	Dutchman Creek	Walden Creek	Hechtic Creek
Baldhead Creek	—	*	*	*	ns
Shellbed Island		—	ns	ns	ns
Dutchman Creek			—	ns	*
Walden Creek				—	*
Hechtic Creek					—

Rotenone station	Baldhead Creek	Dutchman Creek	Walden Creek	Barnards Creek
Baldhead Creek	—	*	*	*
Dutchman Creek		—	ns	*
Walden Creek			—	*
Barnards Creek				—

TABLE 5.—Pooled species abundance for all collections at seine and rotenone sites in the Cape Fear River estuary, N C , listed in order of abundance. Only species composing 0.5% of the total number of individuals and their corresponding percentages are shown. Barnards Creek was not collected until April 1977.

Location species	No	%	Location species	No	%	Location species	No	%
Seine			*Mugil curema*	83	0.6	*Tinectes maculatus*	92	1.1
Baldhead Creek			*Menidia beryllina*	82	0.6	*Penaeus duorarum*	79	1.0
Anchoa mitchili	4 330	28.2	*P. setiferus*	70	0.5	*Citharichthys spilopterus*	54	0.7
Leiostomus xanthurus	3,918	25.5	Shellbed Island			*Gobionellus* sp.	52	0.6
Mugil curema	1,668	10.9	*A. mitchili*	8 927	37.8	*Syngnathus louisianae*	42	0.5
Menidia menidia	1,510	9.8	*M. menidia*	8 758	37.1	Dutchman Creek		
Fundulus heteroclitus	938	6.1	*Leiostomus xanthurus*	3,023	12.8	*L. xanthurus*	12,436	33.7
Penaeus duorarum	657	4.3	*F. heteroclitus*	730	3.1	*F. heteroclitus*	9,278	25.1
F. majalis	541	3.5	*Mugil cephalus*	525	2.2	*Mugil curema*	8,546	23.2
Brevoortia tyrannus	287	1.9	*E. argenteus*	450	1.9	*M. cephalus*	3 713	10.1
P. aztecus	266	1.7	*M. curema*	354	1.5	*B. tyrannus*	909	2.5
Mugil cephalus	263	1.7	*A. hepsetus*	295	1.2	*Lagodon rhomboides*	677	1.8
Callinectes sapidus	162	1.1	*B. chrysura*	115	0.5	*Elops saurus*	273	0.7
Gobiosoma bosci	114	0.7	Hechtic Creek			*Menidia menidia*	242	0.7
Bairdella chrysura	108	0.7	*Brevoorta tyrannus*	7,967	34.4	Walden Creek		
Eucinostomus argenteus	106	0.7	*L. xanthurus*	7,953	34.4	*Leiostomus xanthurus*	11,093	61.0
C. similis	91	0.6	*M. cephalus*	3,009	13.0	*B. tyrannus*	2,531	13.9
Lagodon rhomboides	70	0.5	*P. aztecus*	1,199	5.2	*F. heteroclitus*	910	5.0
Dutchman Creek			*A. mitchili*	660	2.9	*Mugil cephalus*	733	4.0
Leiostomus xanthurus	8 534	32.8	*F. heteroclitus*	590	2.6	*Lagodon rhomboides*	708	3.9
M. cephalus	4,160	16.0	*C. sapidus*	265	1.1	*M. curema*	677	3.7
F. heteroclitus	3,056	11.7	*P. duorarum*	247	1.1	*Eucinostomus argenteus*	329	1.8
M. curema	2,582	9.9	*M. curema*	199	0.9	*Menidia menidia*	318	1.8
Menidia menidia	2,510	9.6	*Menidia beryllina*	199	0.9	*M. beryllina*	241	1.3
Brevoortia tyrannus	1 387	5.3	*P. setiferus*	171	0.7	*Paralichthys* spp.	142	0.8
C. sapidus	938	3.6	*Bairdiella chrysura*	160	0.7	*Bairdiella chrysura*	88	0.5
F. majalis	824	3.2	*Micropogonias undulatus*	122	0.5	Barnards Creek		
P. aztecus	741	2.8				*F. heteroclitus*	2,996	24.4
Bairdiella chrysura	502	1.9	Rotenone			*Leiostomus xanthurus*	2,750	22.4
E. argenteus	231	0.9	Baldhead Creek			*M. menidia*	2,486	20.2
A. mitchili	151	0.6	*L. xanthurus*	1,969	24.2	*Mugil curema*	855	7.0
P. setiferus	132	0.5	*Brevoorta tyrannus*	1 260	15.5	*Lagodon rhomboides*	519	4.2
Walden Creek			*Mugil cephalus*	1,181	14.5	*Mugil cephalus*	406	3.3
L. xanthurus	7,410	49.6	*F. heteroclitus*	799	9.8	*G. boleosoma*	373	3.0
Brevoortia tyrannus	1 666	11.1	*Micropogonias undulatus*	446	5.5	*B. chrysura*	343	2.8
F. heteroclitus	1,240	8.3	*A. mitchili*	373	4.6	*Gobiosoma bosci*	223	1.8
P. aztecus	1,217	8.1	*Symphurus plagiusa*	334	4.1	*Anchoa mitchili*	211	1.7
A. mitchili	1,050	7.0	*Paralichthys* spp.	250	3.1	*Eucinostomus argenteus*	205	1.7
Mugil cephalus	780	5.2	*Gobionellus boleosoma*	213	2.6	*Brevoorta tyrannus*	158	1.3
E. argenteus	304	2.0	*Anguilla rostrata*	209	2.6	*Paralichthys* spp.	123	1.0
C. sapidus	284	1.9	*C. sapidus*	179	2.2	*F. majalis*	85	0.7
Lagodon rhomboides	192	1.3	*Gambusia affinis*	134	1.6	*Penaeus duorarum*	69	0.6
Menidia menidia	175	1.2	*Penaeus aztecus*	117	1.4	*Symphurus plagiusa*	64	0.5
Bairdiella chrysura	112	0.7	*Paralichthys lethostigma*	100	1.2	*Orthopristis chrysoptera*	56	0.5
P. duorarum	101	0.7						

tures might be fatal to the young of many species, especially since they were prolonged (Gunter and Hildebrand 1951; June and Chamberlain 1959; Massman and Pachecho 1960; Joseph 1972).

Seasonality and Growth

In the Cape Fear estuary tidal marshes, peak seasonal abundance (Figure 3) for young commercially and recreationally important species was always associated with the recruitment of postlarvae or early juveniles into the area and subsequent decreases in numbers were due to mortality and/or emigration from the primary nurseries. Although very few postlarval *Micropogonias undulatus* were captured in early 1977, recruitment was improved at the beginning of the 1977-78 larval year, with densities in November 1977 at upriver sites reaching a mean of 31 individuals/400 m^2 (Figure 3, upper left). Concentrations of this species in the river mainstem were much higher than in the marshes (Hodson[6]). Red drum, *Sciaenops ocellata*, were captured in relatively low numbers in the fall although their density approached 34 individuals/400 m^2 in the Dutchman Creek collections in October. *Leiostomus xanthurus* postlarvae dominated the sciaenid catches with average densities in March of 3,099 individuals/400 m^2.

Except during the cold period in early 1977, *Mugil cephalus* were fairly common throughout the estuary (Figure 3, lower left), with primary recruitment of early juveniles occurring in March and April. *Mugil curema*, however, displayed a

[6]R. G. Hodson, Director, Cape Fear Estuarine Laboratory, North Carolina State University, Southport, N.C., pers. commun. July 1978.

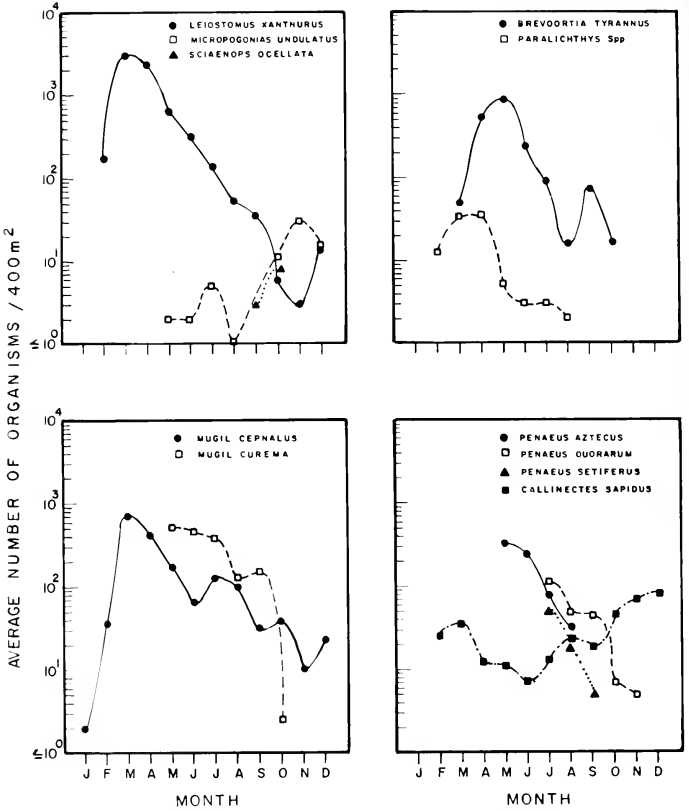


FIGURE 3.—Seasonality for selected estuary species in the Cape Fear River, N.C., 1977

more distinct seasonal presence in the Cape Fear estuary, with young arriving in May and emigrating nearly completely from the estuary in late fall. The more southerly distribution of this species (Anderson 1957; Moore 1974; Richards and Castagna 1976), perhaps related to temperature tolerance, may be responsible for this pattern.

Other winter-spawned species also were common in the Cape Fear. Flounders of the genus *Paralichthys* were most abundant in March and April when postlarvae first entered the marshes (Figure 3, upper right). *Brevoortia tyrannus* reached peak densities in April and May and were fairly abundant throughout summer and early fall, then they generally migrated out of the shallows in October when temperatures decreased markedly. The pooled data for the Atlantic menhaden, however, do not indicate the large monthly variation observed for catches of this species. In a given creek, densities varied over more than an order of magnitude between months, and peaks of abundance were not coincident among marshes. The only consistent pattern exhibited by the Atlantic menhaden was their generally greater association as postlarvae and early juveniles with intermediate to lower salinities. Except for their brief stay in brackish-water marshes as juveniles, Atlantic menhaden did not seem to establish long-term residency in any area, but instead tended to range throughout the lower salinity portions of the estuary, especially the river mainstem. Their mode of feeding may have contributed to this phenomenon (June and Chamberlain 1959; Jefferies 1975; Durbin and Durbin 1975).

All three species of commercial shrimps (Figure 3, lower right) exhibited distinct seasonal presence: *Penaeus aztecus* was recruited to the marshes as early as May, and white, *P. setiferus*, and pink, *P. duorarum*, shrimp were first captured in July. For all three species, peak densities were recorded during the month of first appearances, and young adults emigrated from the shallow marshes during the fall, especially after October. *Callinectes sapidus* (Figure 3, lower right) generally were abundant in all months, with a peak of recruitment in November and December. Apparently, the absence of early juveniles in January and February 1977 catches reflected heavy mortality or emigration due to the extreme cold in these months.

Length-frequency data for abundant 0 year class fishes and brown shrimp indicated that most of these species resided in tidal creeks at relatively small sizes and grew rapidly after April (Table 6). The smaller increments of growth occurring prior to this month for winter-spawned species resulted from the effects of low temperatures and the masking effect of continued recruitment through March. Extended recruitment periods created a similar "lag" in growth for species spawned in other seasons.

Standing Crops at Peak Recruitment

Patterns of distribution for selected species at the peak of postlarval recruitment are shown in Table 7; in all cases, more than 1 mo was averaged since a plateau was indicated in the data. Catches generally were lower at Baldhead Island stations (including Shellbed Island) for most dominant fishes, suggesting the inability of these marshes to support as much juvenile production per unit area as other Cape Fear marshes or perhaps indicating greater predation pressure in this area. *Leiostomus xanthurus* was relatively evenly distributed although catches of this species and those of *Mugil cephalus* and *M. curema* were lower at Baldhead Island; *M. curema* also was captured in reduced numbers at low salinity sites. In addition, both species of mullet were collected where the substrate contained high levels of organic matter.

Atlantic menhaden postlarvae and early juveniles (17–32 mm) predominated upriver at brackish salinities and also were abundant in Walden and Dutchman Creeks. Although salinity was relatively low in Dutchman Creek in April (11.5 and 12.6‰ at the rotenone and seine sites, respectively) the high catch of menhaden in May at the seine site (742 individuals 400 m^2) occurred at a time when salinity (35‰) was at a yearly maximum. Interestingly, the majority of these fish were of a different age-class (probably yearlings, 50–109 mm) than were the postlarvae and early juveniles that predominated in the April and May collections at other stations. These individuals may have already completed their early developmental period in brackish waters (June and Chamberlain 1959) and were moving freely throughout the Cape Fear estuary. They also apparently made forays into the Walden Creek system, and in other months contributed to the patchiness at all stations described previously.

Penaeid shrimp were an important component of the marsh nekton community during the late spring and summer months. Maximum densities

TABLE 6.—Length data for 0 year class individuals of selected species, Cape Fear River estuary, N.C., all station collections combined — data were not available

Species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Leiostomus xanthurus												
Mean length	14.3	19.5	22.4	24.6	33.4	41.3	43.8	49.1	58.4	68.6	89.8	109.4
Range	13-16	13-25	14-30	12-41	16-60	21-69	29-71	36-73	38-98	48-109	54-162	63-174
Sample size	3	412	1 969	1 778	1 275	709	524	373	376	193	41	35
Brevoortia tyrannus												
Mean length	—	—	27.7	27.0	31.9	33.3	47.3	37.2	52.3	56.8	68.0	67.3
Range	—	—	22-31	17-32	24-44	20-46	37-60	41-43	32-64	43-69	42-86	50-82
Sample size	0	0	300	674	693	306	146	5	54	57	3	3
Mugil cephalus												
Mean length	21.0	21.9	22.8	25.6	36.0	45.8	62.1	62.3	69.3	76.1	83.6	78.5
Range	19-22	18-28	16-29	17-37	24-62	28-67	35-92	37-94	40-113	48-131	49-118	55-127
Sample size	4	235	1 025	853	816	403	553	382	277	355	149	372
M. curema												
Mean length	—	—	—	—	25.8	37.0	56.3	61.6	63.1	70.5	75.1	—
Range	—	—	—	—	15-38	21-60	18-87	18-90	18-121	17-135	25-114	—
Sample size	0	0	0	0	718	751	665	392	327	67	71	0
Gobiosoma ocellata												
Mean length	—	—	—	—	—	—	—	14.3	17.5	24.8	39.5	33.5
Range	—	—	—	—	—	—	—	13-15	5-30	12-40	23-47	23-48
Sample size	0	0	0	0	0	0	0	3	39	80	13	10
Paralichthys spp.[1]												
Mean length	—	13.1	15.4	17.6	—	—	—	—	—	—	—	—
Range	—	9-19	12-21	10-30	—	—	—	—	—	—	—	—
Sample size	0	68	100	169	0	0	0	0	0	0	0	0
Anchoa mitchilli												
Mean length	—	—	—	—	—	17.3	20.2	21.0	22.3	22.2	26.5	24.6
Range	—	—	—	—	—	8-23	10-35	10-34	11-53	15-53	17-61	19-48
Sample size	0	0	0	0	0	473	540	391	844	715	447	85
Penaeus aztecus[2]												
Mean length	—	—	—	—	37.7	70.1	88.6	97.6	—	—	—	—
Range	—	—	—	—	18-64	24-113	30-130	24-127	—	—	—	—
Sample size	0	0	0	0	663	421	370	169	0	0	0	0

[1]Probably mostly *Paralichthys lethostigma* which was abundant at upriver stations. 0 year class identified to species after April.
[2]*Penaeus* sp. was collected down to 11 mm TL in May, probably *P. aztecus*.

TABLE 7.—Relative densities (mean number of individuals 400 m²) for selected species at the peak of postlarval and early juvenile recruitment in the Cape Fear River estuary, N.C. Rotenone collection data are not presented for shrimp, *Penaeus* spp.

Species	Peak recruitment months	Baldhead Creek		Shellbed Island		Dutchman Creek		Walden Creek		Hechtic Creek	Barnards Creek
		Seine	Rotenone	Seine	Rotenone	Seine	Rotenone	Seine	Rotenone	Seine	Rotenone
Leiostomus xanthurus	Mar.-Apr.	1 781	972	1 259	3 474	4 520	2 721	4 043	3 762	1 510	
Brevoortia tyrannus	Apr.-May	110	16	24	373	439	505	153	3 821	618	
Mugil cephalus	Mar.-Apr.	80	109	172	1 788	970	209	24	909	803	
M. curema	May-June	712	179	148	979	2 251	21	73	71	0	
Penaeus aztecus	May-June	113	—	0	257	—	525	—	538	—	
P. duorarum	July-Aug.	266		14	2	—	31	—	92	—	
P. setiferus	July-Aug.	0	—	0	60	—	26	—	85	—	

April data only.

of brown shrimp occurred at Hechtic and Walden Creeks. Except for a single individual in August, none were collected at Shellbed Island, and catches were also low at the Baldhead Creek site. The presence of shrimp in high densities in Walden Creek is of interest since the organic (detrital) content of the substratum is the lowest of any of the Cape Fear stations. Except for one tributary where nearby construction activities have added large quantities of fine sediments, this creek is well scoured almost its entire length. White shrimp (*P. setiferus*) were most abundant at Hechtic and Dutchman Creeks, where the sediment contained considerable quantities of organic matter and were absent from the high salinity stations in Baldhead Creek and Shellbed Island. On the other hand, pink shrimp reached maximum abundance in Baldhead Creek, while intermediate numbers were also collected at Hechtic Creek.

Community Patterns

Numerical classification analysis was employed to detect underlying patterns among marsh nekton communities (Figure 4). Two primary station clusters were discerned by this procedure, a group consisting of the Baldhead Island sites (i.e., Baldhead Creek seine and rotenone stations and Shellbed Island) and a second group composed of the Walden and Hechtic Creeks and the Dutchman Creek seine station. The latter cluster was joined by the Walden and Dutchman Creek rotenone sta-

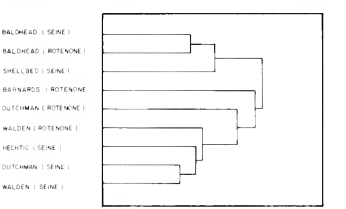


FIGURE 4.—Similarities among all stations collected from February to December 1977 in the Cape Fear River estuary, N.C. Associations in dendogram are based on pooled monthly collections. Sampling was not initiated at Barnards Creek, N.C., until April.

tions and by the Barnards Creek site which exhibited the lowest overall degree of association. Although the physicochemical factors at the Barnards Creek site differed in some respects from those of other stations (particularly with respect to percent organics, Table 1), it should be emphasized that this station was not collected until April and, therefore, did not reflect a large portion of winter recruitment. Since the rotenone stations were not collected uniformly throughout the year, they were omitted from further analysis. Data for individual species, however, are used to support conclusions drawn from seine studies.

A two-way coincidence table (Table 8) was prepared for seine data collected from February to December 1977 by first clustering the matrix for seine station associations and comparing these with a dendrogram for species associations. In this way, comparisons among stations was facilitated by direct cross-referencing against the characteristics species associations at each site. The five seine stations fell into two clusters at the 65% similarity level, designated A and B in the table. Twelve species association clusters were recognized at this same level. Clearly, several subcategories of marsh communities may be distinguished for the Cape Fear region, although the marshes also share many commonalities, as indicated in Figure 4 by the generally high similarity values among station clusters (>55%).

Members of Group III (Table 8) were generally ubiquitous, with most difference being reflected in relative numbers. *Leiostomus xanthurus*, *Mugil cephalus*, and *Brevoortia tyrannus*, for example, were more prevalent at Hechtic, Walden, and Dutchman Creeks, while the bay anchovy, *Anchoa mitchilli*, and *Menidia menidia* dominated at Baldhead Island stations. Species groups I, IV, and X were characterized by the lower salinities at Hechtic and Walden Creeks and included species present in relatively higher densities, such as the tidewater silverside, *M. beryllina*, and species normally associated with lower salinities, such as gizzard shad, *Dorosoma cepedianum*; mosquitofish, *Gambusia affinis*; *Anguilla rostrata*; and juvenile *Micropogonias undulatus*. Two freshwater fishes, the bluegill, *Lepomis macrochirus*, and golden shiner, *Notemigonus crysoleucas*, also were captured at these sites. In rotenone collections, by comparison, tidewater silverside were absent from Baldhead Creek collections and only six specimens were captured at Dutchman Creek. In Walden Creek, this species was a relativley abundant member of the community, contributing 1.3% of the total number of individuals (Table 5). At Barnards Creek, however, only 15 individuals were captured. Several other species were also more abundant in low salinity rotenone collections, postlarval and juvenile *M. undulatus* (9-83 mm), for example, were the fifth most abundant species captured in Barnards Creek samples, and *A. rostrata* and *G. affinis* contributed 2.6 and 1.6% of the total number of individuals, respectively (Table 5).

The Baldhead Creek and Shellbed Island sites form a complex that is influenced by the nearby marine environment. Groups VII, VIII, and IX included many species associated with intermediate to higher salinities and probably also reflected additional parameters such as the substratum composition and proximity to the ocean entrance. Several stenohaline marine species were collected only at these locations. These included rough silverside, *Membras martinica*; several species of searobins, *Prionotus* spp.; windowpane flounder, *Scopthalmus aquosus*; summer flounder, *Paralichthys dentatus*; fringed flounder, *Etropus crossotus*; gag, *Mycteroperca microlepis*; southern blue crab, *Callinectes similis*; inshore lizardfish, *Synodus foetens*; and pigfish, *Orthopristis chrysoptera*. Except for *Scopthalmus aquosus* and *E. crossotus*, these species were also recorded in low to intermediate densities from Baldhead Creek rotenone collections (e.g., pigfish ranked 17th in abundance out of a total of 61 taxa collected). Members of the genus *Prionotus* were not

TABLE 8.—Two-way coincidence table comparing dendograms for station and species associations in the Cape Fear River estuary, N.C., February-December 1977. The two station clusters, designated A and B, are cross-referenced against 12 species clusters derived from previous calculations. Dendrograms are not shown

B			A			
Dutchman Creek	Walden Creek	Hechtc Creek	Shellbed Island	Baldhead Creek	Species	
	2				*Notemigonus crysoleucas*	I
	3				*Morone saxatilis*	
	10				*Alosa aestivalis*	
1	1				*Trinectes maculatus*	II
2	1	2		5	*Cynoscion nebulosus*	III
2	26	16	3	1	*Strongilyura marina*	
741	1,217	1 199	1	266	*Penaeus aztecus*	
2 510	175	57	8 758	1 510	*Menidia menidia*	
231	304	6	405	106	*Eucinostomus argenteus*	
824	50	7	46	541	*Fundulus majalis*	
2 582	83	199	354	1 668	*Mugil curema*	
67	101	247	31	657	*Penaeus duorarum*	
24	192	89	55	70	*Lagodon rhomboides*	
1 387	1 666	7 967	71	287	*Brevoortia tyrannus*	
938	284	265	41	162	*Calinectes sapidus*	
4 160	780	3.009	525	263	*Mugil cephalus*	
502	112	160	115	108	*Bairdiella chrysura*	
3 056	1.240	590	730	938	*Fundulus heteroclitus*	
8 534	7 410	7 953	3 023	3 916	*Leiostomus xanthurus*	
1	29	14	19	48	*Paralichthys* spp.	
151	1 050	660	8 927	4 330	*Anchoa mitchilli*	
1	21	13			*Gambusia affinis*	IV
1	6	10			*Dorosoma cepedianum*	
1	82	199			*Menidia beryllina*	
4	3	122	3		*Micropogonias undulatus*	
3	3	8	2		*Caranx hippos*	
2	1	3	2		*Pomatomus saltatrix*	
6	2	49		1	*Anguilla rostrata*	
27	4	22		2	*Elops saurus*	
132	70	171			*Penaeus setiferus*	
1		15		32	*Syngnathus louisianae*	V
1	1	9		9	*Gobionellus boleosoma*	
		13	3	114	*Gobiosoma bosci*	
		20	1	7	*Lutjanus griseus*	
		2	5		*Citharichthys spilopterus*	VI
		2	4		*Caranx latus*	
			21		*Membras martinica*	VII
			3		*Citharichthys macrops*	
1	2	2	27	48	*Symphurus plagusia*	VIII
	1	2	5	16	*Monacanthus hispidus*	
		1	1	1	*Myrophis punctatus*	
	1		9	3	*Paralichthys dentatus*	
			5	2	*Mycteroperca microlepis*	
			2	1	*Etropus crossotus*	
			295	11	*Anchoa hepsetus*	
			3	1	*Scophthalmus aquosus*	
			3	1	*Prionotus carolinus*	
	1		9	18	*Synodus foetens*	
			34	91	*Callinectes similis*	
			19	29	*Orthopristis chrysoptera*	
			1	2	*Prionotus scitulus*	
			3	10	*Prionotus tribulus*	
				4	*Opsanus tau*	XI
				21	*Syngnathus fuscus*	
				3	*Prionotus evolans*	
				2	*Lutjanus synagris*	
				5	*Astroscopus y-graecum*	
			1	15	*Gobiosoma ginsburgi*	
		2			*Lepomis macrochirus*	X
		2			*Lucania parva*	
		2			*Evorthodus lyricus*	
2		1		1	*Chaetodipterus faber*	IX
62		1		2	*Sciaenops ocellata*	
3					*Pogonias cromis*	XII
3					*Gobionellus hastatus*	
2					*Trachinotus falcatus*	

recorded from low salinity sites with the exception of the two very small, unidentified species from Walden Creek in August (salinity 18.3‰). Also absent from low salinity rotenone collections were *S. aquosus*, *E. crossotus*, and *P. dentatus*; on the other hand, the southern flounder, *P. lethostigma*, was common at low salinity stations and was the 14th most abundant species at Barnards Creek, composing 1.2% of the total captured. A winter visitor to the estuary, striped cusk-eel, *Rissola marginata*, was present in Baldhead Creek rotenone collections; a total of 15 specimens were captured during February-April, and a single specimen was also captured at the seine site. At least three estuarine species with a previously reported preference for higher salinities were collected in larger numbers at Baldhead Island stations, the Atlantic silverside (Johnson 1975), striped killifish (Griffith 1974), and blackcheek tonguefish, *Symphurus plagiusa* (Gunter 1945; Reid 1954), which also was taken in substantial numbers in Dutchman Creek.

The affiliation of Dutchman Creek presents an interesting case among marshes. Recent construction activities nearby have effectively reduced the input of freshwater to this orginally brackish water creek (Birkhead[7]). Thus, apparently in the process of change, Dutchman Creek retains both original similarities to Walden Creek, and "newer" associations with higher salinity marshes (e.g., for the Atlantic silverside and white mullet).

DISCUSSION

Tidal Creeks as Nurseries

Due partly to sampling difficulties, the nursery role of tidal salt marshes, especially the shallow upper reaches of tidal creeks, has seldom been investigated (Herke 1971; Copeland and Bechtel 1974; Cain and Dean 1976). Nevertheless, it is this very habitat that has been defined by Purvis (see footnote 2) and others (Kilby 1955; Herke 1971; Dahlberg 1972) as one of the primary nursery zones where initial postlarval development takes place. Populations of marine-spawned species in the areas Purvis studied in Pamlico Sound, N.C., (low salinity, shallow tributaries with mud or mud-grass bottoms) were uniformly of very early juveniles. In the past, several investigators have pointed to the relationship between the size of organisms in an area and salinity as an indicator of the primary nursery grounds (Gunter 1945, 1961, 1967; Herke 1971; Dahlberg 1972; Copeland and Bechtel 1974). Others, however, have noted that the size-salinity relationship is not a simple one, and that interactions with food supplies, substratum characteristics, and other physicochemical factors dictate preferred zones for nursery utilization (Kilby 1955; Reid 1957; Simmons 1957; Dawson 1958; Reid and Hoese 1958; McHugh 1967; Parker 1971).

Results of my study demonstrate that shallow tidal creeks and marsh shoals of the Cape Fear River estuary harbor dense populations of postlarvae of several marine-spawned species. Field observations showed that young fishes and shellfish were actively seeking the creek headwaters, that in effect, the marshes fill up backwards during recruitment. Postlarval spot, *Mugil* spp., *Paralichthys* spp., red drum, and other species accumulated in great numbers in the upper reaches of the creeks and gradually decreased in densities downstream. Ichthyoplankton tows in the mouths and a short distance upstream in these same creeks yielded much lower concentrations of postlarvae than collections closer to the headwaters (Hodson see footnote 6). Although the gear deployed in these surveys differed, recent studies of gear efficiency indicated that the methods are reasonably similar (Weinstein and Davis in prep.). The period of residency in these habitats is apparently lengthy; winter recruits of several species were abundant throughout the summer (Figure 3); and a mass exodus did not seem to take place until the following fall. Other studies have shown, however, that larger members of the population tend to move downstream as they grow, leaving behind slower growing individuals and newer recruits (Herke 1971: Dunham 1972; Purvis see footnote 2).

Parallel conclusions on the comparative richness of shallow marsh habitats were reached by Marshall (1976). Employing similar sampling techniques, including the use of 1 mm mesh seines, he reported densities of spot, *Mugil* spp., Atlantic menhaden, and brown shrimp in two marsh areas altered by ditching for mosquito control to exceed 0.1 m^2. Standing crops of most species in the natural creeks and ditches he studied were among the highest ever reported for small estuarine nekton. A survey of the literature

[7]W. Birkhead, Associate, Cape Fear Estuarine Laboratory, North Carolina State University, Southport, N.C., pers. commun. April 1978

by Marshall (1976) supported this observation, even higher densities for total nekton were noted in the studies of Turner and Johnson (1974) in South Carolina tidal marshes. However, Marshall cautioned that the efficiency and selectivity of gear used to study various estuarine areas may, in part, be responsible for some of the differences seen among areas. Average densities in my study for the same species listed by Marshall all exceeded 0.1 organism m^2 except for brown shrimp. When seine data alone were considered for this species, however, densities of 0.1 m^2 were recorded.

The utilization of the marsh shallows does not, however, hold for all postlarvae that inhabit the Cape Fear region. Atlantic croaker, for example, occurred primarily in the deeper water of the river from the vicinity of the salt boundary through the mesohaline zone. As postlarvae, this species was noticeably absent in the downstream marshes and densities generally were low at upstream stations. The Atlantic croaker was not listed among the 10 most abundant species captured in each of two marsh areas near Beaufort, N.C., by Marshall (1976), nor was it among the 10 most abundant species collected in six tidal creeks located near Port Royal Sound, S.C. (Turner and Johnson 1974). In my study, only one specimen of the 1976-77 year class was collected before May, when juveniles (27-35 mm) appeared at low salinity stations. In the early stages of recruitment for the 1977-78 year class, however, low densities of postlarval and early juvenile croaker (9-19 mm) were collected, principally at Hechtic and Barnards Creeks. Haven (1957) and Wallace (1940) observed a similar distribution in the Chesapeake Bay, and for most Atlantic and Gulf coast estuaries containing deeper channels, this relationship seems to hold (Welsh and Breder 1923; Suttkus 1955; Nelson 1969). However, the Atlantic croaker also utilizes the marsh shallows extensively in some of the Gulf states, including Louisiana, Texas, and Mississippi (Herke 1971; Parker 1971; Arnoldi et al. 1974; Yakupzack et al. 1977). In the Cape Fear region, where there are extensive marshes, the Atlantic croaker is simply absent. Perhaps minimum temperatures during winter recruitment in the Cape Fear and other middle Atlantic coast estuaries are limiting for this species (Joseph 1972). Another species that seems to prefer open waters is the Atlantic menhaden, which was captured in lower numbers in the interior marshes than on the river shoals and in the ship channel (Hodson see footnote 6). Since postlarvae feed primarily on zooplankton (Thayer et al. 1974) which are found in higher concentrations out in the estuary (Jefferies 1975), this preference for open waters is not surprising.

These observations lead to conjecture as to the mechanisms that may reduce potential competition among the early life stages of species with similar food requirements (Thayer et al. 1974; Kjelson et al. 1975). The results of recent studies (May 1974; Thayer et al. 1974; Lasker 1975; Houde 1977; Laurence 1977) suggested that food supplies are potentially limiting in estuaries and nearshore areas and that critical densities of food items were required at several larval developmental stages. If species were undergoing diffuse competition (MacArthur 1972), they might, therefore, benefit from behavioral patterns that resulted in temporal and/or spatial segregation on the nursery grounds. There are apparently two major nursery areas in the Cape Fear estuary: the interior marshes, including the shallow marsh fringe, and the river mainstem at the head of the estuary. Related or potentially competitive species, by utilizing either one of these zones, may remain spatially segregated.

Seasonal presence also may enhance survival of many species; the data showed this clearly for white and striped mullet and for penaeid shrimp although local variables within each major nursery zone also influenced patterns of distribution for these groups. For example, white and pink shrimp were recruited at similar times of the year, yet they separated within the marsh zones on the basis of salinity. White mullet were much more abundant at high salinities in areas with sediments containing considerable quantities of organic matter; striped mullet were distributed throughout the estuary although they, too, were most abundant where sediments contained a high level of organics.

Salinity preferences for several dominant species are treated statistically in Table 9. Although consistent relationships appeared in the data, monthly values reflected local variations in freshwater flow. In September, for example, heavy rainfall in the vicinity of Dutchman Creek depressed salinities 16‰ below the previous collection date. The resident population of white mullet apparently remained in the area and catches were high (1,112 individuals/400 m^2 at the rotenone site). Along with lower catches for this species elsewhere in the system, this observation suggests

TABLE 9.—Partial correlations (given temperature) of species abundance with salinity in the Cape Fear River estuary, N.C. Collections with < 10 individuals of a given species in any month were omitted from the calculations. N.C. = 10 individuals collected. $^{**}P < .01$

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Pooled	χ^2	df
Leiostomus xanthurus	0.449	0.808	0.582	0.176	0.237	0.493	0.783	0.751	0.210	0.449	0.577	0.409**	13.870	10
Menidia menidia	.387	.983	.747	.856	.799	.546	.673	.676	.722	.799	.732	.727**	10.244	10
M. beryllina	.509	N.C.	N.C.	N.C.	.547	.604	.719	.755	.469	.820	.855	.693**	2.705	7
Mugil cephalus	.525	.132	.080	.637	.501	.118	.304	.769	.374	.418	.060	.291*	8.312	10
M. curema	N.C.	N.C.	N.C.	.769	.757	.627	.624	.067	.252	N.C.	N.C.	.560**	3.783	5
Symphurus plagiusa	N.C.	N.C.	N.C.	N.C.	N.C.	.018	.217	.068	.625	.523	N.C.	.092	4.428	4
Brevoortia tyrannus	N.C.	.001	.735	.570	.555	.274	.334	.537	.110	N.C.	N.C.	.426**	3.243	7
Fundulus heteroclitus	.293	.397	.269	.675	.438	.343	.441	.094	.169	.043	.082	.060	7.622	10
F. majalis	.665	.669	.887	.514	.700	.544	.600	.873	.453	.460	.654	.673**	4.827	10
Micropogonias undulatus	N.C.	N.C.	N.C.	.765	.724	.781	N.C.	N.C.	.580	.648	.576	.688**	0.732	5
Bairdiella chrysura	N.C.	N.C.	N.C.	N.C.	.146	.015	.516	.628	N.C.	N.C.	N.C.	.353	1.761	3
Anchoa mitchilli	N.C.	N.C.	N.C.	.449	.537	.271	.084	.109	.058	.030	.242	.130	3.090	7
A. hepsetus	N.C.	N.C.	N.C.	N.C.	.355	.324	.542	.585	N.C.	N.C.	N.C.	.459	0.421	3
Lagodon rhomboides	.111	.474	.032	.099	.162	.289	.384	.290	.332	N.C.	.857	.003	11.804	9
Sample size (stations)	7	8	9	9	9	9	9	9	9	9	9			

$^{1}\chi^2$ values are based on tests of equality among correlations of the 11 monthly collections; none were significant; therefore, all individual correlation values were pooled.

a lack of correlation of distribution with salinity. This effect occurred in other months for other species and is consistent with the patterns of distribution of estuarine organisms and their ability to withstand wide ranges of salinity, at least over the short term. What is important, however, is that during the course of residency in the marshes, the presence of several species was significantly correlated with salinity. Gunter (1961) draws a similar conclusion by stating that correlation is not necessarily with a given salinity but rather with the gradient as a whole.

Of the species tested (Table 9), striped mullet; blackcheek tonguefish; mummichogs; silver perch, *Bairdiella chrysura*; pinfish, *Lagodon rhomboides*; bay anchovy; and striped anchovy, *A. hepsetus*, were distributed independently of salinity. In several instances, a considerable portion of the variance associated with abundance data was explained by salinity alone; this was true for the Atlantic and tidewater silversides and for the striped killifish and Atlantic croaker. Although other r values were significant ($P = 0.01$) it is obvious that factors other than salinity were contributing to patterns of distribution.

Substrate characteristics have been shown to influence invertebrate populations and the structure of fish communities (Mills 1975). In this study, the distribution of several species also appeared influenced by properties of the sediment (Table 10). The abundance of *Menidia menidia* and *M. beryllina* was negatively correlated with percent organics, and the former species displayed a similar relationship with sorting coefficient. This is not at all surprising in light of their mode of feeding and the presence of currents which probably act to carry food items through the area. On the other hand, young striped mullet which relies heavily on detritus in its diet (Odum 1968) was expected to display a positive association with percent organics, but this did not occur with respect to all creeks concerned. If Barnards Creek was omitted from the calculations, however, the relationship became highly significant. The extremely high organic content of Barnards Creek sediments probably is indicative of highly reducing conditions, and may, in fact, have contributed to the low total fish catch in this creek.

TABLE 10.—Partial correlations (given salinity) of species abundances with several sediment parameters in the Cape Fear River estuary, N.C. Collections with < 10 individuals of a given species in any month were omitted from the calculations. Values in parentheses do not include Barnards Creek. $^{**}P < .01$

Species	Percent organics	Sorting coefficient	Fine sand
Menidia menidia	0.410**	0.468**	0.234
M. beryllina	.655**	.123	.009
Mugil cephalus	.065 (.562**)	.588**	.364
M. curema	.136 (.743**)	.620**	.399**
Symphurus plagiusa	.628**	.326	.210
Micropogonias undulatus	.553**	.366	.193
Fundulus heteroclitus	.297	.565**	.353**
Anchoa mitchilli	.031	.310	.511**

Two other species exhibited a positive relationship with percent organics, the blackcheek tonguefish and the Atlantic croaker. The blackcheek tonguefish commonly is associated with muddy bottoms and high salinity (Gunter 1945; Kilby 1955) although salinity did not seem to play a role in governing its distribution in the Cape Fear region (Table 7). Darnell (1958) has described the feeding preference of young croaker for organic matter and since this species tends to accumulate toward the headwaters of many sys-

tems (where deposition is greatest), this result may have been expected.

Thus, both spatial and seasonal programming seem to play an integral role in habitat partitioning among ocean-spawned recruits utilizing Cape Fear estuary primary nurseries. Whether or not this partitioning results in enhanced survival of otherwise competing species remains an area for fruitful research.

Community Composition

Each marsh community in the Cape Fear estuary displayed several unique characteristics. In addition to seasonal differences in species richness, abundance relationships varied among marsh complexes (Tables 5, 8). Although some species appeared in relatively low numbers, they only occurred in certain areas or were much more abundant in a specific marsh complex. The Atlantic croaker, southern flounder, mosquitofish, and the seasonal capture of freshwater species including white catfish, *Ictalurus catus*, bluegill, golden shiner, *Notemigonus crysoleucas*, and largemouth bass, *Micropterus salmoides*, were associated with low salinity sites (Walden, Hechtic, and Barnards Creeks). More abundant members of these communities also seemed to display a preference for lower salinities including tidewater silverside and 0 year class Atlantic menhaden (see also Table 9).

Two groups apparently set the high salinity marshes apart from other areas. Several species, usually associated with estuaries during the early part of their life cycle, were restricted mainly to the polyhaline zone. Pigfish, white mullet, red drum, and southern blue crab were in this category and along with two permanent marsh residents, Atlantic silverside and striped killifish were much more abundant or were only captured at high salinities.

The predominance of sandy areas near Baldhead Island, in combination with higher salinity, attracted several species—e.g., the windowpane, rough silverside, spotted whiff, *Citharichthys macrops*, inshore lizardfish, and bighead sea robin, *Prionotus tribulus*—were in this group.

The proximity of the Baldhead Island marsh to the ocean entrance also provided suitable conditions for invasion by several stenohaline species not usually associated with estuaries. Many of these species were seasonal visitors to the area and their general rarity suggests that the marsh is not a primary nursery habitat. Young sergeant major, *Abudefduf saxatilis*; great barracuda, *Sphyraena barracuda*; Atlantic spadefish, *Chaetodipterus faber*; lookdown, *Selene vomer*; lane snapper, *Lutjanus synagris*; gag, and others are seldom collected in marshes and, in fact, would probably be classified as reef species. McHugh (1967) has described these species as adventitious invaders of the estuary.

The majority of community dominants captured in this study were transient in the marshes, being resident for only part of their life cycle. The only permanent residents which were dominant members of the marsh community were mummichog, striped killifish, and Atlantic silversides. Thus, energy flow at higher trophic levels is predominantly through those species that utilize the marsh nurseries in the first year of life. Although larger individuals of these species probably make feeding forays into the upper tidal creeks, their importance in these areas is not known.

Not surprisingly then, species richness was greatest in areas (Baldhead Island and upriver) influenced by the marine and freshwater biotas. It is tempting to relate higher species diversity to more stable physicochemical conditions existing at these sites, yet as indicated in Table 1, salinity and temperature variations were generally similar at all stations. A more plausible explanation of these phenomena may lie in what has been described as an "edge effect" (Odum 1971). Thus, Baldhead Island forms a mixing zone for estuarine, shelf, and reef faunas as evidenced by the seasonal invasion of the latter forms. Similarly, Barnards and Hechtic Creeks are influenced by fresh and brackish faunas at various times of the year.

It is a remarkable observation that if all the transient members of the shallow marsh community were removed, that the remaining, permanent estuarine residents would form a community distinguished by the paucity of its members (Emery and Stevenson 1957). The importance of the link, or continuum, between the estuary and the nearshore marine environment and the energy transfers therein, is highlighted by this observation. It seems obvious that the functional integrity of the estuarine ecosystem is as much dependent on the marine fish community as the members of that community are dependent on the estuary for part of their life cycle. Continued productivity, within the estuary and marine environment for certain species important to man may indeed, depend on the continued health of this relationship.

CONCLUSIONS

Shallow marsh habitats are demonstrably critical areas for the earliest developmental stages of fishes and shellfish. Postlarvae of most species important to man were found to reside in immense numbers at the headwaters of shallow tributary creeks and along the marsh fringe at the rivers edge. With few exceptions these species were the community dominants at all study sites.

Salinity seemed to play an important role in governing spatial distributions of many species and to a lesser extent substratum characteristics interacted with salinity to restrict certain species to a narrow range of habitats. Based partly on these observations, a hypothesis has been established whereby seasonal programming and spatial distributions mediated by salinity and substratum preferences (and probably other factors) may serve to reduce competition among species recruited to the estuary throughout the year.

Similarly, these and other physicochemical parameters, which affect individual tolerances, create unique conditions in each marsh complex that affects the composition of the nekton community. Species richness was highest in the marshes closest to the ocean entrance where higher salinities allowed seasonal invasion by marine forms otherwise unable to reside in the estuary. An apparently similar phenomenon, more limited in extent, occurred at the head of the estuary for freshwater species. Despite the seasonal progression of species, it is apparent that marsh communities in the Cape Fear are highly structured and are able to maintain a specific identity throughout the year.

ACKNOWLEDGMENTS

I am grateful to J. P. Lawler of the Lawler, Matusky & Skelly (LMS) Engineers and W. T. Hogarth of the Carolina Power and Light Co. for the opportunity to conduct these studies. I am also grateful to the biotechnicians of LMS, in particular, R. Beatty, R. Davis, L. Gerry, J. Hecht, W. Pollard, and P. Woodard for their conscientious efforts in the field and laboratory; the quality of their work added measurably to the success of this study. Several individuals have provided constructive criticism of the manuscript including K. L. Heck, J. P. Lawler, G. W. Thayer, R. L. Wyman, and two anonymous reviewers. S. Weiss contributed significantly with his expertise in statistics, and J. Berkun, B. McKenna, and S. Kaufman provided editorial and typing assistance. This program was funded by the Carolina Power and Light Co.

LITERATURE CITED

ANDERSON, W. W.
1957. Early development, spawning, growth, and occurrence of the silver mullet (*Mugil curema*) along the south Atlantic coast of the United States. U.S. Fish Wildl. Serv., Fish. Bull. 119: 397-414.

ARNOLDI, D. C., W. H. HERKE, AND E. J. CLAIRAIN, JR.
1974. Estimate of growth rate and length of stay in a marsh nursery of juvenile Atlantic croaker, *Micropogon undulatus* (Linnaeus), "sandblasted" with fluorescent pigments. Gulf Caribb. Fish. Inst. Proc. 26th Annu. Sess., p. 158-172.

AMERICAN SOCIETY FOR TESTING AND MATERIALS.
1963. Standard method for particle-size analysis of soils. Am. Soc. Test. Mater. D422-63, p. 200-211.

BEARDEN, C. M.
1964. Distribution and abundance of Atlantic croaker, *Micropogon undulatus*, in South Carolina. Contrib. Bears Bluff Lab. 40, 23 p.

CAIN, R. L., AND J. M. DEAN.
1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. (Berl.) 36: 369-379.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75: 657-702.

CLIFFORD, H. T., AND W. STEPHENSON.
1975. An introduction to numerical classification. Academic Press, N.Y., 229 p.

COPELAND, B. J., AND T. J. BECHTEL.
1974. Some environmental limits of six Gulf coast estuarine organisms. Contrib. Mar. Sci. 18: 169-204.

DAHLBERG, M. D.
1972. An ecological study of Georgia coastal fishes. Fish. Bull., U.S. 70: 323-353.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Ponchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5: 353-416.

DAWSON, C. E.
1958. A study of the biology and life history of the spot, *Leiostomus xanthurus*. Lacepede, with special reference to South Carolina. Contrib. Bears Bluff Lab. 28, 48 p.

DE SYLVA, D. P.
1975. Nektonic food webs in estuaries. *In* L. E. Cronin (editor), Estuarine research. Vol. 1, p. 420-447. Academic Press, N.Y.

DUNHAM, F.
1972. A study of commercially important estuarine-dependent industrial fishes. La. Wildl. Fish. Comm. Tech. Bull. 4, 63 p.

DURBIN, A. G., AND E. G. DURBIN.
1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. (Berl.) 33: 265-277.

EMERY, K O , AND R E STEVENSON
1957 Estuaries and lagoons *In* J W Hedgpeth (editor), Treatise on marine ecology and paleoecology Vol 1, p 673-693 Geol Soc Am Mem 67

FISHER, R A
1973 Statistical methods for research workers Hafner Publ Co , N Y , 362 p

FOLK, R L
1974 Petrology of sedimentary rocks Hemphill Publ Co , Austin, Tex , 182 p

GAINEY, L F , JR , AND M J GREENBERG
1977 Physiological basis of the species abundance-salinity relationship in molluscs A speculation Mar Biol (Berl) 40 41-49

GRIFFITH, R W
1974 Environmeot and salinity tolerance in the genus *Fundulus* Copeia 1974 319-331

GUNTER, G
1945 Studies on marine fishes of Texas Publ Inst Mar Sci Univ Tex 1 1-190
1961 Some relations of estuarine organisms to salinity Limnol Oceanogr 6 182-190
1967 Some relationships of estuaries to the fisheries in the Gulf of Mexico *In* G H Lauff (editor), Estuaries, p 621-638 Am Assoc Adv Sci , Publ 83, Wash , D C

GUNTER, G , AND H H HILDEBRAND
1951 Destruction of fishes and other organisms on the South Texas Coast by the cold wave of January 28 - February 3, 1951 Ecology 32 731-736

HACKNEY, C T , W D BURBANCK, AND O P HACKNEY
1976 Biological and physical dynamics of a Georgia tidal creek Chesapeake Sci 17 271-280

HANSEN, D J
1970 Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-65 Fish Bull , U S 68 135-146

HAVEN, D S
1957 Distribution, growth, and availability of juvenile croaker, *Micropogon undulatus*, in Virginia Ecology 38 88-97

HEDGPETH, J W
1957 Biological aspects *In* J W Hedgpeth (editor), Treatise on marine ecology and paleoecology Vol 1, p 693-749 Geol Soc Am Mem 67.

HERKE, W H
1971 Use of natural, and semi-impounded, Louisiana tidal marshes as nurseries for fishes and crustaceans Ph D Thesis, Louisiana State Univ , Baton Rouge, 264 p

HOLDE, E D
1978 Critical food concentrations for larvae of three species of subtropical marine fishes Bull Mar Sci 28 395-411

HURLBERT, S H
1971 The nonconcept of species diversity a critique and alternative parameters Ecology 52 577-586

JEFFERIES, H P
1975 Diets of juvenile Atlantic menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents J Fish Res Board Can 32 587-592

JOHNSON, M S
1975 Biochemical systematics of the atherinid genus *Menidia* Copeia 1975 662-681

JOSEPH, E B
1972 The status of the sciaenid stocks of the middle Atlantic coast Chesapeake Sci 13 87-100

JUNE, F C , AND J L CHAMBERLIN
1959 The role of the estuary in the life history and biology of Atlantic menhaden Proc Gulf Caribb Fish Inst 11th Annu Sess , p 41-45.

KHLEBOVICH, V V
1969 Aspects of animal evolution related to critical salinity and internal state Mar Biol (Berl) 2 338-345.

KILBY, J D
1955 The fishes of two Gulf coastal marsh areas of Florida Tulane Stud Zool 2 173-247.

KJELSON, M A , D S PETERS, G W THAYER, AND G N JOHNSON
1975 The general feeding ecology of postlarval fishes in the Newport River estuary Fish Bull , U S 73 137-144

LASKER, R
1975 Field criteria for survival of anchovy larvae The relation between inshore chlorophyll maximum layers and successful first feeding. Fish Bull ,U S 73 453-462

LAURENCE, G C
1977 A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. Fish Bull , U S 75 529-546

MACARTHUR, R H
1972 Geographical ecology patterns in the distribution of species Harper and Row, N Y , 269 p

MARSHALL, H L
1976 Effects of mosquito control ditching on *Juncus* marshes and utilization of mosquito control ditches by estuarine fishes and invertebrates Ph D Thesis, Univ North Carolina, Chapel Hill, 204 p

MASSMAN, W H , AND A L PACHECHO
1960 Disappearance of young Atlantic croakers from the York River Virginia Trans Am Fish Soc 89 154-159

MAY, R C
1974 Larval mortality in marine fishes and the critical period concept *In* J H S Blaxter (editor), The early life history of fish, p 3-19 Springer-Verlag, Berl

MCHUGH, J L
1967 Estuarine nekton *In* G H Lauff (editor), Estuaries, p 581-620 Am Assoc Adv Sci , Publ 83, Wash , D C

MILLS, E L
1975 Benthic organisms and the structure of marine ecosystems J Fish Res Board Can 32 1657-1663.

MOORE, R H
1974 General ecology, distribution and relative abundance of *Mugil cephalus* and *Mugil curema* on the South Texas coast Contrib Mar Sci 18 241-255

NELSON, W R
1969 Studies on the croaker, *Micropogon undulatus* Linnaeus, and the spot, *Leiostomus xanthurus* Lacepede, in Mobile Bay, Alabama J Mar Sci Ala 1 1-14-92

ODUM, E P
1971 Fundamentals of ecology 3d ed W B Saunders Co , Phila , 574 p

ODUM, W E
1968 The ecological significance of fine particle selection by the striped mullet *Mugil cephalus* Limnol Oceanogr 13 92-98

PARKER, J. C.
1971. The biology of the spot, *Leiostomus xanthurus* Lacepede, and the Atlantic croaker, *Micropogon undulatus* (Linnaeus), in two Gulf of Mexico nursery areas. Ph.D. Thesis, Texas A&M Univ., College Station. 236 p.

REID, G. K.
1957. Biologic and hydrographic adjustment in a disturbed Gulf Coast estuary. Limnol. Oceanogr. 2:198-212.

REID, G. K., AND H. D. HOESE
1958. Size distribution of fishes in a Texas estuary. Copeia 1958:225-231.

REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1-94.

REMANE, A.
1934. Die brackwasserfauna. Zool. Anz. (Suppl.) 7:34-74.

RICHARDS, C. E., AND M. CASTAGNA
1976. Distribution, growth, and predation of juvenile white mullet (*Mugil curema*) in oceanside waters of Virginia's eastern shore. Chesapeake Sci. 17:308-309.

SHANNON, C. E., AND W. WEAVER
1949. The mathematical theory of communication. Univ. Ill. Press, Urbana. 117 p.

SIMMONS, E. G.
1957. An ecological survey of the Upper Laguna Madre of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 4(2):156-200.

SNEATH, P. H. A., AND R. S. SOKAL
1973. Numerical taxonomy. W. H. Freeman Co., San Franc., 573 p.

SUTTKUS, R. D.
1955. Seasonal movements and growth of the Atlantic croaker (*Micropogon undulatus*) along the east Louisiana coast. Proc. Gulf Caribb. Fish. Inst., 7th Annu. Sess. p. 151-158.

THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACKEY
1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15:9-16.

THOMAS, J., AND H. LOESCH
1970. Some notes on fish collected in the Barataria Bay, Louisiana, region. *In* Coastal studies bulletin 5, p. 53-57. Spec. Sea Grant Issue, La. State Univ., Baton Rouge.

TURNER, W. R., AND G. N. JOHNSON
1974. Standing crops of aquatic organisms in tidal streams of the lower Cooper River system, South Carolina. *In* F. Nelson (editor), The Cooper River environmental study, p. 13-20. S.C. Water Res. Comm. 177.

U.S. ARMY CORPS OF ENGINEERS
1953. The unified soil classification system. U.S. Army Corps Eng., Tech. Memo. 3-357, 3 vol.

WALLACE, D. H.
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.

WELSH, W. W., AND C. M. BREDER, JR.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.

WHITTAKER, R. H., AND C. W. FAIRBANKS
1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39:46-65.

WINSOR, C. P., AND G. L. CLARKE
1940. A statistical study of variation in the catch of plankton nets. J. Mar. Res. 3:1-34.

YAKUPZACK, P. M., W. H. HERKE, AND W. G. PERRY
1977. Emigration of juvenile Atlantic croakers, *Micropogon undulatus*, from a semi-impounded marsh in southwestern Louisiana. Trans. Am. Fish. Soc. 106:538-544.

LARVAL DEVELOPMENT OF THE CUBAN STONE CRAB, *MENIPPE NODIFRONS* (BRACHYURA, XANTHIDAE), UNDER LABORATORY CONDITIONS WITH NOTES ON THE STATUS OF THE FAMILY MENIPPIDAE[1]

LIBERTA E. SCOTTO[2]

ABSTRACT

The complete larval development of the Cuban stone crab, *Menippe nodifrons*, is described and illustrated. Larvae reared in the laboratory passed through a prezoeal, five and uncommonly six zoeal, and one megalopal stage. At 30° C the megalopal stage was attained in 16-17 days, at 20° C, 28-37 days. The six zoeal stages of *M. nodifrons* are compared with those of its sympatric congener *M. mercenaria* and with the first zoeal stage of the Indo-Pacific species *M. rumphii*. Larvae of the genus *Menippe* may be distinguished from other xanthid larvae by a combination of morphological features, including antennal development (exopodite at least three-fourths the length of protopodite), lack of setae on the basal segment of the second maxillipedal endopodite, and number of larval stages (*Menippe*, 5 or 6, most other xanthids, 4). Using Lebour's criteria (emphasizing antennal development and number of zoeal stages) to determine the primitive or advanced status of decapod larvae, the genus *Menippe* is more closely related to the phylogenetically primitive family Cancridae than to most of the Xanthidae. The possible reestablishment of the family Menippidae is discussed in view of new larval evidence.

The Cuban stone crab, *Menippe nodifrons* Stimpson 1859, is a medium-sized xanthid crab closely allied to the common commercial stone crab, *Menippe mercenaria* (Say 1818). The type-locality of *M. nodifrons* is the Indian River region located on the central eastern Florida coast between lat. 27° and 29° N. The western Atlantic range of the species extends from the Indian River, Fla., to the state of Santa Catherina, Brazil. Although Rathbun (1930) listed Cameron, La., as a collection site, subsequent sampling in this and other areas of the northwestern Gulf of Mexico had failed to produce any more specimens (Felder[3]). In the eastern Atlantic, specimens attributed to *M. nodifrons* have been recorded from Senegal to Angola, West Africa (Monod 1956).

Studies on *M. nodifrons* have been primarily taxonomic. Since Rathbun's monograph on the American cancroid crabs (1930), the major studies dealing with this species include faunal investigations of West Africa (Capart 1951; Monod 1956), a survey of stomatopod and decapod crustaceans of Portuguese Guiana (Vilela 1951), and an ecological investigation of the species on Floridan sabellariid worm reefs (Gore et al. 1978).

Although there are five (possibly seven) species in the genus *Menippe*, four occurring in the New World, *M. mercenaria* is the only species whose complete larval development has been described (Hyman 1925; Porter 1960). The first zoeal stage of a species identified as *M. rumphii* (Fabricius 1798) was described by Prasad and Tampi (1957) from an ovigerous female collected from the Indian Ocean (Mandapam Camp, South India). However, the taxonomy of *M. rumphii* is confused and the species is distinguished from *M. nodifrons* primarily by the presence of stridulating ridges on the palm (Stimpson 1871; Milne-Edwards 1873). Whether Rathbun (1930) and Monod (1956) were correct in synonymizing *M. rumphii* with *M. nodifrons*, remains to be seen; the former is also considered to be a Caribbean-Western Atlantic species (Dana 1852; Milne-Edwards 1873). If *M. rumphii* is indeed synonymous with *M. nodifrons* and not a separate species, Prasad and Tampi's Mandapam Camp record would be a remarkable range extension for *M. nodifrons*. Further investigation on larval morphology and development may answer this question.

[1]Scientific Contribution No. 118, from the Smithsonian Institution-Harbor Branch Foundation, Inc., Scientific Consortium, Link Port, Fort Pierce, FL 33450. This paper is Article XII, Studies on Decapod Crustacea from the Indian River region of Florida.

[2]Smithsonian Institution, Fort Pierce Bureau, Fort Pierce, FL 33450.

[3]Felder, D. 1973. An annotated key to the crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. LSU-SG-73-02, 103 p. Louisiana State University, Baton Rouge, LA 70803.

Manuscript accepted January 1979.
FISHERY BULLETIN: VOL. 77, NO. 2, 1979.

To provide evidence for this problem, the complete larval development of *M. nodifrons*, reared under laboratory conditions, is described and illustrated here. Larvae of *M. nodifrons* are compared insofar as possible with descriptions of *M. mercenaria* and *M. rumphii*, and features used in separating the various larvae are noted.

MATERIALS AND METHODS

A 66.0 mm CW (carapace width) female with bright orange eggs was collected from a sabellarid worm, *Phragmatopoma lapidosa*, reef at Seminole Shores, Martin County, Fla. (Gore et al. 1978) on 15 June 1977. Ovigerous females were found from May through August. The berried crab was retained in a nonflowing marine aquarium at the Smithsonian Institution, Fort Pierce Bureau, and fed mullet, *Mugil* sp., strips daily. The egg mass progressively darkened from bright orange to dark brown until hatching on 26 June 1977. The larvae were cultured in the laboratory using methods developed by Costlow and Bookhout (1960, 1962), Gore (1968), and Provenzano (1967). Six 24-compartmented trays were used, and each compartment contained three zoeae. Equal numbers of zoeae were reared in oceanic water (35‰) at 20 C (±0.5) in constant light; at room temperature (range = 21–26.5 C; $\bar{x}$ = 24.5 C) in diurnal light; and at 30 C (±0.5) in a constant temperature unit (CTU) in 12 h of light, 12 h of darkness. Seawater in the trays was changed and zoeae were fed freshly hatched *Artemia salina* nauplii daily. The number of zoeae was reduced to one per compartment on completion of the molt to the second zoeal stage.

Throughout the course of larval development all molts, dead zoeae, and some living representatives were preserved in 70% ethanol. Usually 10 specimens at each stage of development were dissected and examined for morphological characters using procedures described in studies by Gore (e.g., 1968). In the description that follows the first four zoeal stages of *M. nodifrons* are denoted as zoeae one (Z I) to zoeae four (Z IV). However, the fifth zoeal stage is discussed as either the penultimate fifth stage (Z Vp) which molts to a sixth stage before molting to megalopa, or the ultimate fifth stage (Z Vu) which molts directly to megalopa. Both fifth stages possess pleopods, appendages that typically develop in the stage preceding megalopa. Because there are few morphological differences between the penultimate and ultimate fifth stages, as noted in the larval descriptions, they are each considered one stage, and not substages. The sixth stage is referred to as an intercalated stage because it is inserted between the seemingly regular molt from fifth stage (i.e., Z Vu) to megalopa.

The measurement for each zoeal stage is the arithmetic mean of all specimens examined. Carapace length was measured from the base of the rostrum to the posterior edge of the carapace along the midline. Carapace width, in the megalopal stage, was measured across the widest part of the carapace. Direction of setation formulae in the descriptions progress proximal to distal.

A complete series of larvae, and or their molts, were deposited in the National Museum of Natural History, Washington, D.C.; the Allan Hancock Foundation, University of Southern California, Los Angeles; the British Museum (Natural History), London; the Rijksmuseum van Natuurlijke Historie, Leiden; the Geneva Museum of Natural History, Geneva; and the Museum National d'Histoire Naturelle, Paris.

DESCRIPTION OF THE LARVAE

First Zoeae

Carapace length: 0.55 mm.
Number of specimens examined: 10

Carapace (Figure 1A, B). Cephalothorax smooth, globose, with dorsal, rostral, and 2 lateral spines. Posteriorly curving dorsal spine usually 0.1 × longer, but in some specimens equal to or shorter than straight rostral spine. Length of dorsal spine about 2.75 × that of short, ventrally curving lateral spines. A minute seta found posterior to and at base of dorsal spine throughout all zoeal stages. A dorsal tubercle present in all stages midway between bases of dorsal and rostral spines. Eyes unstalked.

Abdomen (Figure 1A, B). Five somites and telson; second through fifth with 2 small setae on posterodorsal margin (remaining throughout all zoeal stages); second with small pair of lateral spines or knobs curving anteriorly; third with pair curving posteriorly (both pair present in all stages); fifth with pair of large ventrally curved spines at dorsolateral angle, present in all zoeal stages.

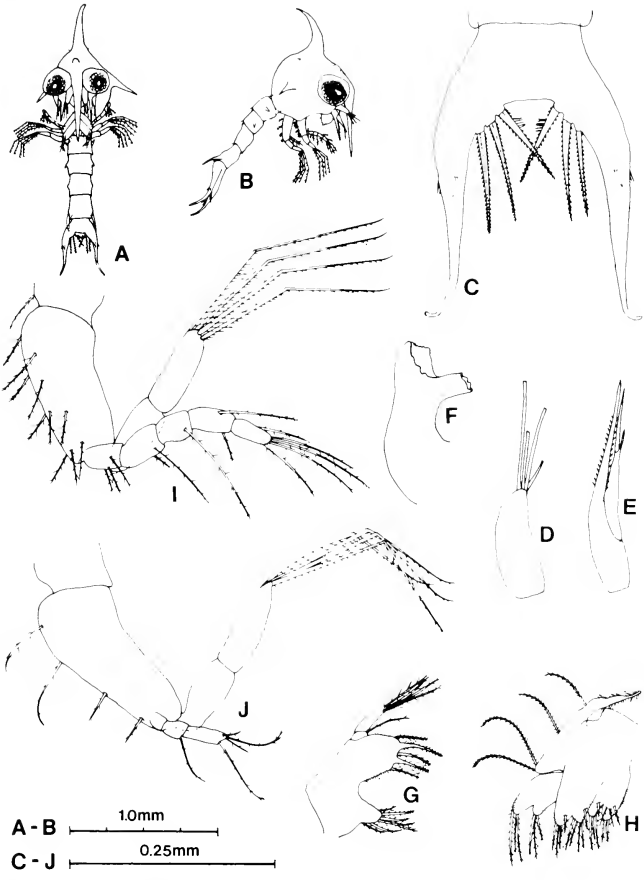


FIGURE 1.—First zoeal stage of *Menippe nodifrons*. (A) Ventral view, (B) lateral view, (C) telson, (D) antennule, (E) antenna, (F) left mandible (in ventral view as illustrated here and throughout all zoeal stages), (G) maxillule, (H) maxilla, (I) maxilliped 1, (J) maxilliped 2.

Telson (Figure 1C). One dorsal and two smaller lateral spines present on median portion of each upcurved furca. Three spines, each with three rows of spinules, on inner margin of each furca (present in all zoeal stages); setae replace spinules at midpoint of innermost spines, number variable but setae present in all zoeal stages.

Antennule (Figure 1D). Conical rod with 4 unequal aesthetases terminally.

Antenna (Figure 1E). Protopodite a slender process bearing two rows of small teeth from about midlength to one-fifth from the distal tip. Exopodite tapered, approximately 0.75 × length of protopodal process, with a slender spine (present in all zoeal stages) near distal end extending almost as far as tip of protopodal process; slender spine about 0.4 × length of exopodite.

Mandible (Figure 1F). Assymetrically dentate, scoop-shaped process. Incisor process elongate with indistinct dentation. Molar process irregularly serrate on outer margin; left molar process with 2 or 3 small prominences along inner margin and at junction with incisor process; right side either smooth or with a prominence.

Maxillule (Figure 1G). Endopodite with two segments, proximal short with 1 long feathery seta laterally, distal with 4 long setae; 2 terminal, 2 subterminal. Coxal endite with 7 plumodentate setae (armed with hair proximally, spinules distally). Basal endite with 5 plumodentate setae, 2 of which are stouter; lower margin of endite with rows of fine hairs.

Maxilla (Figure 1H). Endopodite bilobed, each with 3 setae. Coxal and basal endites with 5 and 4 setae respectively, placed as shown. Anterior and posterior margins of endopodite, as well as basal and coxal endites, pubescent. Scaphognathite with 4 plumose setae on outer margin; distal portion tapering to a thin plumose process.

Maxilliped 1 (Figure 1I). Coxopodite with 1 seta; basipodite with 10 ventral setae progressing distally 2,2,3,3. Endopodite five-segmented, ventral setae 3,2,1,2,4 + I (Roman numeral denotes dorsal setae). Exopodite two-segmented; 4 natatory setae terminally.

Maxilliped 2 (Figure 1J). Coxopodite naked; basipodite with 4 ventral setae. Endopodite three-segmented, ventral setae progressing distally 0,1,4 (3 terminal plus 1 subterminal). Exopodite two-segmented, 4 natatory setae terminally.

Color. Zoeae transparent, appearing gold with emerald green eyes under reflected light. Chromatophore position follows Aikawa (1929). Single brown chromatophores placed as follows: precardiac, occasionally one at posterior tip of dorsal spine, postcardiac, carapacial (posterolateral margin of cephalothorax), labral, mandibular, and maxillipedal (distally on the basipodites of the first and second maxillipeds). Two brown chromatophores placed ventrally on all abdominal somites and telson. Singular orange chromatophores placed as follows: precardiac, postcardiac, and carapacial (posterolateral margin of cephalothorax).

Second Zoeae

Carapace length: 0.68 mm.
Number of specimens examined: 10.

Carapace (Figure 2A, B). Cephalothorax as in stage I, but with additional setae placed as follows: 1 on lateral, 2 on posterolateral margin, a pair of minute setae posterolateral to dorsal tubercle, 2 minute interocular setae. Dorsal and rostral spines increased in length, now 2 × longer than lateral spines. Eyes stalked.

Abdomen (Figure 2A, B). First somite with 1 or 2 dorsal setae; second unchanged; third and fourth with an additional pair of small spines at posteroventral angle; fifth often with small blunt tooth at posteroventral angle.

Telson (Figure 2C). Dorsal and lateral spines on medial portion of elongate furcae now minute. A pair of small setae along posterior telsonal margin. Six spines between furcae as previously described and illustrated.

Antennule (Figure 2D). Similar in form to first stage; basal region swollen; aesthetases increased to 5 or 6, unequal in length.

Antenna (Figure 2E). Similar in form to first stage; protopodal basal region produced as a small hump (= endopodite primordium); exopodite spine

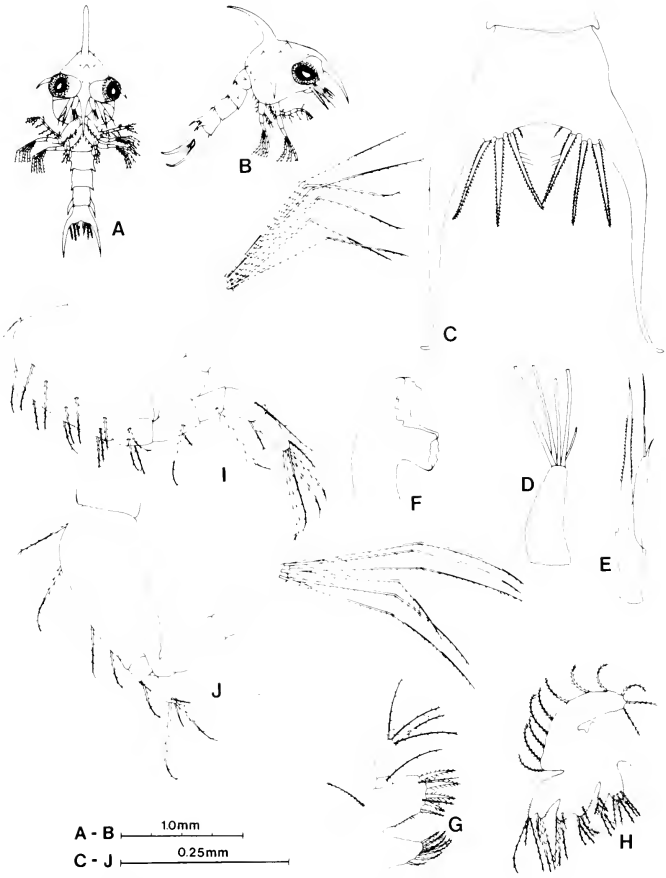


FIGURE 2.—Second zoeal stage of *Menippe nodifrons*. (A) Ventral view, (B) lateral view, (C) telson; (D) antennule, (E) antenna, (F) mandible; (G) maxillule, (H) maxilla, (I) maxilliped 1, (J) maxilliped 2.

equal to or surpassing protopodal process, about 0.5 × length of exopodite.

Mandible (Figure 2F). Incisor process stouter, dentation irregular. Left molar process with 3 irregular teeth along inner margin to junction with incisor process, right molar process with 1 tooth.

Maxillule (Figure 2G). Setae on endopodite and coxal endites unchanged; basal endite now with 5 spines and 2 setae, plus 1 long feathery seta laterally.

Maxilla (Figure 2H). Setae on endopodite; coxal and basal endites unchanged. Scaphognathite with 11 plumose setae, no elongate distal process.

Maxilliped 1 (Figure 2I). Coxo-, basi-, and endopodites unchanged. Exopodite with 6 natatory setae.

Maxilliped 2 (Figure 2J). Coxo-, basi-, and endopodites unchanged. Exopodite with 6 natatory setae.

Color. Darker orange-brown, though chromatophore number and position unchanged from first stage; eyes with an orange-rose hue.

Third Zoeae

Carapace length: 0.80 mm.
Number of specimens examined: 10.

Carapace (Figure 3A, B). Cephalothorax inflated, posterolateral border with 8 (7-9) setae. Three pair of minute setae along dorsal midline as in stage II. Dorsal and rostral spines increased in length, usually 3.5 × longer than lateral spines. Buds of third maxillipeds and thoracic appendages barely visible through carapace.

Abdomen (Figure 3A, B). Now with 6 somites, sixth with 2 dorsal setae posteriorly but no spines. Posterolateral spines of third, fourth, and dorsolateral spines of fifth somites elongate. Three dorsal setae on first somite.

Telson (Figure 3C). Dorsal and lateral spines on median portion of furcae miniscule. Spination and setation of posterior margin as before, occasionally an additional median seta. Furcae 0.75 × length of telson.

Antennule (Figure 3D). Similar in form to second stage; terminal aesthetascs usually 4 (3-5); 3 long, 1 short.

Antenna (Figure 3E). Endopodal bud enlarged. Exopodal spine extended slightly beyond slender protopodal process, and equal in length to exopodite.

Mandible (Figure 3F). Incisor process similar in form to second stage, 3 or 4 irregular teeth on left side, 2 on right.

Maxillule (Figure 3G). Basal endite with 1 additional seta, now 5 spines, 3 setae, plus lateral seta as before. Setae of endopodite and coxal endites unchanged.

Maxilla (Figure 3H). Endopodal setation as in stage II: basal endite lobes 5,5; coxal endite lobes usually 5,4 (6,4). Scaphognathite with 19 or 20 marginal plumose setae.

Maxilliped 1 (Figure 3I). Similar in form to second stage; coxo- and basipodal setae unchanged; exopodite with 8 natatory setae; endopodite usually with an additional lateral seta on the distal segment (formula now 3,2,1,2,5+1; rarely 3,2,1,2,4+1).

Maxilliped 2 (Figure 3J). Similar in morphology to second stage; exopodite with 8 natatory setae.

Color. Two orange chromatophores ventrally on first through fifth abdominal somites; other chromatophores as before. Entire zoea dark orange-rose; rose coloration concentrated on posterior and posterolateral margins of cephalothorax. Lateral carapace and abdominal spines, now pale orange-rose. Dorsal carapace spine clear except for orange-rose hue at base and along posterior margin. Mandible and labrum dark brown. Eyes with rose coloration concentrated dorsally. Abdominal somites 1 through 5 darker orange-brown than in previous stage. Sixth somite pale orange-brown.

Fourth Zoeae

Carapace length: 1.0 mm.
Number of specimens examined: 10.

Carapace (Figure 4A, B). Cephalothorax

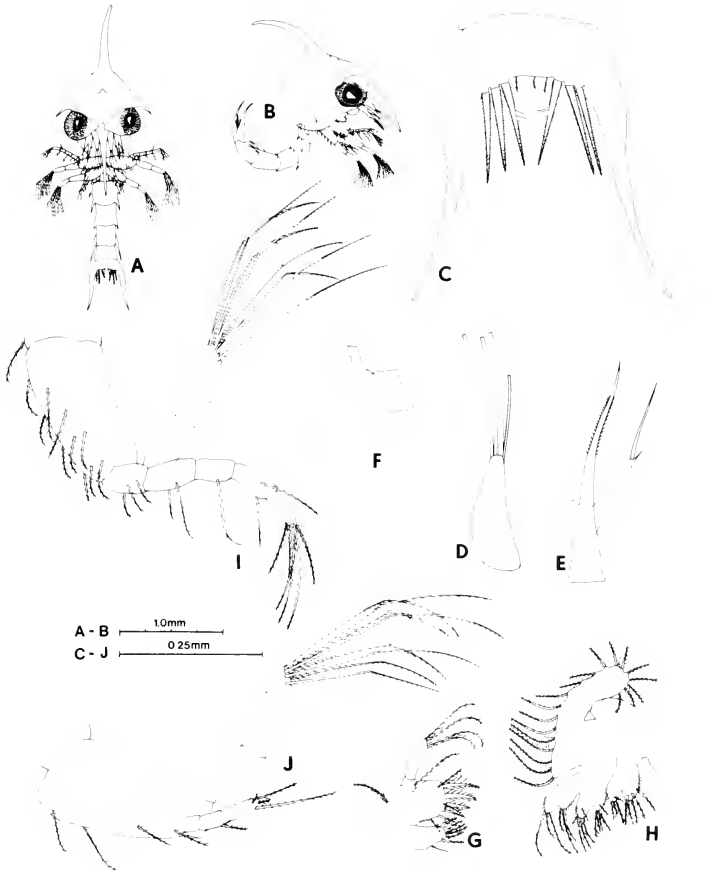


FIGURE 3.—Third zoeal stage of *Menippe nodifrons*. (A) Ventral view, (B) lateral view, (C) telson, (D) antennule, (E) antenna, (F) mandible, (G) maxillule, (H) maxilla, (I) maxilliped 1, (J) maxilliped 2

globose, enlarged, posterolateral border with 11 or 12 setae; three pairs of minute interocular setae; other setae as in stage III. Bud of third maxilliped and thoracic appendages enlarged, more evident under carapace.

Abdomen (Figure 4A, B). Pleopod buds now present on second through sixth somites, but much reduced on sixth. First somite with 5-7 setae on dorsal posterior margin; sixth with a pair of small posterolateral spines or knobs. Posterolateral spines on third, fourth, and dorsolateral spines on fifth somites more elongate than in previous stage.

Telson (Figure 4C). Similar in form to third stage; 4 setae on posterior telsonal margin. Dorsal and lateral spines on median portion of furcae miniscule as in previous stage.

Antennule (Figure 4D). Similar in form to third stage aesthetascs increased to 7 or 8, arranged in three tiers progressing distally: 2 small, 1 small, 3 large plus 1 or 2 small.

Antenna (Figure 4E). Exopodal spine usually extending 0.1 × beyond protopodal process and only 0.75 × length of exopodite. Terminal tip of endopodal bud extending to base of lateral spinules of protopodal process and about 0.4 × its length.

Mandible (Figure 4F). Left molar process unchanged, right molar process with 2 or 3 irregularly rounded prominences which join margin of incisor process.

Maxillule (Figure 4G). Endopodal setation unchanged; basal endite with 12 setae (6 or 7 strong, 5 or 6 thinner) plus a long plumose lateral seta as in previous stage; coxal endite with 8 setae (5 strong plus 3 thinner).

Maxilla (Figure 4H). Endopodite unchanged; setae on each basal endite usually 6,5 (5-7, 5-6); coxal endite setae 6,4 (uncommonly 7,4). Scaphognathite with 25-29 plumose setae.

Maxilliped 1 (Figure 4I). Coxopodite now with 2 setae; basi- and endopodite setae unchanged. Exopodite with 10 natatory setae.

Maxilliped 2 (Figure 4J). Coxo-, basi-, and endopodal setae unchanged. Exopodite with 10 natatory setae.

Maxilliped 3 (Figure 4K). Bilobed, rudimentary process, without setae, visible through carapace.

Color. Zoeae similar in color to third stage. Basipodite of first and second maxillipeds now orange-yellow. In lateral view, abdomen gold dorsally, brown medially, deep orange-rose ventrally. Ommatidia more evenly rose colored, cornea emerald green. Other chromatophore placement and color unchanged.

Fifth Zoeae (ultimate)

Carapace length: 1.55 mm.
Number of specimens examined: 11.
Remarks: Ultimate fifth stage zoeae molted directly to megalopae without an intercalated molt to sixth stage.

Carapace (Figure 5A, B). Distinctly increased in size from fourth stage. Carapace length, as in previous stages, about 1.2-1.3 × longer than dorsal and rostral spines. Posterolateral margin with 15-20 setae. Other carapacial setae as described and illustrated for fourth stage. Third maxilliped and pereiopods increased in size, visibly extended from beneath carapace, segmentation evident.

Abdomen (Figure 5A, B). First somite usually with 10 (8-10) dorsal setae. Setae on second through fifth somites unchanged, each bearing 2 on posterodorsal margin. Small lateral spines on second and third, posteroventral spines on third and fourth, and dorsolateral spines on fifth somite elongate. Posteroventral prominence of sixth somite broad, unlike slender spines of preceding somites. Pleopods on second to fifth somites, each with well-developed exopodite and a rudimentary endopodite; sixth rudimentary.

Telson (Figure 5C). An additional fifth seta may occur on the posterior margin of the telson. When exopodite of the second maxilliped has 12 plus 1 setae, telson exhibits 2 small medial setae dorsally near telsonal posterior margin as shown; if there are only 12 natatory exopodal setae, telson is naked.

Antennule (Figure 5D). Endopodal bud now present below tiers of aesthetascs, latter progressing distally 7,7,1,5; basal region swollen but unsegmented, with 2 small basal setae.

FIGURE 4.—Fourth zoeal stage of *Menippe nodifrons*. (A) Ventral view, (B) lateral view, (C) telson; (D) antennule; (E) antenna; (F) mandible, (G) maxillule, (H) maxilla, (I) maxilliped 1, (J) maxilliped 2, (K) maxilliped 3.

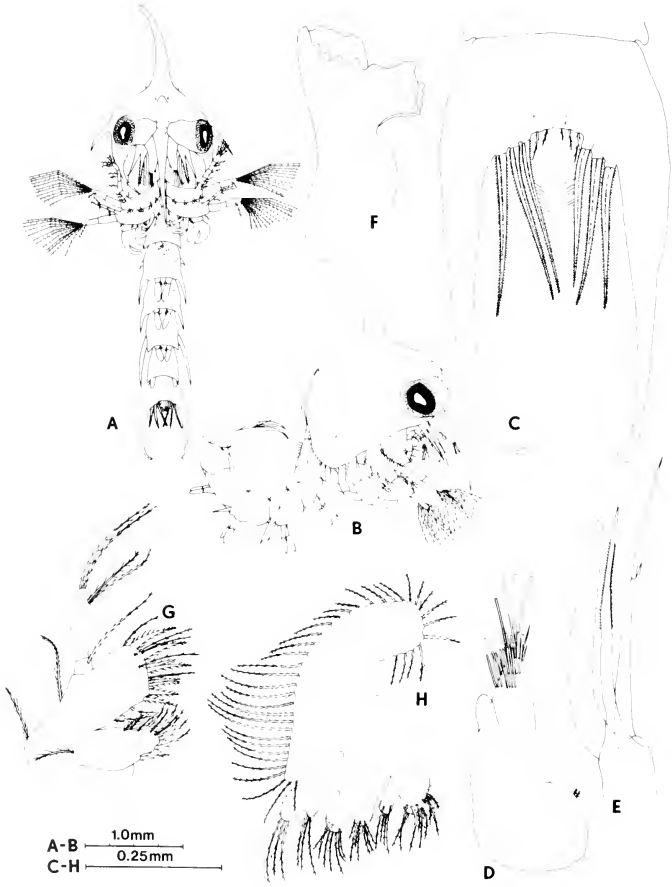


FIGURE 5.—Fifth (ultimate) zoeal stage of *Menippe nodifrons*. (A) Ventral view, (B) lateral view, (C) telson; (D) antennule; (E) antenna; (F) mandible, (G) maxillule; (H) maxilla

Antenna (Figure 5E). Exopodal spine extending (as in stage IV) beyond distal tip of protopodal process and remaining 0.75× length of exopodite. Endopodal bud elongate, unsegmented, about 0.7× length of protopodal process.

Mandible (Figure 5F). Palp bud now present on anterior surface. Left molar process with 4 or 5 rounded to angular prominences along margin of inner angle and junction with incisor process, right molar process with 2 or 3 prominences.

Maxillule (Figure 5G). Endopodite unchanged. Lateral margin of basal endite with 2 long feathery setae; usually 8 (8-10) spines and 8 (8-10) setae terminally; coxal endite with 6 strong plus 5 thinner setae distally and 1 long feathery seta basally.

Maxilla (Figure 5H). Endopodite unchanged; basal endites with 7,7 processes; coxal endite lobes with 8 or 9, and 4 or 5 processes, respectively. Scaphognathite with 36-45 plumose setae.

Maxilliped 1 (Figure 6A). Coxopodite with 5 (5 or 6) setae; basi- and endopodal setae unchanged. Exopodite with usually 11 distal plus 1 lateral natatory setae.

Maxilliped 2 (Figure 6B). Coxopodite with 1 seta; basi- and endopodal setae unchanged. Exopodite with 12 distal and commonly 1 smaller lateral setae.

Maxilliped 3 (Figure 6C). Exopodite two-segmented, distal segment with up to 6 terminal setae of variable length; endopodite indistinctly four- or five-segmented; unsegmented naked epipodite now present, commonly with 1 seta.

Color. Cephalothorax and abdominal coloration similar to fourth stage. Placement and color of chromatophores unchanged except for additional orange chromatophore at the posterior margin of the yellow telson. In lateral view, abdomen gold dorsally, brown medially, and orange ventrally; pleopods colorless carapace rose-gold dorsally, brown medially, rose posteroventrally, and brown anteroventrally. Ommatidia light rose throughout but concentrated dorsally; cornea reflecting emerald green to irridescent turquoise depending on the position of the larvae. Mandibles and labrum dark brown; antennules and antenna colorless. On the first day in stage V, chelae barely visible and colorless except for dark brown chromatophores on the interior margin of each manus. Chelae progressively turn deep orange-rose and continue to extend beneath the carapace by the fourth day.

Fifth Zoeae (penultimate)

Number of specimens examined: 10.

Remarks: Penultimate fifth stage zoeae molted to an atypical sixth stage before molting to megalopae. The morphological characters compared and discussed below are the ones that differ from the regular fifth stage and may be used as a guide to distinguish between the two fifth stages. The abdominal setation should be one of the first characters to check in distinguishing between the two fifth stages.

Carapace. Carapace similar to ultimate fifth stage zoeae. Setation on the posterolateral border of penultimate fifth stage zoeae 15 or 16 (15-20 in ultimate stage).

Abdomen. First abdominal somite usually with 8 (7-10) dorsal setae (10 in ultimate stage).

Antennule. Endopodal bud less developed, its distal tip not extending beyond the midpoint between the base of the first tier of aesthetascs and the base of the bud itself (ultimate stage bud extends about one-fourth past this midpoint). Aesthetascs arranged in tiers; progressing distally 3-7,7,1,5 (the ultimate stage proximal tier usually has 7 aesthetascs).

Antenna. Endopodal bud less elongate, often not reaching distal end of protopodal spinules, never surpassing them (as in ultimate stage).

Mandible. Palp bud smaller in penultimate stage, other prominences equal in both fifth stages.

Maxilliped 1. Coxopodite with 4 setae (5 in ultimate stage). Exopodite with either 11 or 11 plus 1 natatory setae (latter condition usual in ultimate stage).

Maxilliped 2. Exopodite exhibits either 12 or (as usual in ultimate stage) 12 plus 1 natatory setae.

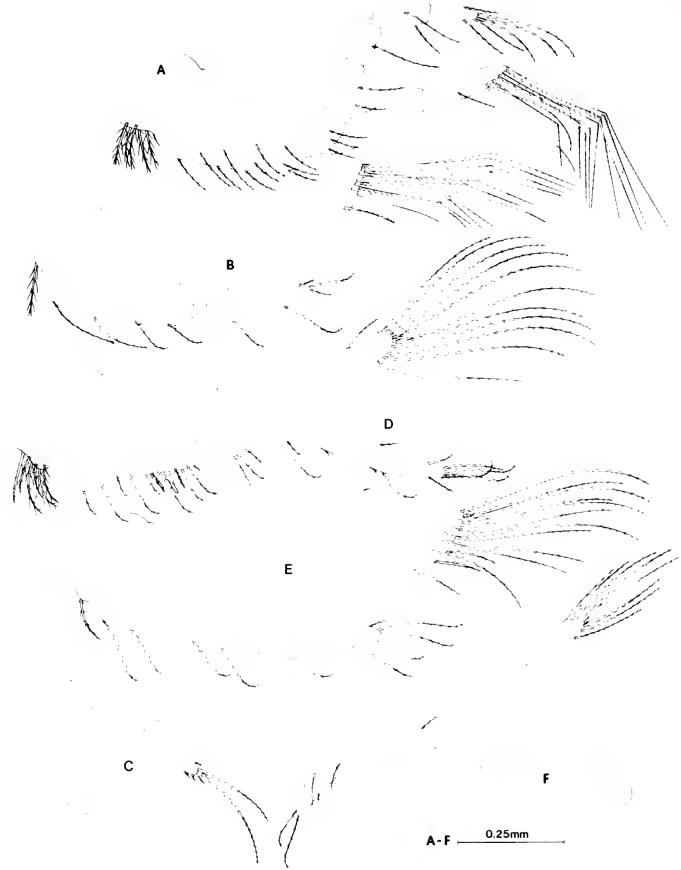


FIGURE 6.—Fifth (ultimate) (A-C) and sixth (D-F) zoeal stages of *Menippe nodifrons*. (A) Maxilliped 1, (B) maxilliped 2, (C) maxilliped 3, (D) maxilliped 1, (E) maxilliped 2, (F) maxilliped 3.

Maxilliped 3. Epi- and endopodites usually naked.

Sixth Zoeae (intercalated)

Carapace length: 1.60 mm.
Number of specimens examined: 5.

Carapace. Cephalothorax little inflated from previous stage. Posterolateral border with 20-22 setae, other setation and armature unchanged.

Abdomen. Pleopods elongate, one specimen with setae partially extruded. First abdominal somite with 11-14 dorsal setae.

Telson. Similar in morphology to fifth stage.

Antennule (Figure 7A). Endopodal bud elongate with up to 3 setae on distal end. Exopodite showing evidence of five segments; aesthetasc number variable, arranged in tiers: (progressing distally) 0,6-11,9-10,7-9,2 subterminal plus 5 terminal (note: not all aesthetases illustrated); unsegmented basal region swollen with 2 small setae placed as shown.

Antenna (Figure 7B). Endopodite surpassing protopodal spinous process, showing evidence of five segments; setation variable, 0 or 1 on proximal segment, 0-3 on remaining four. Distal tip of exopodal spine surpassing protopodal process but attaining length of endopodal distal tip. Exopodal spine now 0.5 × length of exopodite; latter about equal in length to protopodal process.

Mandible (Figure 7C). Palp unsegmented, elongate, with up to 3 distal setae. Molar process similar in form to fifth stage, 4 or 5 rounded to angular prominences along margin of inner angle and junction with incisor process; right molar process with 2 or 3 prominences.

Maxillule (Figure 7D). Proto- and endopodal setation unchanged; basal endite with 11 spines plus 10-12 stout setae plus 2 laterally; coxal endite with 6 strong plus 7 thinner setae plus 1 basally.

Maxilla (Figure 7E). Endopodite unchanged, basal endite lobes with usually 8 (8 or 9), 10 (8-10) setae respectively; coxal endite setae usually 11,7. Scaphognathite with 43-50 plumose setae on outer margin plus 2 small setae on lower surface of the blade.

Maxilliped 1 (Figure 6D). Coxopodite with 6 setae; basipodal setal formula similar to fifth stage with 2-4 additional setae dispersed as illustrated; endopodal setae 3,2,1,2-3,5 + I; exopodite with usually 11 (11 or 12) plus 1 lateral natatory setae.

Maxilliped 2 (Figure 6E). Coxo- and basipodal setation unchanged, 1 and 4 setae, respectively; endopodal setae 0,1,5; exopodite with 12 plus 2 natatory setae.

Maxilliped 3 (Figure 6F). Exopodite two-segmented with 8 setae on distal segment; unsegmented endopodite unchanged from previous stage; epipodite with up to 6 setae.

Color. Entire zoea much lighter orange-rose than in previous stage. Eyestalks each with one brown-orange chromatophore anteriorly. Rostrum pale rose. Proximal segment of exopodites of maxillipeds 1 and 2 now yellow. Brown-orange postcardiac chromatophores, present in first five zoeal stage, now absent.

Megalopae

Carapace length × width: 1.50 × 1.31 mm.
Number of specimens examined: 10.
Remarks: Megalopae (VI) molting from stage VI zoeae differed only slightly from those megalopae (V) molting from stage V zoeae. These differences are noted under the appropriate headings.

Carapace (Figure 8A). Cephalothorax subquadrate overall, sparsely covered with hairs as shown; posterior and posterolateral border with up to 60 setae. Frontal region rectangular, rostrum strongly deflexed, nearly vertical, bluntly rounded with distinct median cleft, slightly expanded laterally to meet bluntly angular interorbital prominence. Orbit excavated, nearly rectangular; eyes large, eyestalks with 5 anterior setae.

Abdomen (Figures 8A, 9A). Pleurae 1 through 5 with lobes at posteroventral angles, that of somite 6 subquadrate. First abdominal somite with up to 32 setae arranged in a transverse row, somites 2 through 6 sparsely covered with setae.

FIGURE 7.—Sixth (A-E) zoeal stage of *Menippe nodifrons*. (A) Antennule (not all aesthetases illustrated), (B) antenna, (C) mandible, (D) maxillule, (E) maxilla. Megalopa (F-J). (F) Antennule (not all aesthetascs illustrated), (G) antenna, (H) mandible, (I) maxillule (J) maxilla

FIGURE 8.—Megalopal stage of *Menippe nodifrons* (A) Dorsal view, (B) maxilliped 1; (C) maxilliped 2; (D) maxilliped 3

Telson (Figure 9A). Subquadrate, posterior angles rounded, 5 setae on posterior margin, other setation variable.

Antennule (Figure 7F) Biramous. Peduncle three-segmented; bulbous basal segment partially bilobed; middle segment subcylindrical, smaller than proximal segment, setae appearing distally as shown; distal segment ovoid, setation variable in all segments. Lower ramus one-segmented with 8 setae; upper ramus five-segmented, aesthetascs arranged in tiers: usually 0,12,10,8 (+ 2 setae), 5 subterminal plus 3 terminal (note: all aesthetascs not illustrated).

Antenna (Figure 7G). Peduncle with lateral lobe extending to about midpoint of the first basal segment. First basal segment the largest; setation of the 11 flagellar segments variable, usually 4,3,2,0,0,4,0,4,0,4,5.

Mandible (Figure 7H). With truncately spade-shaped cutting edge; palp two-segmented, setae 0, 10-13.

Maxillule (Figure 7I). Protopodite with 1 long feathery seta on the dorsal margin; endopodite two-segmented, longer and more swollen proximal segment with 1 lateral seta, distal segment with 4 setae; basal endite with 28-33 spines and setae; coxal endite with 15-19 setae.

Maxilla (Figure 7J). Endopodite now unsegmented with 4-6 setae; setation of basal endites variable: 10-13, 11-15, setae on coxal endites also variable: 9-15, 4-10. Scaphognathite of megalopae (V) usually with 66 plumose setae on the outer margin plus up to 12 small setae on blade, megalopae (VI) with 76 plus 18.

Maxilliped 1 (Figure 8B). Exopodite two-segmented, proximal segment usually with 5 (4-6) setae distally, distal segment usually with 6 (5-7) setae. Endopodite unsegmented, usually with 6 (6-9) setae. Basal endite setation variable, 30-34 on megalopae (V), 40-44 on megalopae (VI); coxal endite setae 12-18 on megalopae (V), 20-25 on megalopae (VI). Epipodite with naked processes (in appearance similar to antennular aesthetascs), 12-20 on megalopae, (V), 26 on megalopae (VI).

Maxilliped 2 (Figure 8C). Exopodite two-segmented, proximal segment with 2 small setae medially, distal segment with 8 terminal setae. Endopodite four-segmented, setation variable usually: 8-12, 0-5, 6-10, 9-12, placed generally as shown. Epipodite with up to 10 naked aesthetasclike setae.

Maxilliped 3 (Figure 8D). Exopodite two-segmented, 4 medial setae on proximal segment, 6-10 on distal segment. Endopodite five-segmented, third and fourth segments partially bilobed, setation on all segments variable, usually: 25, 14, 10, 11, 8. Epipodite usually with 18 naked aesthetasclike setae on distal two-thirds plus 8 normal setae on proximal one-third in megalopae (V); 28 plus 8 in megalopae (VI). Protopodal setation variable (example illustrated).

Pereiopods (Figure 9B, C, c, D, d). Chelipeds (B) elongate, equal; dactyl with 4 irregular teeth in gape, propodus with 3, the curved tips overlapping distally. Second to fourth pereiopods (e.g., C) similar; dactyls with 5 teeth ventrally. Fifth pereiopod dactyl (D, d) with 3 long pectinate setae distally (= brachyuran feelers) in megalopae (V), 4 on megalopae (VI).

Pleopods (Figure 9A, E, F). Pleopods of decreasing size on second to sixth abdominal somites; pleopods (uropods) of sixth somite without endopodite. Megalopae (V) with 20-21, 20-21, 20-21, 16-17, and 11 plumose setae on the exopodite respectively; megalopae (VI) with 22-23, 22-23, 21-22, 19-20, and 12 plumose setae. Endopodites of pleopods (= appendices internae) 1-4 and both (V) and (VI) megalopae with 3 hooked setae.

Color. Under incident light, the megalopae exhibit a rose-orange coloration especially pronounced around posterolateral borders of carapace. Eyes iridescent turquoise. Eyestalks with black chromatophores dorsally, rose colored posteriorly. Cephalothorax with iridescent turquoise chromatophores on epibranchial, posterolateral, and entire gastric region. Abdomen with 1 large black chromatophore on first somite, 2 each on second to sixth somites. Second to fifth pereiopods light rose, darker at joints. Chelipeds deep orange-rose with black chromatophores interspersed, teeth of hand colorless.

DISCUSSION OF REARING RESULTS

Few brachyuran decapod larvae exhibit vari-

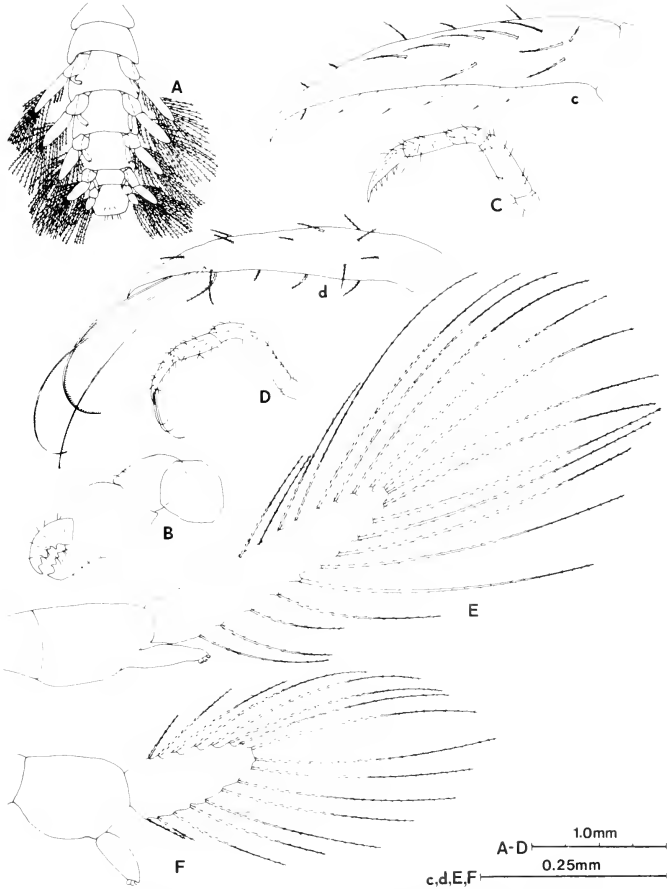


FIGURE 9.—Megalopal stage of *Menippe nodifrons*. (A) Abdomen, (B) chelped, (C) third pereiopod, (c) third pereiopod dactyl, (D) fifth pereiopod, (d) fifth pereiopod dactyl, (E) first pleopod, (F) fourth pleopod.

ability in number of larval stages. *Callinectes sapidus*, *Dromidia antillensis*, *Rhithropanopeus harrisii*, *Menippe mercenaria*, and now *M. nodifrons* larvae have exhibited an extra instar at the end of larval development (Knowlton 1974). In summarizing earlier studies, Knowlton (1965, 1974) speculated that the amount of food, temperature, and photoperiod contribute to controlling the number of instars in decapod crustaceans. Knowlton (1974) reared *Palaemonetes vulgaris*, a caridean shrimp, under varying environmental conditions and concluded that "larvae maintained at increasingly higher temperature levels were inclined to pass through more instars." In contrast, Sandifer (1973) found that larvae of *P. vulgaris* "passed through fewer instars at the moderate temperature (25°C) than at higher or lower temperatures, ..."

Menippe nodifrons has five or (uncommonly) six zoeal stages, and one megalopal stage, as does its congener *M. mercenaria* (Porter 1960; Ong and Costlow 1970). As expected (Ong and Costlow 1970; Costlow and Bookhout 1971; Gore 1971; Christiansen and Costlow 1975) larval development of *M. nodifrons* was substantially slower at 20°C than at 30°C. The first five zoeal stages exhibited modal durations ranging from 5 to 8 days at 20°C, 4 to 5 days at room temperature ($\bar{x}$ = 24.5°C), and 2 to 4 days at 30°C (Table 1). A decrease in the number of zoeal stages was observed concomitant with this decrease in duration of each stage at the higher temperature, i.e., only five zoeal stages were attained at 30°C, while an atypical sixth stage was infrequently obtained at both room temperature and 20°C.

In summary, duration of larval development, duration in days of each stage, and number of zoeal stages of *M. nodifrons*, are all temperature-dependent (Figure 10). Although similar results were obtained by Ong and Costlow (1970) with regard to larval development of *M. mercenaria*, a difference in survival rate can be noted. At 30°C none of the *M. nodifrons* larvae survived to crab stage 1, while 30 (60%) *M. mercenaria* larvae (in 35‰) attained crab stage 1. At similar room temperatures (about 25°C), 1 *M. nodifrons* larva (2%) reached crab stage 1, while 37 (74%) *M. mercenaria* larvae attained crab stage 1. At 20°C, *M. nodifrons* exhibited the highest survival with 7 (15%) megalopae molting to crab stage 1, while survival of *M. mercenaria* sharply decreased to 0% with no first crab stages reached (Ong and Costlow 1970).

TABLE 1.—Duration of larval stages of *Menippe nodifrons* at three temperatures

Temp (°C)	Stage	Duration (days) Min	Mean	Mode	Max	Total no molting to next stage
20	Zoeae I	5	5 8	6	7	48
	II	3	4 3	5	5	42
	III	4	5 1	5	7	39
	IV	5	6 0	6	7	38
	V(p)[1]	5	5 2	5	6	5
	V(u)[2]	6	7 6	8	9	24
	VI	8	8 7	9	9	3
	Megalopa (V)[3]	15	16 8	17 5	18	6
	(VI)[4]	16	16 0	16 0	16	1
24 5° (mean room temp)	Zoeae I	3	4 7	5	6	48
	II	3	3 9	4	6	44
	III	3	5 1	5	8	28
	IV	3	4 2	4	5	25
	V(p)[1]	3	4 4	5	5	7
	V(u)[2]	5	6 3	5	11	9
	VI	6	6 0	6	6	1
	Megalopa (VI)[4]	13	13 0	13	13	1
30	Zoeae I	3	3 2	3	4	48
	II	2	2 5	2 5	3	48
	III	1	2 6	3	4	47
	IV	2	3 1	3	5	46
	V	3	4 0	4	5	35
	Megalopa	(1)			(9)	0

[1]Zoea V molting to Zoea VI (penultimate)
[2]Zoea V molting to Megalopa (ultimate)
[3]Megalopa molted from Zoea V
[4]Megalopa molted from Zoea VI
( ) Died in stage

Ong and Costlow (1970) suggested that 30°C is the optimum survival temperature for the larvae of *M. mercenaria* with optimum salinity ranging from 30 to 35‰. The megalopal stage was attained in 14 days, first crab on day 21, with total larval survival ranging from 60 to 72%. Conversely, my results indicate highest survival of *M. nodifrons* (15%) at 20°C. The megalopal stage was attained in 28-34 days and first crab on days 45-49 from fifth stage zoeae. Because of the additional sixth stage, the megalopal stage in that series was attained in 36-37 days and first crab on day 52.

DISCUSSION

Comparative Morphology of *Menippe* Larvae

The only other species of *Menippe* whose complete larval development has been described is *M. mercenaria*. Hyman (1925) described the prezoeal and first zoeal stages of that species, and Porter (1960) obtained a complete series of five (atypically six) zoeal stages. *Menippe nodifrons* also attains five and atypically six zoeal stages, depending on the rearing temperature.

There is but one easily observed and recurring feature which may be used to distinguish between all zoeal stages of *M. nodifrons* and *M. mercenaria*. The fourth abdominal somite of *M. mercenaria* has

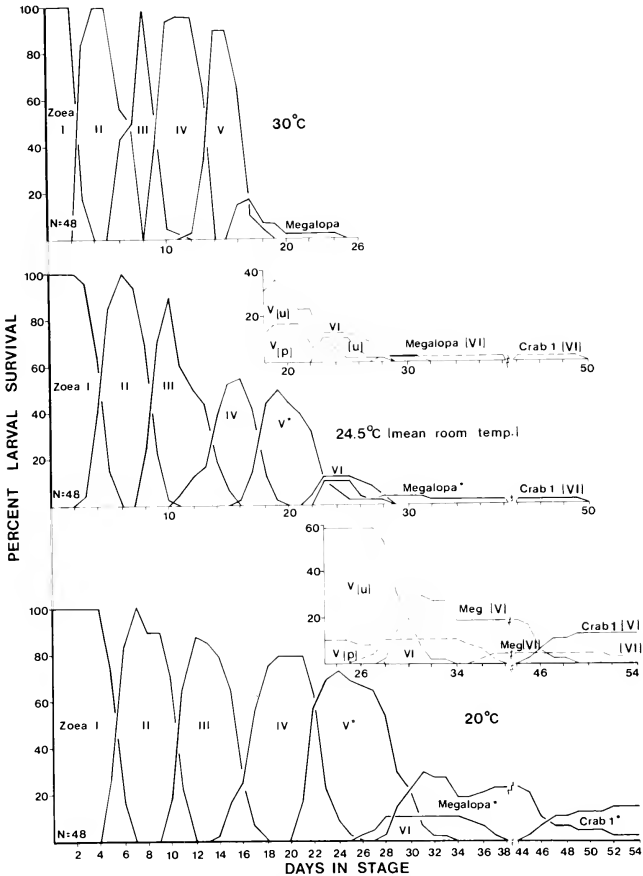


FIGURE 10.—Percentage survival and stage duration of *Menippe mercenaria* larvae reared under laboratory conditions. N = number of larvae cultured at each temperature, * = combined stages; u = ultimate stage, p = penultimate stage.

a dorsolateral spine not found in *M. nodifrons*. Additionally, in the first zoeal stage several differences (Table 2) include: antennular aesthetase number, maxillulary coxal endite setation, and segmentation of the exopodites of the first and second maxillipeds. Setation differences in other stages are relatively minor (Table 3), and include: setation of the first maxilliped, in zoeal stage 2; setation of the maxillary basal endite and endopodite of the second maxilliped, in zoeal stage 3; and setation of the maxillulary basal endite, in zoeal stage 4.

Setation on the larval appendages of *M. nodifrons* becomes particularly variable in the fifth stage; because of this, distinguishing characters between *M. nodifrons* and *M. mercenaria* in this stage are not discussed. However, in *M. nodifrons* there are several differences between ultimate fifth stage zoeae [ZV(u)] that molt directly to megalopae and penultimate fifth stage zoeae [ZV(p)] that molt to sixth stage. These include (Table 4): coxopodal setation of the first maxilliped, antennular aesthetasc number, exopodal setation of the third maxilliped, and setation on the first abdominal somite. In addition, the antennal endopodite bud reaches the tip of the protopodite in ZV(u); in ZV(p) it is less elongate, reaching only to distal end of protopodite process spinules.

Differences between the sixth zoeal stages of *M. nodifrons* and *M. mercenaria* concern setation of the maxillary scaphognathite and first maxillipedal basipodite (Table 5). Other distinguishing characters include evidence of antennular exopodite and antennal endopodite segmentation, also observed in *Callinectes sapidus* (Costlow and Bookhout 1959).

Kurata[4] described the complete larval development, including the megalopal stage, of *M. mer-*

[4]Kurata, H. 1970. Part III. Larvae of decapod Crustacea of Georgia. *In* Studies on the life histories of decapod Crustacea of Georgia. Unpubl. manuscr., 274 p. University of Georgia, Marine Institute, Sapelo Island, GA 31327.

TABLE 2.—Taxonomically important first zoeal characters in three species of *Menippe*.[1]

Character	*M. nodifrons*	*M. rumphii* (Prasad and Tampi 1957)	*M. mercenaria* (Porter 1960)
Carapace			
Rostrum	Straight, unarmed	Straight, unarmed	Straight, unarmed
Dorsal spine	Posteriorly curved	Posteriorly curved	Posteriorly curved
Lateral spine	Ventrally curved	Ventrally curved	Ventrally curved
Margin	Unarmed	Unarmed	Unarmed
Antennule	Conical rod	Conical rod	Conical rod
Exopodite	4 aesthetascs	4 aesthetascs	6 aesthetascs
Antenna	Exopodite ¾ protopodite	Exopodite protopodite	Ratio not given
Exopodite	Tapered, long subterminal spine	Tapered, single spine	Tapered, 1 long heavy spine
Mandible	Scoop-shaped incisor and molar processes indistinctly dentate and serrate; no palp	Cutting edge serrate; no palp	Lateral and posterior cutting edge indistinct teeth; no palp
Maxillule			
Endopodite	Two-segmented, 1 4 setae	Two-segmented, 1 4 setae	Two-segmented, 1 4 setae
Basal endite	5 hirsute setae	5 hirsute setae	5 stout hairy setae
Coxal endite	7 hirsute setae	6 hirsute setae	6 stout hairy setae
Maxilla			
Endopodite	Bilobed, 3 3 setae	Bifid, 3 3 setae	Bilobed, 3 3 setae
Basal endite	Bilobed, 5 4 setae	Bifid, 5 4 setae	Bilobed, 5 4 setae
Coxal endite	Bilobed, 5 4 setae	Bifid, 5 4 setae	Bilobed, 5 4 setae
Scaphognathite	4 plumose setae; distal plumose prorera	4 plumose setae; posterior plumose process	4 plumose setae; distal plumose process
Maxilliped 1			
Coxopodite	1 seta	1 seta	Not given
Basipodite	10 setae, 2 2 3 3	6 setae	10 setae
Endopodite	Five-segmented, 3 2 1 2 5	Five-segmented, 2 2 1 2 4	Five-segmented, 2 2 1 2 5
Exopodite	Two-segmented; 4 natatory setae	4 natatory setae	Partially bisegmented; 4 natatory setae
Maxilliped 2			
Coxopodite	Naked	Not given	Not given
Basipodite	4 setae	Few setae	4 setae
Endopodite	Three-segmented, 0 1 4 setae	Three-segmented, 0 2 4 setae	Three-segmented, 0 1 4 setae
Exopodite	Two-segmented; 4 natatory setae	4 natatory setae	Partially bisegmented; 4 natatory setae
Abdomen	Somites 2 to 5 with 2 posterodorsal setae; somite 4 without spines in all stages	Somites 2 to 4 with a pair of short hairs; somite 4 without spines	Somites 1 to 5 with 2 posterodorsal setae; somite 4 with pair of dorsolateral spines in all stages

[1]Characters taken from authors descriptions and illustrations.

TABLE 3.—Taxonomically important zoeal characters in two species of *Menippe*. Data on *M. mercenaria* taken from Porter (1960).

	Stage II		Stage III		Stage IV	
Character	*M. nodifrons*	*M. mercenaria*	*M. nodifrons*	*M. mercenaria*	*M. nodifrons*	*M. mercenaria*
Carapace						
Margin	3 setae	Several setae	8 setae	5 setae	11-12 setae	12 setae
Antennule					Base swollen,	Base swollen
aesthetascs	5-6	5	4	5	7-8	7
Antenna						
Endopodite	Small hump	Not given	Bud	Hump	Bud terminal tip at mid-point of antenna	Terminal tip bud at mid-point of antenna
Maxillule setation						
Endopodite	1 4	1 4	1 4	1 4	1 4	1 4
Basal endite	7 + 1 laterally	7 + 1 laterally	8 + 1 laterally	8 + 1 laterally	12 + 1 laterally	12 + 2 laterally
Coxal endite	7	7	7	7	8	8
Maxilla setation						
Endopodite	3 3	3 3	3 3	3 3	3 3	3 3
Basal endite	5 4	5 4	5 5	5 4	6 5	6 5
Coxal endite	5 4	5 4	5 4	5 4	6 4	6 4
Scaphognathite	11 plumose	11-12 plumose	19-20 plumose	18 plumose	25-29 plumose	27-28 plumose
Maxilliped 1 setation						
Coxopodite	1	Not given	1	Not given	2	Not given
Basopodite	2,2,3,3 (10)	10	2 2 3 3 (10)	10	2 2 3 3 (10)	10
Endopodite	3,2,1,2,5	2,2,1,2,5	3,2,1,2,6	3,2,1,2,5	3,2,1,2,6	3,2,1,2,6
Exopodite	6 natatory	6 natatory	8 natatory	8 natatory	10 natatory	10 natatory
Maxilliped 2 setation						
Coxopodite	Naked	Not given	Naked	Not given	Naked	Not given
Basopodite	4	4	4	4	4	4
Endopodite	0 1 4	0 1 4	0 1 4	0 1 4	0 1 4	0 1 4
Exopodite	6 natatory	6 natatory	8 natatory	8 natatory	10 natatory	10 natatory
Maxilliped 3					Bilobed bud	Bud
Abdomen					Pleopod buds	Pleopod buds
First somite	1-2 setae	1 setae	3 setae	3 setae	5-7 setae	5-7 setae
Sixth somite			2 dorsal setae	Unarmed	2 dorsal setae	Unarmed

cenaria. His data show that differences between megalopae of the two species are exhibited chiefly in the spination of the pereiopods. *Menippe mercenaria* has 5 or 6, 2 or 3, and 1 small spine on the ischia of walking legs, one, two, and three, respectively; and 2 small spines on the proximal inner edge of the merus of the first walking leg. *Menippe nodifrons* exhibits variable setation on these same segments but lacks spines. Kurata also stated that the ischium of the third maxilliped of *M. mercenaria* has 9 small spines; in *M. nodifrons* variable setation occurs, but 25 setae are usually found.

Among other species of *Menippe* only the first zoeal stage of the Indo-Pacific *M. rumphii* has been described (Prasad and Tampi 1957). As indicated in Table 2, the three congeners have a similar first stage, but differ in antennular aesthetasc number, setation of the maxillary coxal endite, setation of the basi- and endopodite of the first maxilliped, and endopodite setation of the second maxilliped. As noted in the introduction, there is some question as to whether *M. rumphii* is synonymous with *M. nodifrons*. The complete larval development of *M. rumphii* is needed to establish the status of this species and its taxonomic relationship to *M. nodifrons*.

Distinguishing Morphology of Xanthidae Larvae

According to Lebour (1928), larvae of the family Xanthidae exhibit the following characters:

1. One prezoeal and four zoeal stages.
2. Carapace with dorsal, rostral, and one pair of smaller lateral spines.
3. Antenna with rudimentary exopodite, or with one nearly as long as the spinous protopodal process.
4. Abdomen with lateral knobs on somites 2 and 3, somites 3-5 or 6 with lateral spines in all stages.
5. Telson furcae with 3 lateral spines or with 1 tending to disappear in later stages.

Wear (1970) reviewed the diagnostic characters of certain xanthid larvae and enumerated several conclusions about *Menippe*. Known larvae of the genus *Menippe*, reared under laboratory con-

TABLE 4.—Taxonomically important characters of the fifth zoeal stage in two species of *Menippe*

Character	*M. nodifrons* (ultimate)	*M. nodifrons* (penultimate)	*M. mercenaria* (Porter 1960)
Carapace			
Margin	15-20 setae	15-16 setae	20-22 setae
Antennule			
Endopodite	Bud	Bud less elongate	Bud elongate
Exopodite	7.7.1.5	3-7.7.1.5	2-7.6-8.1.4-5
Antenna			
Endopodite	Bud elongate	Bud less elongate	Bud elongate
Mandible	Palp present	Palp smaller	Palp present
Maxillule setation			
Endopodite	1.4	1.4	1.4
Basal endite	16 - 2 laterally	16 - 2 laterally	14-17 - 2 laterally
Coxal endite	11 - 1 basally	11 - 1 basally	11-12
Maxilla setation			
Endopodite	3.3	3.3	3.3
Basal endite	7.7	7.7	8.7
Coxal endite	8-9. 4-5	8-9. 4-5	6-10. 4-5
Scaphognathite	36-45 plumose	34-42 plumose	36-39 plumose
Maxilliped 1 setation			
Coxopodite	5	4	Not given
Basipodite	2.2.3.3.(10)	2.2.3.3.(10)	10
Endopodite	3.2.1.2.6	3.2.1.2.6	3.2.1.2.6
Exopodite	11 - 1 natatory	11 or 11 - 1 natatory	11 - 1 natatory
Maxilliped 2 setation			
Coxopodite	1	1	Not given
Basipodite	4	4	4
Endopodite	0.1.4	0.1.4	0.1.4
Exopodite	12 - 1 natatory	12 or 12 - 1 natatory	12 - 1 natatory
Maxilliped 3 setation			
Endopodite	Indistinctly 4-5 segmented	Reduced	Partially five-segmented
Exopodite	Two-segmented 0. 0-6	Naked	Unsegmented
Epipodite	Unsegmented, naked	Reduced	Unsegmented, naked
Abdomen setation			
First somite	Usually 10	Usually 8	8-9
Pleopods	Pair 1 to 4 with exopod and rudimentary endopod, pair 5 a bud	Pair 1 to 4 with exopod and rudimentary endopod, pair 5 a bud	Pair 1 to 4 with protopod, exopod and endopod, pair 5 a bud

ditions, are distinguished from other xanthid genera by attaining five and atypically six zoeal stages; other xanthid larvae exhibit only four zoeal stages. Larvae of the genus *Menippe* (and *Eriphia*) are distinguished from other xanthids by antennal development, i.e., the larval exopodite is about 0.75 + the length of the spinous protopodal process (see Aikawa 1937; Porter 1960; Sandifer 1974). *Menippe* (and *Sphaeroxtus*) larvae are distinguished from other closely related xanthid genera by the absence of setae on the basal segment of the second maxillipedal endopodite (Aikawa 1937; Porter 1960).

Number of Zoeal Stages

According to descriptions to date, every genus of xanthid crab has four zoeal stages except *Menippe*. In this study, *M. nodifrons* attained five zoeal stages, occasionally a sixth, and a prezoeal stage occurred. These stages also appeared in the larval development of *M. mercenaria* (Porter 1960). The prezoeal stage exhibited by both *M. mercenaria* and *M. nodifrons* was never observed to molt to a first stage zoea. Larvae of both species, collected within seconds after hatching, were almost always found to be in the first stage, indicating that the observed *M. nodifrons* prezoeae were those zoeae too weak to molt to stage I. Porter also indicated that *M. mercenaria* prezoeae, which were seen most often when subsequent survival was poor, may not be a normal stage in planktonic existence of the larvae. However, Lebour (1928), Chamberlain (1957), and Wear (1970) established that larvae of other xanthid genera hatch from the egg as prezoeae. Based on data obtained in this experiment, it seems possible that the prezoeal stage of *M. nodifrons* may occur in nature under certain conditions, as may the sixth zoeal stage.

Porter (1960) suggested that, based on the variability of morphological characters and the fact that no stage VI zoeae molted to megalopae, the sixth stage in *M. mercenaria* may not be a true stage but an advanced fifth stage. As noted in the rearing results, the observation of temperature-dependency in relation to number of zoeal stages

TABLE 5.—Taxonomically important characters of the sixth zoeal stage in two species of *Menippe*. Data on *M. mercenaria* taken from Porter (1960).

Character	*M. nodifrons*	*M. mercenaria*
Carapace		
Margin	20-22 setae	20-22 setae
Antennule		
Endopodite	Bud elongate, 0-3 setae	Bud elongate, occasional setae
Exopodite	Five-segmented, 0-6-11, 9-10, 7-9, 2 subterminal + 5 terminal	Unsegmented, 4-6-8, 1, 4-5
Antenna		
Endopodite	Five-segmented, 0-1-0-3, 0-3, 0-3, 0-3	Unsegmented
Mandible	Palp elongate, 0-3 setae	Palp as in stage 5
Maxillule setation		
Endopodite	1,4	1,4
Basal endite	22-23 - 2 laterally	23-29 - 2 laterally
Coxal endite	13	11-12
Maxilla setation		
Endopodite	3,3	3,3
Basal endite	8(8-9), 10(8-10)	9-11, 8-9
Coxal endite	11,7	8-11, 4-5
Scaphognathite	43-50 - 2 plumose	39-44 plumose
Maxilliped 1 setation		
Coxopodite	6	Not given
Basipodite	12-4	10
Endopodite	3,2,1,2-3,6	3,2,1,2,6
Exopodite	11 - 1 natatory	11 - 1 natatory
Maxilliped 2 setation		
Coxopodite	1	Not given
Basipodite	4	4
Endopodite	0,1,5	0,1,4
Exopodite	12 - 2 natatory	12 - 1 natatory
Maxilliped 3 setation		
Endopodite	Unsegmented, naked	Not given
Exopodite	Two-segmented, 0-8	0-8
Epipodite	Unsegmented, 0-6	Not given
Abdomen setation		
First somite	11-14	9-11
Pleopods	Exopodite setae only partially extruded	Exopodites with setae on all or only last pair

indicates that his supposition may not hold for all members of the genus, notably for *M. nodifrons*.

Regardless of whether a sixth zoeal stage is a laboratory artifact, the appearance of which seems to be temperature-dependent, it is apparent that larvae of at least two species of *Menippe* undergo at least five zoeal stages. The ramifications of this fact will be discussed below.

Few other brachyuran species exhibit an inconsistent number of instars in their larval development. Boyd and Johnson (1963) reported that out of 20 species of brachyuran crabs observed by Costlow, only two species, both Portunidae, exhibited variation in the number of zoeal stages. The phylogenetically primitive Portunidae have at least seven and sometimes eight zoeal stages (Bookhout and Costlow 1974, 1977). The extra stages resulted in reduced viability, with only a few zoeae developing to megalopae. Boyd and Johnson (1963) also suggested that the sixth stage in some normally five-staged Brachyura is a result of laboratory conditions because the extra stage has never been found in the plankton. This supports Gurney's (1942) and Porter's (1960) contentions that laboratory conditions produce aberrant larval forms. However, Boyd and Johnson (1963) also stated that extra stages might possibly occur in nature under certain conditions. Now that larvae of *M. nodifrons* are known it should be relatively easy to identify a sixth stage zoea of this species in the plankton based on criteria produced earlier in my study.

Plesiomorphy and Larval Development

Lebour (1928) set forth the genus *Portunus* as the most primitive of the Brachyrhyncha, based on the following characters: many zoeal stages (up to eight, Bookhout and Costlow 1977); telson with 6 long internal setae plus 3 lateral spines on each furca, making 7 spines on each side, with 2 extra pair of internal setae in later stages; knobs on the second and third abdominal somites, those on the third disappearing in later stages; and antenna with a well-developed exopodite, about one-half as long as the spinous protopodital process.

Larvae of the western North Atlantic species of *Menippe* also exhibit these characters, differing only in the number of larval stages (up to six) and in the retention of the knob on the third abdominal somite. Larvae of the Cancridae, considered to be more primitive than the Xanthidae (Rathbun 1930; Gurney 1939) and by some authors (Borradaile 1907; Lebour 1928; Glaessner 1969) than the Portunidae, also exhibit the primitive characters enumerated by Lebour for the Portunidae, differing mainly in number of zoeal stages (five), armature of the telson (2 lateral spines on each furca), and possession of a knob only on the second abdominal somite.

Based on the assumption that a greater number of zoeal stages is a primitive character, I agree with the phylogenetic arrangement of Rathbun (1930) and Gurney (1939), both of whom placed the Cancridae primitive to the Xanthidae but more advanced than the Portunidae. However, in comparing the number of larval stages, the genus *Menippe* shows a closer relationship to the Cancridae than to the Xanthidae. This relationship is discussed below in light of additional larval characters.

Excluding *Menippe*, the laboratory cultured genera of xanthids have four zoeal stages (e.g.,

Palumnus dasypodus, Sandifer 1974; *Eurypanopeus depressus*, Costlow and Bookhout 1961a). These xanthids usually possess 8 or 9 natatory maxillipedal setae in the third zoeal stage and pleopod buds first appear in this instar. However, third zoeae of *Menippe*, which also possess 8 natatory maxillipedal setae, lack pleopod buds and the latter do not appear in known *Menippe* larvae until the fourth stage (10 natatory maxillipedal setae). *Menippe* larvae, as do other xanthid larvae, otherwise attain the sixth abdominal somite in the third stage.

A similar situation is found among known larvae of the Cancridae (e.g., *Cancer borealis*, Sastry 1977b; *C. irroratus*, Sastry 1977a), which exhibit 8 natatory maxillipedal setae but no pleopod buds in the third zoeal stage, while 10 natatory maxillipedal setae and pleopod buds are exhibited in the fourth stage, as in *Menippe*. Thus *Menippe* again shows, in this respect, a closer relationship to the Cancridae than to the Xanthidae.

Another heterochronic feature is the mandibular palp, which appears in the fourth (i.e., last) zoeal stage in all xanthid genera except *Menippe*. Fourth stage *Menippe* larvae in the western North Atlantic may thus be distinguished from other stage IV xanthid larvae in lacking a mandibular palp as well as in possessing 10 natatory maxillipedal setae, as noted above. In all other laboratory cultured xanthid genera with 9 or 10 natatory maxillipedal setae the mandibular palp is present. Again, *Menippe* larvae seem closer to cancrid larvae than to xanthid larvae, in that the mandibular palp appears in the fifth (usually the last) zoeal stage.

Comparison of *M. nodifrons* maxillipedal coxopodal setation with that of other xanthid and cancrid larvae, which may be a significant feature, was not analyzed because of the lack of descriptions and illustrations of this larval character. The coxopodal setation has been described for only one other xanthid, *Neopanope texana* (McMahan 1967). Setal number of *M. nodifrons* agreed with that of *N. texana* for the first four zoeal stages, increasing in the fifth and sixth stages of *M. nodifrons*.

Assuming then, that data just presented are evidence of retained, primitive features, it can then be postulated that *Menippe* larvae are recapitulating, in the sense of retarded heterochronic maturation (Gould 1977), a larval development now accelerated in other xanthid larvae. The presence of the fifth zoeal stage, the irregular occurrence of the sixth stage, the delayed appearance of mandibular palp and pleopod buds, and retention of coxopodal setation in cultured species of *M. nodifrons* and *M. mercenaria* are all evidence which indicates this might have happened. Evolution has apparently acted in the larvae of other xanthid genera to reduce the number of zoeal stages.

In summary, because of the greater number of zoeal stages and the tardy appearance of both pleopod buds and mandibular palp, *Menippe* may be the most primitive genus of the family Xanthidae. Whether the genus is transitional between the Cancridae and the Xanthidae remains speculative. As noted above, larvae of the family Cancridae, phylogenetically primitive to the Xanthidae, also exhibit five zoeal stages and pleopodal and mandibular features which appear in a similar developmental sequence to those of *Menippe*. The more advanced xanthid larvae, on the other hand, pass through only four zoeal stages and exhibit sequential features typical of larvae of the family Goneplacidae, a group considered to be more advanced than xanthids (Lebour 1928; Kurata 1968).

Carapacial Armature

Menippe larvae have well-developed dorsal, rostral, and smaller lateral spines, a feature found in all cancrid and most xanthid larvae. Thus, little can be inferred regarding phylogenetic relationships using these features.

The reason for such spines remains conjectural. Lebour (1928) stated that these well-developed carapacial spines were used "in directing movement and keeping up [the larvae in] the surface-layers, and their reduction appears to be associated with habits near the bottom." Her supposition may be correct. *Menippe nodifrons* larvae reared in this study were active swimmers near the surface in earlier stages. Their locomotion was usually in a forward direction with the dorsal spine pointed anteriorly.

Antennal Morphology

In considering antennal features, xanthid larvae were first divided into either two (Hyman 1925) or three (Lebour 1928) groups. In the former, both authors noted that the length of the antennal exopodite is either about equal to the protopodite (primitive) or rudimentary (advanced). In the

third group, also considered primitive, the antennal exopodite is about three-fourths the length of the protopodal process (this group was established by Lebour to include *Menippe* and *Eriphia*). Therefore, regardless of classification scheme (Hyman's or Lebour's), larvae of the genus *Menippe* exhibit a primitive antennal morphology. However, as will be seen, the degree of primitiveness is relative.

Aikawa (1929) classified four types of antennae (A, B, C, and D) based on the ratio of length of peduncle to that of exopodite. In the A type antenna the exopodite and peduncle (= protopodal process) are nearly equal in length. Aikawa also considered this to be the most primitive condition because other authors (e.g., Calman 1909) have noted that the long exopodite is homologous with the antennal scale of the Caridea.

Xanthid larvae exhibiting A type antennae are *Pilumnus* (considered by Hyman 1925 to be the most primitive xanthid), *Heteropanope*, and *Actumnus* (Aikawa 1929, 1937; Lebour 1928).

The typical B type antenna occurs most frequently in brachyuran larvae. The exopodite is about one-half to three-fourths the length of the peduncle. Type B antennae are found in the larvae of the xanthids *Menippe*, *Eriphia*, *Sphaerozius*, and *Trapezia* (Aikawa 1937). This antennal morphology, primitive by Hyman's standards, is considered by Aikawa (1929) to be intermediate in development, but less advanced than the following C type.

The C type antenna consists of a long peduncle and a very short spine (= exopodite). This highly advanced antenna is exhibited in the larvae of the xanthids *Panopeus* (considered by Hyman 1925 to be the most advanced xanthid), *Eurypanopeus*, and *Neopanope*, among others (Aikawa 1929).

Aikawa (1929) briefly described the D type antenna (seen in the oxystome crab *Philyra pisum* (Leucosiidae)) as a simple, inconspicuous spiny process shorter than either the rostrum or the antennule, and considered it to be a deviation.

The cancrids exhibit the intermediate B type antenna seen in *Menippe*. Thus, in antennal features, larvae of both *Menippe* and the Cancridae would be more advanced than some of the xanthids, and equal to or less advanced than others.

Abdominal Morphology

A lateral knob occurs on the second abdominal somite of most brachyuran larvae also on the third somite of some xanthid larvae (Lebour 1928). Lebour did not attribute much significance to the abdominal processes and was ambivalent in regarding these as either a primitive or advanced feature. Later, Wear (1970), noted that "the posterior pair of papillae [knobs] may be absent" and that "lateral spines on the third to fifth abdominal segments is also a variable character, but these occur in a great majority of xanthid larvae." Both *M. nodifrons* and *M. mercenaria* exhibit the lateral papillae on the second and third abdominal somites, as well as ventrolateral spines on the third, fourth, and fifth somites, thereby agreeing with the great majority of xanthid larvae. As noted above, *M. mercenaria* larvae may be distinguished from *M. nodifrons* larvae by possession of a pair of dorsolateral spines on the fourth abdominal somite. In the more primitive Cancridae, lateral knobs only occur on the second abdominal somite, and lateral spines on the third to fifth somites are much smaller than those of the xanthid larvae (Aikawa 1937; Sastry 1977a, b). Thus *Menippe* larvae are more advanced than cancrid larvae if additional spines indicate apomorphy.

Telsonal Armature

Menippe nodifrons larvae have a typically forked brachyuran telson with 6 setae anterior to the furcae. However, 3 setae which become reduced in later stages, appear on the median portion of the furcae, and one to three pair of extra, shorter setae occur in posterior telsonal margin. Lebour (1928) suggested that this type of telson is "most near the embryonic form, and therefore probably nearest the primitive form . . . ." The extra internal setae along the posterior telsonal margin first appear in the second zoeal stage of both the xanthid *M. nodifrons* and the cancrid *Cancer borealis* (Sastry 1977b). These internal setae, if present in other xanthid larvae, do not appear until the third zoeal stage, e.g., in *Panopeus herbstii* (Costlow and Bookhout 1961b), *Eurypanopeus depressus* (Costlow and Bookhout 1961a), and *Hexapanopeus angustifrons* (Costlow and Bookhout 1966), all more advanced forms than *Menippe*. These data lend further support to the primitive status of *Menippe* as compared with other xanthid genera.

In summary, using larval characters suggested by Lebour (1928) to determine the primitive or advanced status of decapod larvae, the genus *Menippe* is phylogenetically more primitive than

most of the Xanthidae. It appears to be closer, in most features, to the family Cancridae.

Status of the Family Menippidae

Ortman (1894) established the family Menippidae, which included the subfamilies Menippinae, Myomenippinae, and Pilumninae, based on the following adult characters: a) the second segment of each antenna is short, not overreaching the frontal region; and b) the palate is with or without a ridge. However, because of the reigning taxonomic confusion in this group, this familial rank was not recognized by other authors of that time. Indeed, many present day xanthid species were placed under differing familial and subfamilial names (e.g., Pilumnidae, Cancridae) before the taxon Xanthidae became firmly established (Rathbun 1930). Later authors notwithstanding, Aikawa (1929, 1937), using Lebour's larval characters (with emphasis on antennal development), again recognized the family Menippidae, considering it to be more primitive than the Xanthidae. Subsequent study of the larval development of *Menippe*, reported by Porter (1960) and in this paper, supports Aikawa's phylogenetic arrangement based on larval morphology, as well as adding evidence using larval development, i.e., the fact that *Menippe* attains up to six zoeal stages (more stages = primitive). The establishment by Ortmann (1894) of the Menippidae as a family, although based only on adult characters, seems to be supported also by larval traits.

Guinot (1977) proposed a new classification scheme for brachyuran decapods based on placement of female and male genital openings. She divided the brachyurans into three sections as follows: 1) Podotremata—female and male openings coxal, a primitive condition (i.e., Homoloidea); 2) Heterotremata—female openings sternal, male openings either sternal or coxal, an intermediate condition (i.e., Xanthoidea); 3) Thoracotremata—female and male openings sternal, an advanced condition (i.e., Gecarcinoidea). Guinot[5] listed the family Menippidae under the superfamily Xanthoidea, based on adult characters emphasizing genital opening placement. Thus she provided additional evidence, based on adult gonopore/gonopod characters, for the reestablishment of the family Menippidae. Investigations of the larval development of other species of *Menippe* could provide further support warranting reestablishment of the family.

[5]Guinot, D. 1977. Projet d'une nouvelle classification des Brachyoures. Unpubl. tables. Museum National d'Histoire Naturelle, Laboratoire de Zoologie (Arthropodes), Paris, Fr.

NOTE ADDED IN PROOF

After this paper was sent to the printer, a publication—Larval development of *Epixanthus dentatus* (White) (Brachyura, Xanthidae) by M. Saba, M. Takeda, and Y. Nakasone published 1978 in Bulletin of the National Science Museum (Tokyo), Series A (Zoology) 4(3):151-161—was received indicating that three genera of xanthids developed through less than four zoeal stages. *Epixanthus dentatus* and *Heterozius rotundifrons* attain two larval stages, while *Pilumnus lumpinus* attains only one larval stage. These three species live in specialized and restricted habitats.

ACKNOWLEDGMENTS

I wish to express my appreciation to the Smithsonian Institution for granting a summer internship and use of the facilities at the Fort Pierce Bureau. I also thank the members of my thesis committee: Robert H. Gore, Smithsonian Institution, Fort Pierce Bureau; and Frank M. Truesdale, William H. Herke, Clyde H. Moore, Louisiana State University, for their assistance. I express my gratitude to Anthony J. Provenzano, Jr. and Paul A. Sandifer who also critically reviewed the manuscript. I also wish to thank Joan Dupont, Applied Biology, Inc., Atlanta, Ga., for pointing out morphological differences between *M. nodifrons* and *M. mercenaria*; and Suzanne Bass, Karen Rodman, and Kim Wilson who provided moral support and aid in the laboratory.

LITERATURE CITED

AIKAWA, H.
1929. On larval forms of some Brachyura. Rec. Oceanogr. Works Jpn. 2:17-55.
1937. Further notes on brachyuran larvae. Rec. Oceanogr. Works Jpn. 9:87-162.

BOOKHOUT, C. G., AND J. D. COSTLOW, JR.
1974. Larval development of *Portunus spinicarpus* reared in the laboratory. Bull. Mar. Sci. 24:20-51.
1977. Larval development of *Callinectes similis* reared in the laboratory. Bull. Mar. Sci. 27:704-728.

BORRADAILE, E. A.
1907. On the classification of the decapod crustaceans. Ann. Mag. Nat. Hist., Ser. 7, 19:457-486.

BOYD, C M , AND M W JOHNSON
1963. Variations in the larval stages of a decapod crustacean, *Pleuroncodes planipes* Stimpson (Galatheidae) Biol Bull (Woods Hole) 124 141-152
CALMAN, W T
1909 A treatise on zoology Part VII Appendiculata Third Fascicle, Crustacea Adam and Charles Black, Lond , 346 p
CAPART, A
1951 Crustacea Decapodes, Brachyures Exped Oceanogr Belg Eaux côtieres Afr Atl. Suc (1948-1949) III, fasc 1, p 11-205
CHAMBERLAIN, N A
1957 Larval development of the mud crab *Neopanope texana sayi* (Smith) Biol Bull (Woods Hole) 113 338
CHRISTIANSEN, M E , AND J D COSTLOW, JR
1975 The effects of salinity and cyclic temperature on larval development of the mud-crab *Rhithropanopeus harrisii* (Brachyura Xanthidae) reared in the laboratory Mar Biol (Berl) 32 215-221
COSTLOW, J D , AND C G BOOKHOUT.
1959 The larval development of *Callinectes sapidus* Rathbun reared in the laboratory Biol Bull (Woods Hole) 116 373-396
1960 A method for developing brachyuran eggs *in vitro* Limnol Oceanogr 5 212-215
1961a The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions Crustaceana 2 6-15
1961b The larval stages of *Panopeus herbstii* Milne-Edwards reared in the laboratory J Elisha Mitchell Sci Soc 77 33-42
1962 The effect of environmental factors on larval development of crabs *In* C M Tarzwell (Chairman), Biological problems in water pollution Third Seminar, p 77-86 U S Publ Health Serv , Cinc , Ohio
1966 Larval development of the crab, *Hexapanopeus angustifrons* Chesapeake Sci 7 148-156
1971 The effects of cyclic temperatures on larval development in the mud-crab *Rhithropanopeus harrisii* *In* D J Crist (editor), Fourth European Marine Biology Symposium, p 211-220 Camb Univ Press, Lond
DANA, J D
1852 Crustacea *In* United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842 Under the command of Charles Wilkes U S N , Vol 13, Part 1, 685 p C Sherman, Phila
FABRICIUS, J D.
1798 Supplementum entomologiae systematicae Hafniae, 572 p [Not seen]
GLAESSNER, M F
1969 Decapoda *In* R C Moore (editor), Treatise on invertebrate paleontology Part R Arthropoda 4, Vol 2, p 400-651 Geol Soc Am , Inc , Boulder, Colo
GORE, R H
1968 The larval development of the commensal crab *Polyonyx gibbesi* Haig, 1956 (Crustacea Decapoda) Biol Bull (Woods Hole) 135 111-129
1971 *Petrolisthes tridentatus* The development of larvae from a Pacific specimen in laboratory culture with a discussion of larval characters in the genus (Crustacea Decapoda, Porcellanidae) Biol Bull (Woods Hole) 141 485-501
GORE, R H , L E SCOTTO, AND L J BECKER
1978 Community composition, stability, and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellarid worm reefs. Studies on decapod crustacea from the Indian River region of Florida IV Bull Mar Sci 28 221-248
GOULD, S J
1977 Ontogeny and phylogeny The Belknap Press of Harv Univ Press, Camb , Mass , 501 p
GUINOT, D
1977 Propositions pour une nouvelle classification des Crustacés Decapodes Brachyoures C R Hebd Seances Acad Sci Ser D, Sci Nat 285 1049-1052
GURNEY, R
1939 Bibliography of the larvae of decapod crustacea Ray Soc , Lond , 123 p
1942 Larvae of decapod Crustacea Ray Soc , Lond , Publ 129, 306 p
HYMAN, O W
1925 Studies on the larvae of crabs of the family Xanthidae Proc U S Natl Mus 67, Art 3, 22 p
KNOWLTON, R E
1965 Effects of some environmental factors on the larval development of *Palaemonetes vulgaris* (Say) J Elisha Mitchell Sci Soc 81 87
1974 Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea Thalassia Jugosl. 10 138-158
KURATA, H
1968 Larvae of Decapoda Brachyura of Arasaki, Sagami Bay — III. *Carcinoplax longimanus* (De Haan) (Goneplacidae) [In Jpn , Engl abstr] Bull Tokai Reg Fish Res Lab 56 167-171
LEBOUR, M V
1928 The larval stages of the Plymouth Brachyura Proc Zool Soc Lond 1928 473-560
MCMAHAN, M R
1967 The larval development of *Neopanope texana texana* (Stimpson) (Xanthidae) Fla State Board Conserv , Leafl Ser 2(1) 1-16
MILNE-EDWARDS, A
1873 Etudes sur les Xiphosures et les Crustacés de la region Mexicaine (5-6) 185-264 *In* Mission scientifique au Mexique et dans l'Amerique centrale, pt 5, 368 p Rec Zool Hist Faune Am centr Mex
MONOD, TH
1956 Hippidea et Brachyura ouest-africains Mem Inst Fr Afr Noire 45, 674 p
ONG, K -S , AND J D COSTLOW, JR
1970 The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory Chesapeake Sci 11 16-29
ORTMANN, A
1894 Die Decapoden-Krebse des Strassburger Museums VII Theil Abtheilung Brachyura (Brachyura genuina Boas) II Unterabtheilung, Cancrodea, 2 Section Cancrinea, 1 Gruppe Cyclometopa Zool Jahrb Abt Syst DeKol Geogr Tiere 7 411-495
PORTER, H J
1960 Zoeal stages of the stone crab, *Menippe mercenaria* Say Chesapeake Sci 1 168-177
PRASAD, H J , AND P R TAMPI
1957 Notes on some decapod larvae J Zool Soc India 9(1) 23-39

PROVENZANO, A J, JR
1967 Recent advances in the laboratory culture of decapod larvae *In* Symposium on Crustacea, p 940-945 Mar Biol Assoc India, Symp Ser 2

RATHBUN, M J
1930 The cancroid crabs of America of the Families Eurylidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae U S Natl Mus Bull 152, 609 p

SANDIFER, P A
1973 Effects of temperature and salinity on larval development of grass shrimp, *Palaemonetes vulgaris* (Decapoda, Caridea) Fish Bull, U S 71 115-123
1974 Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory Bull Mar Sci 24 378-391

SASTRY, A N
1977a The larval development of the rock crab, *Cancer irroratus* Say, 1817, under laboratory conditions (Decapoda Brachyura) Crustaceana 32 155-168
1977b The larval development of the Jonah crab, *Cancer borealis* Stimpson, 1859, under laboratory conditions (Decapoda Brachyura) Crustaceana 32 290-303

SAY, T
1818 Appendix to the account of the Crustacea of the United States J Acad Nat Sci Phila 1 445-458

STIMPSON, W
1859 Notes on North American Crustacea, No 1 Ann Lyceum Nat Hist N Y 7(1862) (2) 49-93
1871 Notes on North American Crustacea in the Museum of the Smithsonian Institution No III Ann Lyceum Nat Hist N Y 10 92-136

VILELA, H
1951 Crustaceos decapodes e estomatopodes da Guine Portuguesa An Junta Invest Colon Lisboa 4(1949) 47-70

WEAR, R G
1970 Notes and bibliography on the larvae of xanthid crabs Pac Sci 24 84-89

ASSESSMENT OF COMPOSITION OF STOCK MIXTURES

JEROME J. PELLA[1] AND TIMOTHY L. ROBERTSON[2]

ABSTRACT

Stocks of fish can occur in mixtures, and knowledge of the composition of such a mixture may be needed. An estimate of the proportion of the mixture arising from each stock potentially present as well as a measure of the precision of this estimate may suffice. To develop these estimators, we posit that the distributions of characters of individuals differ among the stocks and that rules have been developed by others with which some success in stock identification of individuals can be had. We require test samples of individuals from each stock included in the mixture with which to evaluate the rules; these samples must be other than the learning samples used to develop the rules. The rules are also applied to a sample from the mixture. Using the numbers of individuals in each test sample and sample of the mixture which are assigned to each stock, we can estimate the composition of the mixture and the precision of this estimation.

Approximations based on large samples underlie the estimation. Numerical studies provide some idea of the sample sizes required for the approximations to be satisfactory as well as of the behavior of the estimators as related to performance of rules and sample sizes.

We note that the roles of the learning and test samples from the segregated stocks may be interchanged, allowing a repetition of the procedure.

Stocks of fish frequently occur in mixtures. When these stocks are of the same species at the same life stage, the stock identity of an individual may be difficult or impossible to ascertain. Yet if the distributions of characters of individuals differ among stocks, some success may be had in identification of individuals in a mixture by use of discriminant analysis (e.g., Hill 1959; Fukuhara et al. 1962; Anas and Murai 1969; Parsons 1972; Cook and Lord 1978) or more simply by a verbal key (Konovalov 1975). In most important applications the correct identification of individuals is not of direct value. Rather the accurate determination of the proportions of the mixture belonging to each stock is desired.

Critical to accurate assessment of composition of a mixture are the rules of assignment of individuals to stocks. The rules applied to a vector of measurements on an individual assign the individual to one stock of those possible. Among rules, those with lowest error rates of assignments provide the most accurate assessments, of course. If individuals of known stocks, either those used in developing the rules or new individuals, are assigned to stocks using the rules, a measure of error rates is provided. Although some sense of the accuracy of the rules is obtained, this does not provide a satisfactory evaluation of possible errors in estimates of stock proportions from new mixtures.

Worlund and Fredin (1962) began to attack this problem. They developed an estimation procedure for stock proportions in a mixture of an arbitrary number of stocks. Further, under restrictive assumptions concerning knowledge of the accuracy of assignments, Worlund and Fredin developed an approximate variance expression for the estimates of stock proportions in the mixture when only two stocks composed the mixture. We extend their approach now, developing methodology to estimate stock proportions in mixtures of an arbitrary number of stocks as well as the variances of such estimates under less restrictive conditions.

BACKGROUND SITUATION AND SAMPLING THEORY

We assume K stocks are known to potentially occur in the mixture. Random samples of individuals are taken from each stock at a time when the stocks are completely segregated; these may be taken before or after the mixing. A random sample of individuals from the mixture is also taken.

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

[2]Division of Fisheries, University of Alaska, Juneau, Box 1447, Juneau, AK 99802; present address: Alaska Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Road, Anchorage, AK 99502.

Manuscript accepted November 1978.
FISHERY BULLETIN VOL. 77, NO. 2, 1979

The sample from a stock at time of segregation is partitioned into two subsamples, called the learning and test samples after Cook and Lord (1978). Learning samples from the K stocks are used to develop rules of assignment; the assumptions and methods used are arbitrary for our purpose. The realism of the assumptions forming the basis of the rules is not critical; performance of the rules and some knowledge of this performance is important. Performance of the rules is determined by their application to the test samples. The rules are also applied to the sample of the mixture. Using the numbers assigned to each of the stocks by application of rules to the test samples from the segregated stocks and the sample from the mixture, we can estimate the composition of the mixture and the precision of this estimation.

A caveat concerning situations in which the methodology is not appropriate is needed before we begin. What follows presumes the individuals of a stock in both the test sample and mixture sample are drawn from a common distribution of characters used in the rules. When the condition is violated, performance of the rules would differ impermissibly between test samples and that of the mixture. We must avoid characters on which a selection process occurs between the mixture and the separate stocks.

Test Sample Theory and Analysis

Once particular rules have been established from the learning samples (e.g., using discriminant analysis), individuals forming each stock in effect have been partitioned into K mutually exclusive groups corresponding to those assigned by the rules to one of each of the K stocks. We define ϕ_{kj} to be the proportion of the individuals comprising the kth stock which is assigned by the rules to the jth stock. Also we let t_{kj} be the number of individuals in the test sample from stock k assigned by the rules to stock j, and let $T'_k = (t_{k1}, t_{k2}, \ldots, t_{kK})$. Assuming the number of individuals in the test and learning samples is small as compared with the number of individuals composing the stock, the probability of the occurrence of vector T_k is, to a good approximation, given by the multinomial probability function, i.e.,[3]

$$P(T_k) = \binom{t_{k\cdot}}{t_{k1}\, t_{k2} \ldots t_{kK}} \phi_{k1}^{\,t_{k1}}\ \phi_{k2}^{\,t_{k2}} \ldots \phi_{kK}^{\,t_{kK}} . \quad (1)$$

Because the probabilities ϕ_{kj} are usually unknown, we estimate them from T_k by the well-known maximum likelihood estimator

$$\Phi'_k = (t_{k1}/t_{k\cdot}, t_{k2}/t_{k\cdot}, \ldots, t_{kK}/t_{k\cdot}) \quad (2)$$

corresponding to the parameter vector $\Phi'_k = (\phi_{k1}, \phi_{k2}, \ldots, \phi_{kK})$. $\hat{\Phi}_k$ is unbiased and has the variance-covariance matrix

$$\Sigma_{\hat{\Phi}_k} = \begin{bmatrix} \frac{\phi_{k1}(1-\phi_{k1})}{t_{k\cdot}} & -\frac{\phi_{k1}\phi_{k2}}{t_{k\cdot}} & \cdots & -\frac{\phi_{k1}\phi_{kK}}{t_{k\cdot}} \\ -\frac{\phi_{k2}\phi_{k1}}{t_{k\cdot}} & \frac{\phi_{k2}(1-\phi_{k2})}{t_{k\cdot}} & \cdots & -\frac{\phi_{k2}\phi_{kk}}{t_{k\cdot}} \\ & & \ddots & \\ & & & \frac{\phi_{kK}(1-\phi_{kK})}{t_{k\cdot}} \end{bmatrix}, \quad (3)$$

Test samples from different stocks are statistically independent and covariance between elements of $\hat{\Phi}_k$ and $\hat{\Phi}_{k'}$ are zero for $k \neq k'$.

Mixed Sample Theory and Analysis

The mixture of stocks at the time of sampling is comprised of possibly as many as K stocks. Ignoring for the moment the actual stock composition of the mixture, our rules established from the learning samples partition the mixture into K mutually exclusive groups again corresponding to the K stocks to which individuals are assigned. We define λ_j to be the proportion of the individuals composing the entire mixture which would be assigned to the jth stock by the rules. Also we let m_j be the actual number of fish in the sample from the mixture which are assigned to stock j. If the size of the sample from the mixture is small compared with the number of fish composing the mixture, the probability of observing the vector $M' = (m_1, m_2, \ldots, m_K)$ is given by the multinomial probability function, i.e.,

[3]The dot notation implies summation over the subscript. Thus, $t_{k\cdot} = \sum_j t_{kj}$; $t_{k\cdot}$ is the size of the test sample from the kth stock.

$$P(M) = \binom{m_.}{m_1\ m_2\ \ldots\ m_K} \lambda_1^{m_1} \lambda_2^{m_2} \cdots \lambda_K^{m_K}. \quad (4)$$

We can estimate the probabilities λ_j from M by the maximum likelihood estimator

$$\Lambda' = (m_1/m_.,\ m_2/m_.,\ \ldots,\ m_K/m_.) \quad (5)$$

corresponding to the parameter vector $\Lambda' = (\lambda_1, \lambda_2, \ldots, \lambda_K)$. $\hat{\Lambda}$ is unbiased and has the variance-covariance matrix

$$\Sigma_{\hat{\Lambda}} = \begin{bmatrix} \frac{\lambda_1(1-\lambda_1)}{m_.} & -\frac{\lambda_1\lambda_2}{m_.} & \cdots & -\frac{\lambda_1\lambda_K}{m_.} \\ -\frac{\lambda_2\lambda_1}{m_.} & \frac{\lambda_2(1-\lambda_2)}{m_.} & \cdots & -\frac{\lambda_2\lambda_K}{m_.} \\ & & \ddots & \\ & & & \frac{\lambda_K(1-\lambda_K)}{m_.} \end{bmatrix}. \quad (6)$$

$\hat{\Lambda}$ is a natural estimator of stock composition of the mixture. Unfortunately as we see next, its expected value, Λ, depends not only on stock composition, but also on the behavior of the rules.

Basic Relation Between Parameters of Test Samples and Those of the Sample from the Mixture

We know the mixture consists of individuals from at most K stocks. Let θ_k be the proportion of the individuals composing the entire mixture which are of the kth stock, where $0 \leq \theta_k \leq 1$ for all k and

$$\sum_{k=1}^{K} \theta_k = 1.$$

The parameter vector $\Theta' = (\theta_1, \theta_2, \ldots, \theta_K)$ is unknown; its estimation is our objective. If the individuals of each of the stocks occurring in the mixture are a random sample from the character distribution of that stock, then the probability that a randomly sampled individual from the mixture is assigned to the jth stock, λ_j, is related to previously defined probabilities by the equation system

$$\lambda_j = \sum_{k=1}^{K} \theta_k \phi_{kj}, \qquad j = 1, 2, \ldots, K. \quad (7)$$

The term, $\theta_k \phi_{kj}$, represents the probability a randomly sampled individual from the mixture is of stock k and assigned to stock j; summing over the K stocks gives the total probability the individual is assigned to stock j. This basic set of relationships can be expressed in matrix notation,

$$\Lambda = \Phi'\Theta \quad (8)$$

where $\Phi = \begin{bmatrix} \Phi_1' \\ \Phi_2' \\ \vdots \\ \Phi_K' \end{bmatrix} = \begin{bmatrix} \phi_{11}\ \phi_{12}\ \ldots\ \phi_{1K} \\ \vdots \\ \phi_{K1}\ \phi_{K2}\ \ldots\ \phi_{KK} \end{bmatrix}$.

ESTIMATION OF STOCK COMPOSITION OF MIXTURE

If $|\Phi| \neq 0$, we can solve Equation (8) for Θ,

$$\Theta = (\Phi')^{-1}\Lambda. \quad (9)$$

When the rules assign individuals from the stocks without error, $\Phi = I$, and $\Theta = \Lambda$. Then the natural estimator $\hat{\Lambda}$ is appropriate. But the rules will usually be imperfect, yet Equation (9) shows we can still solve for Θ without error provided Φ and Λ are known. Unfortunately neither Φ nor Λ is known in usual circumstances; however, we saw how to estimate them from the test and mixed samples using Equations (2) and (5). When Λ and Φ in Equation (8) are replaced by estimates from Equations (2) and (5), the problem of estimating Θ is a special case of estimation of the solution of a system of linear equations with random coefficients. Fuller[4] has provided several solutions for the general problem; these are applicable in the present case for large test and mixed samples. Later we indicate how large these samples must be.

[4]Fuller, W. A. 1970. Mimeographed class notes, Statistics 638, winter 1969-70. Iowa State Univ. Stat. Lab., 56 p., on file at the library of Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

Fuller (see footnote 4) begins with the simple estimator

$$\hat{\boldsymbol{\theta}} = (\hat{\boldsymbol{\Phi}}')^{-1}\,\hat{\boldsymbol{\lambda}} \tag{10}$$

with the restriction that the event $|\hat{\boldsymbol{\Phi}}| = 0$ must be impossible. The asymptotic variance-covariance matrix of $\hat{\boldsymbol{\theta}}$, $\boldsymbol{\Sigma}_{\hat{\boldsymbol{\theta}}}$, is given by

$$\boldsymbol{\Sigma}_{\boldsymbol{\theta}} = (\boldsymbol{\Phi}')^{-1}\,(\boldsymbol{\Sigma}_{\lambda} + \boldsymbol{\Sigma}_{\Phi\theta})\,\boldsymbol{\Phi}^{-1} \tag{11}$$

and $\boldsymbol{\Sigma}_{\lambda}$ is defined by Equation (6).

We remark that variation in estimates of $\boldsymbol{\theta}$ arises additively from two sources: 1) sampling variation in estimation of the assignment composition of the mixture which is represented by $\boldsymbol{\Sigma}_{\lambda}$; and 2) sampling variation in estimation of the probability of assignment matrix $\boldsymbol{\Phi}$ which is represented by $\boldsymbol{\Sigma}_{\Phi\theta}$. The diagonal elements of the $\boldsymbol{\Sigma}_{\boldsymbol{\theta}}$ are the variances of the elements of $\hat{\boldsymbol{\theta}}$; the square roots of these are the standard errors.

where

$$\boldsymbol{\Sigma}_{\Phi\theta} = \begin{bmatrix} \sum_i \dfrac{\theta_i^2\phi_{i1}(1-\phi_{i1})}{l_{i\cdot}} & -\sum_i \dfrac{\theta_i^2\phi_{i1}\phi_{i2}}{l_{i\cdot}} & \cdots & -\sum_i \dfrac{\theta_i^2\phi_{i1}\phi_{iK}}{l_{i\cdot}} \\ -\sum_i \dfrac{\theta_i^2\phi_{i2}\phi_{i1}}{l_{i\cdot}} & \sum_i \dfrac{\theta_i^2\phi_{i2}(1-\phi_{i2})}{l_{i\cdot}} & \cdots & -\sum_i \dfrac{\theta_i^2\phi_{i2}\phi_{iK}}{l_{i\cdot}} \\ \vdots & \vdots & & \vdots \\ -\sum_i \dfrac{\theta_i^2\phi_{iK}\phi_{i1}}{l_{i\cdot}} & -\sum_i \dfrac{\theta_i^2\phi_{iK}\phi_{i2}}{l_{i\cdot}} & \cdots & \sum_i \dfrac{\theta_i^2\phi_{iK}(1-\phi_{iK})}{l_{i\cdot}} \end{bmatrix}$$

Bias in estimation of $\boldsymbol{\theta}$ is approximately given by

$$B \cong (\boldsymbol{\Phi}')^{-1}\,G\boldsymbol{\theta}, \tag{12}$$

where

$$G = \begin{bmatrix} \dfrac{\phi^{11}\phi_{11}(1-\phi_{11})}{l_{1\cdot}} - \sum_{k\neq 1} \dfrac{\phi^{k1}\phi_{11}\phi_{1k}}{l_{1\cdot}} & \dfrac{\phi^{12}\phi_{21}(1-\phi_{21})}{l_{2\cdot}} - \sum_{k\neq 1} \dfrac{\phi^{k2}\phi_{21}\phi_{2k}}{l_{2\cdot}} & \cdots \\ \dfrac{\phi^{21}\phi_{12}(1-\phi_{12})}{l_{1\cdot}} - \sum_{k\neq 2} \dfrac{\phi^{k1}\phi_{12}\phi_{1k}}{l_{1\cdot}} & \dfrac{\phi^{22}\phi_{22}(1-\phi_{22})}{l_{2\cdot}} - \sum_{k\neq 2} \dfrac{\phi^{k2}\phi_{22}\phi_{2k}}{l_{2\cdot}} & \cdots \\ \vdots & \vdots & \\ \dfrac{\phi^{K1}\phi_{1K}(1-\phi_{1K})}{l_{1\cdot}} - \sum_{k\neq K} \dfrac{\phi^{k1}\phi_{1K}\phi_{1k}}{l_{1\cdot}} & \dfrac{\phi^{K2}\phi_{2K}(1-\phi_{2K})}{l_{2\cdot}} - \sum_{k\neq K} \dfrac{\phi^{k2}\phi_{2K}\phi_{2k}}{l_{2\cdot}} & \cdots \end{bmatrix}$$

$$\begin{bmatrix} \dfrac{\phi^{1K}\phi_{K1}(1-\phi_{K1})}{l_{K\cdot}} - \sum_{k\neq 1} \dfrac{\phi^{kK}\phi_{K1}\phi_{Kk}}{l_{K\cdot}} \\ \dfrac{\phi^{2K}\phi_{K2}(1-\phi_{K2})}{l_{K\cdot}} - \sum_{k\neq 2} \dfrac{\phi^{kK}\phi_{K2}\phi_{Kk}}{l_{K\cdot}} \\ \vdots \\ \dfrac{\phi^{KK}\phi_{KK}(1-\phi_{KK})}{l_{K\cdot}} - \sum_{k\neq K} \dfrac{\phi^{kK}\phi_{KK}\phi_{Kk}}{l_{K\cdot}} \end{bmatrix}$$

and ϕ^{ij} is the element in the ith row and jth column of Φ^{-1}.

Improved estimators with smaller bias than $\hat{\Theta}$ can also be developed from Fuller's (see footnote 4) general results. These are the new estimators:

$$\tilde{\Theta} = (\hat{\Phi}' + \hat{G})^{-1}\ \hat{\gamma} \text{ and} \tag{13}$$

$$\ddot{\Theta} = [I - (\hat{\Phi}')^{-1}\hat{G}]\,(\hat{\Phi}')^{-1}\ \hat{\gamma}. \tag{14}$$

Here $\hat{G}$ is obtained by substituting the estimates for the unknown parameters of G. To the order of approximation provided by Fuller, these estimators have the same variance-covariance matrix as $\hat{\Theta}$. An internal estimate of this variance-covariance matrix $\Sigma_{\hat{\Theta}}$ can be obtained by substitution of observed values for parameters in Equation (11). We can substitute in Equation (11) for elements of Θ the corresponding elements of either $\tilde{\Theta}$, $\hat{\Theta}$, or $\ddot{\Theta}$. To distinguish between these possibilities, we label the internal estimators of $\Sigma_{\hat{\Theta}}$ as $\hat{\Sigma}_{\hat{\Theta}}$, $\hat{\Sigma}_{\tilde{\Theta}}$, or $\hat{\Sigma}_{\ddot{\Theta}}$, respectively. With the internal estimate of $\Sigma_{\hat{\Theta}}$, we can estimate not only Θ but also how precisely the estimation is accomplished.

To establish confidence intervals on the elements of Θ, we assume test and mixed samples are sufficiently large so that the estimators $\hat{\Theta}$, $\tilde{\Theta}$, or $\ddot{\Theta}$ are each approximately distributed as the multivariate normal with mean Θ and known variance-covariance matrix $\hat{\Sigma}_{\hat{\Theta}}$, $\hat{\Sigma}_{\tilde{\Theta}}$, or $\hat{\Sigma}_{\ddot{\Theta}}$, respectively. Then a $100(1 - \alpha)\%$ set of confidence intervals such that all the unknown elements of Θ are simultaneously covered by their respective intervals with a probability $1 - \alpha$ is for the estimator $\hat{\Theta}$ (say) as follows (see Morrison 1967, section 4.4):

$$\begin{aligned}
&\hat{\theta}_1 - (\hat{\sigma}_{11}{}^2\chi_{\alpha;K-1}{}^2)^{1/2} \leqslant \theta_1 \leqslant \hat{\theta}_1 + (\hat{\sigma}_{11}{}^2\chi_{\alpha;K-1}{}^2)^{1/2}\\
&\hat{\theta}_2 - (\hat{\sigma}_{22}{}^2\chi_{\alpha;K-1}{}^2)^{1/2} \leqslant \theta_2 \leqslant \hat{\theta}_2 + (\hat{\sigma}_{22}{}^2\chi_{\alpha;K-1}{}^2)^{1/2}\\
&\quad\vdots \qquad\qquad \vdots \qquad\qquad \vdots\\
&\hat{\theta}_k - (\hat{\sigma}_{kk}{}^2\chi_{\alpha;K-1}{}^2)^{1/2} \leqslant \theta_k \leqslant \hat{\theta}_k + (\hat{\sigma}_{kk}{}^2\chi_{\alpha;K-1}{}^2)^{1/2}\\
&\quad\vdots \qquad\qquad \vdots \qquad\qquad \vdots\\
&\hat{\theta}_K - (\hat{\sigma}_{KK}{}^2\chi_{\alpha;K-1}{}^2)^{1/2} \leqslant \theta_K \leqslant \hat{\theta}_K + (\hat{\sigma}_{KK}{}^2\chi_{\alpha;K-1}{}^2)^{1/2}
\end{aligned} \tag{15}$$

where $\hat{\sigma}_{kk}{}^2$ is the element in the kth row and column of $\hat{\Sigma}_{\hat{\Theta}}$, and $\chi_{\alpha;K-1}{}^2$ is the value associated with a chi-square distribution with K-1 degrees of freedom such that $100\alpha\%$ of the distribution lies above it. When only two stocks occur in the mixture, this set of simultaneous intervals reduces to the familiar univariate normal approximation for setting confidence intervals:

$$\begin{aligned}
&\hat{\theta}_1 - z_{\alpha/2}(\hat{\sigma}_{11}{}^2)^{1/2} < \theta_1 < \hat{\theta}_1 + z_{\alpha/2}(\hat{\sigma}_{11}{}^2)^{1/2}\\
&\hat{\theta}_2 - z_{\alpha/2}(\hat{\sigma}_{22}{}^2)^{1/2} < \theta_2 < \hat{\theta}_2 + z_{\alpha/2}(\hat{\sigma}_{22}{}^2)^{1/2}
\end{aligned} \tag{16}$$

where $z_{\alpha/2}$ is the standardized normal deviate such that $100(\alpha/2)\%$ of the distribution lies below $-z_{\alpha/2}$ and $100(\alpha/2)\%$ lies above $z_{\alpha/2}$. These expressions are in terms of the estimator $\hat{\Theta}$; they apply as well to the other estimators when elements of $\tilde{\Theta}$ or $\ddot{\Theta}$ replace those of $\hat{\Theta}$ within them.

Worlund and Fredin (1962) developed the estimator $\hat{\Theta}$ in Equation (10). To translate their notation to ours, let

$$\begin{aligned}
\phi_{ij} &= P_{ij}\\
\theta_t &= F_t\\
\lambda_j &= R_j
\end{aligned} \tag{17}$$

and permit the subscripts to take on letter values $a, b, c, \ldots$. In the special case when the mixture is comprised of only two stocks, they developed an asymptotic expression for the variance of θ_1 (the variance of θ_2 necessarily equals that of θ_1 since $\theta_2 = 1 - \theta_1$). In deriving the variance expression, they assumed Φ is known without error so that $\Sigma_{\hat{\theta}\,\theta}$ is a null matrix; such is approximately true as $t_{1.}$ and $t_{2.}$ become large.

We consider two examples now to illustrate our notation and method in concrete terms. The first case restricts our general approach to the simplest situation of two stocks in the mixture; the second

provides numerical computations for three stocks so that users may verify their understanding of the formulas.

Special Case of Two Stocks

We assume a set of rules based on learning samples from each stock has been developed which assigns each individual to one of the two stocks. Individuals in two test samples, size t_1 from stock 1 and size t_2 from stock 2, are assigned by the rules to either of the stocks. Of the t_1 individuals, t_{11} are assigned to stock 1 and t_{12} to stock 2. Of the t_2 individuals, t_{21} are assigned to stock 1 and t_{22} to stock 2. A sample from the mixture of size m is assigned by the rules to the stocks—m_1 to stock 1 and m_2 to stock 2. Then

$$\Phi = \begin{bmatrix} \phi_{11} & \phi_{12} \\ \phi_{21} & \phi_{22} \end{bmatrix} = \begin{bmatrix} t_{11}/t_1 & t_{12}/t_1 \\ t_{21}/t_2 & t_{22}/t_2 \end{bmatrix} \quad (18)$$

$$\Lambda = \begin{bmatrix} \lambda_1 \\ \lambda_2 \end{bmatrix} = \begin{bmatrix} m_1/m \\ m_2/m \end{bmatrix} \quad (19)$$

$$(\Phi')^{-1} = \begin{bmatrix} \phi^{11} & \phi^{21} \\ \phi^{12} & \phi^{22} \end{bmatrix} = \frac{1}{\phi_{11}\phi_{22} - \phi_{12}\phi_{21}} \begin{bmatrix} \phi_{22} & -\phi_{21} \\ -\phi_{12} & \phi_{11} \end{bmatrix} \quad (20)$$

$$\Theta = (\Phi')^{-1}\Lambda = \begin{bmatrix} \dfrac{\lambda_1 - \phi_{21}}{\phi_{11} - \phi_{21}} \\ \dfrac{\phi_{11} - \lambda_1}{\phi_{11} - \phi_{21}} \end{bmatrix}. \quad (21)$$

The form of $\hat{\Theta}$ has been chosen to agree with the solution of Worlund and Fredin (1962); in developing this form, we used the facts for this special case that

$$\begin{aligned} \hat{\phi}_{22} &= 1 - \hat{\phi}_{21} \\ \hat{\phi}_{12} &= 1 - \hat{\phi}_{11} \\ \text{and } \lambda_2 &= 1 - \lambda_1 \end{aligned} \quad (22)$$

$$G = \begin{bmatrix} \dfrac{\phi^{11}\phi_{11}(1-\phi_{11}) - \phi^{21}\phi_{11}\phi_{12}}{t_1} & \dfrac{\phi^{12}\phi_{21}(1-\phi_{21}) - \phi^{22}\phi_{21}\phi_{22}}{t_2} \\ \dfrac{\phi^{21}\phi_{12}(1-\phi_{12}) - \phi^{11}\phi_{12}\phi_{11}}{t_1} & \dfrac{\phi^{22}\phi_{22}(1-\phi_{22}) - \phi^{12}\phi_{22}\phi_{21}}{t_2} \end{bmatrix} \quad (23)$$

$$\Sigma_\Lambda = \frac{\lambda_1\lambda_2}{m} \begin{bmatrix} 1 & -1 \\ -1 & 1 \end{bmatrix} \quad (24)$$

$\Sigma_{\Phi\Theta}$ =

$$\left(\frac{\theta_1{}^2\phi_{11}\phi_{12}}{t_1} + \frac{\theta_2{}^2\phi_{21}\phi_{22}}{t_2} \right) \begin{bmatrix} 1 & -1 \\ -1 & 1 \end{bmatrix}. \quad (25)$$

$\hat{G}$, $\hat{\Sigma}_\Lambda$ and $\hat{\Sigma}_{\Phi\Theta}$ are obtained by substituting estimates for the corresponding parameters. Then

$$\Sigma_\Theta = (\Phi')^{-1}(\Sigma_\Lambda + \Sigma_{\Phi\Theta})\Phi^{-1} \quad (26)$$

provides internal estimates of the variance of θ_1 or θ_2 as well as their covariance.

Expressions for $\hat{\Theta}$ and $\hat{G}$ follow directly from specialization of Equations (13) and (14) to two stocks; substitution of their elements into Equation (26) in place of those of $\hat{\Theta}$ provides $\hat{\Sigma}_\Theta$ and $\hat{\Sigma}_\Theta$, respectively.

Numerical Computations for Three Stocks

To illustrate the computations for a three-stock situation, we use the information reported by Cook and Lord (1978) regarding stock composition of high-seas mixtures of sockeye salmon, *Oncorhynchus nerka*. Their purpose was to estimate proportions of the mixture arising from each of three river systems — Egegik, Kvichak, and Naknek — of the Bristol Bay region of Alaska. Actu-

ally the application of our methods is inappropriate because Cook and Lord used individuals of test samples from the segregated stocks both to modify an original set of rules from the learning samples as well as to estimate Φ. Because our purpose is only to illustrate the computations, we will treat their observations as though the test samples had been used exclusively to estimate Φ. Using the test samples in developing the rules, as Cook and Lord did, should produce greater precision in estimation of composition of a mixture; the disadvantage at present is the inability to assess the precision of these enhanced estimates. In developing the variance-covariance matrix $\hat{\Sigma}_{\hat{\Theta}}$, we assumed $\hat{\Phi}$ and $\hat{\Lambda}$ are statistically independent. Such is untrue if the test samples are used as by Cook and Lord both to develop the rules used to estimate Λ as well as to estimate Φ.

Test samples from the segregated stocks of the three rivers were assigned by the rules to these stocks (Table 1). Then the rules were applied to 101 fish caught on the high seas. Of these, 25 were assigned to Egegik, 22 to Kvichak, and 54 to Naknek. We identify Egegik, Kvichak, and Naknek as the first, second, and third streams in our subscript use. Computations using these data produce the following results:

$$\hat{\Phi} = \begin{bmatrix} 0.80000 & 0.08000 & 0.12000 \\ 0.04000 & 0.74000 & 0.22000 \\ 0.16667 & 0.20833 & 0.62500 \end{bmatrix}.$$

(Our $\hat{\Phi}$ is the transpose of $\hat{C}$ of Cook and Lord (1978).)

$$\hat{\Lambda} = \begin{bmatrix} 0.24752 \\ 0.21782 \\ 0.53465 \end{bmatrix}.$$

(Our $\hat{\Lambda}$ is the same statistic as R_u of Cook and Lord (1978); apparently they have numerical errors in their evaluation of R_u.)

TABLE 1.—Numbers of sockeye salmon in test samples from three Bristol Bay (Alaska) rivers—Egegik, Kvichak, and Naknek—assigned by rules to these rivers (source: Cook and Lord 1978)

Actual river	Assigned river		
	Egegik	Kvichak	Naknek
Egegik	40	4	6
Kvichak	2	37	11
Naknek	8	10	30

$$\hat{\Phi}^{-1} = \begin{bmatrix} 1.30019 & -0.07801 & -0.22218 \\ 0.03641 & 1.49782 & -0.53422 \\ -0.35885 & -0.47847 & 1.83732 \end{bmatrix}$$

$$\hat{G} = \begin{bmatrix} 0.00480 & -0.00086 & -0.00424 \\ -0.00154 & 0.00737 & -0.00666 \\ -0.00326 & -0.00651 & 0.01090 \end{bmatrix}$$

$$\hat{\Theta} = \begin{bmatrix} 0.138 \\ 0.051 \\ 0.811 \end{bmatrix} \qquad \tilde{\Theta} = \begin{bmatrix} 0.145 \\ 0.062 \\ 0.793 \end{bmatrix} \qquad \ddot{\Theta} = \begin{bmatrix} 0.145 \\ 0.062 \\ 0.793 \end{bmatrix}.$$

(Our $\hat{\Theta}$ is $\hat{U}$ of Cook and Lord (1978); their errors in evaluating R_u are responsible for the discrepancy with our estimate $\hat{\Theta}$.)

$$\hat{\Sigma}_{\Lambda} = \begin{bmatrix} 0.00184 & -0.00053 & -0.00131 \\ & 0.00169 & -0.00115 \\ & & 0.00246 \end{bmatrix}$$

$$\hat{\Sigma}_{\hat{\Phi}\hat{\Theta}} = \begin{bmatrix} 0.00197 & -0.00050 & -0.00146 \\ & 0.00230 & -0.00180 \\ & & 0.00326 \end{bmatrix}$$

$$\hat{\Sigma}_{\hat{\Theta}} = \begin{bmatrix} 0.00975 & 0.00208 & -0.01184 \\ & 0.01454 & -0.01662 \\ & & 0.02846 \end{bmatrix}.$$

In computing $\hat{\Sigma}_{\hat{\Phi}\hat{\Theta}}$ and $\hat{\Sigma}_{\hat{\Theta}}$, $\hat{\Theta}$ is used as the estimate of Θ.

The 90% confidence set from Equation (15) using $\hat{\Theta}$ is as follows:

$$-0.074 \leq \theta_1 \leq 0.350$$
$$-0.208 \leq \theta_2 \leq 0.310$$
$$0.449 \leq \theta_3 \leq 1.173.$$

The elements of Θ must lie between 0 and 1; therefore, we can set the lower limits of the first two intervals to 0, and the upper limit of the third interval to 1. The actual composition was estimated by Cook and Lord (1978) from returning adults to Bristol Bay as

$$\Theta = \begin{bmatrix} 0.325 \\ 0.061 \\ 0.614 \end{bmatrix},$$

which falls within the intervals of the confidence set as would be expected. However, recall that the condition that test samples be used exclusively to evaluate the rules was violated; therefore, the confidence set is not valid. Further, Cook and Lord

(1978) have misgivings of probable occurrence of additional unaccounted stocks in the high-seas mixture.

BEHAVIOR OF ESTIMATORS AND ASYMPTOTIC FORMULAS

Of interest to investigators beginning studies of stock composition of mixtures is the behavior of our estimators as test and mixed sample sizes vary for fixed rules and the influence of rules on the estimators. Further, we remarked that our solution of the stock mixture problem assumes large test and mixed samples. Of concern is how large specifically the samples must be for the asymptotic expressions to be reasonably accurate. This examination will be restricted to the two-stock case which is general for our purpose in that any number of stocks can be partitioned into two groups; that is, we can evaluate the estimators for a particular stock when the remaining stocks are lumped into a second group after assignment by the rules to the individual stocks. Bias and variance for the particular stock would be unchanged then even if the stocks of the second group were treated severally.

We evaluate estimation behavior and asymptotic approximation for three choices of Φ representing rules of increasing accuracy:

$$\text{Case 1. } \Phi = \begin{bmatrix} 0.75 & 0.25 \\ 0.25 & 0.75 \end{bmatrix}$$

$$\text{Case 2. } \Phi = \begin{bmatrix} 0.75 & 0.25 \\ 0.10 & 0.90 \end{bmatrix}$$

$$\text{Case 3. } \Phi = \begin{bmatrix} 0.90 & 0.10 \\ 0.10 & 0.90 \end{bmatrix}$$

We let $\mathbf{O}' = (0.6, 0.4)$ for all three cases. Based on experience in identification of sockeye salmon in Bristol Bay, Alaska, using discriminant functions on scale features, the ranges of elements of Φ are realistic. The choice of $\mathbf{O}$ is arbitrary, of course.

Given Φ, $\mathbf{O}$, and sample sizes t_1, t_2, and m, we can enumerate all possible sample points — t_{11}, t_{12}, t_{21}, t_{22}, m_1, and m_2 — as well as compute their probabilities of occurrence. In our evaluations, we always used equal test sample sizes. For each sample point, we can compute $\mathbf{O}$, $\hat{\mathbf{O}}$, $\tilde{\mathbf{O}}$, $\boldsymbol{\Sigma}_{\hat{\mathbf{O}}}$, $\boldsymbol{\Sigma}_{\tilde{\mathbf{O}}}$, and $\boldsymbol{\Sigma}_{\ddot{\mathbf{O}}}$. With these calculations for each point we can compute the mean and variance of each estimator by weighting its value at a sample point by the probability of that point.

Estimation of $\mathbf{O}$ by $\hat{\mathbf{O}}$, $\tilde{\mathbf{O}}$, or $\ddot{\mathbf{O}}$ requires the probability that $|\Phi| = 0$ be zero; this condition is not met. If we supplement the procedure by assigning arbitrary values to the estimators when $|\Phi| = 0$, means and variances of such modified estimators will approach the values we obtained by omission of such sample points. The probability that $|\Phi| = 0$ rapidly decreases with increasing test sample sizes. For case 1 with test samples of 20, it is $\cdot 5 \times 10^{-4}$, and with test samples of 40, about 5×10^{-7}. The probability also decreases with improved identification of stocks. For case 3 with test samples of 20, the probability is $\cdot 4 \times 10^{-6}$. Weighting the arbitrary values of the estimators corresponding to such points by their probabilities makes their contributions to expectation computations negligible.

We found these numerical studies to be expensive, especially with large sample sizes. Therefore, we began omitting sample points whose probability was small even if $|\Phi| \neq 0$. Criteria for omission of points are indicated in our tables; the justification is again their negligible contributions in expectation computations. Results will be discussed in terms of the first stock only.

We consider bias first. Bias of any estimator, θ_1, $\hat{\theta}_1$, or $\ddot{\theta}_1$, is unaffected by changes in mixed sample size; however, bias decreases with increasing test sample size. For example, we computed biases for case 1 with three mixed sample sizes—20, 30, and 40 — at each of two choices of equal sized test samples — 20 and 30 (Table 2, lines 1 to 6). The occasional change in the last digit for biases at varying mixed sample sizes within fixed test sample sizes is probably caused by omission of improbable sample points in evaluation of expectations. Bias of θ_1 also is predicted by the asymptotic formula (Equation (12)) to vary only with test sample sizes, not mixed sample size (Table 2, last column).

Bias of $\hat{\theta}_1$ is of opposite sign from that of either θ_1 or $\ddot{\theta}_1$ (Table 2, column $b_{\hat{\theta}}$ as compared with columns b_θ and $b_{\ddot{\theta}}$). Absolute value of bias of $\hat{\theta}_1$ is less than that of either θ_1 or $\ddot{\theta}_1$. Generally, absolute value of bias of $\ddot{\theta}_1$ is also less than that of θ_1; the sole exception is case 1 with test samples of only 20.

Bias of θ_1 or $\ddot{\theta}_1$ decreases with improved rules as we go from case 1 to case 2 to case 3, holding test and mixed sample sizes fixed. Biases computed for $\hat{\theta}_1$ decreased between case 1 and case 3 for which the Φ-matrices are both symmetric; however, for

TABLE 2.—Biases, (b_{θ_1}, b_{θ_2}, and b_{θ_3}), of estimators and asymptotic bias, $b_{\hat{\theta}_1}$, from Equation (12) for indicated Φ-matrices, indicated test and mixed sample sizes, and $\Theta = (0.6, 0.4)$

Φ	Test sample sizes	Mixed sample size	b_{θ_1}	b_{θ_2}	b_{θ_3}	$b_{\hat{\theta}_1}$
Case 1	20	120	-0.01077	0.00363	-0.01873	-0.00750
		330	-.01076	.00362	.01873	-.00750
$\begin{bmatrix} 0.75 & 0.25 \\ 0.25 & 0.75 \end{bmatrix}$		540	-.01076	.00364	.01873	-.00750
	30	120	-.00637	.00123	.00381	-.00500
		330	-.00637	.00124	.00381	-.00500
		540	-.00636	.00124	.00382	-.00500
	40	540	-.00438	.00063	.00108	-.00375
Case 2	20	120	-.01053	.00090	.00186	-.00905
$\begin{bmatrix} 0.75 & 0.25 \\ 0.10 & 0.90 \end{bmatrix}$	30	330	-.00660	.00037	.00060	-.00604
	40	540	-.00481	.00022	.00033	-.00453
Case 3	20	120	-.00155	.00014	.00018	-.00141
$\begin{bmatrix} 0.90 & 0.10 \\ 0.10 & 0.90 \end{bmatrix}$	30	330	-.00099	.00007	.00008	-.00094

[1]Evaluated at all sample points except when $\Phi = 0$.
[2]Evaluated only at sample points for which probability of observing the outcomes of the test samples $< 10^{-6}$ and $\Phi \neq 0$.

two of three combinations of test and mixed sample sizes, repeated under case 1 and case 2, bias increased between case 1 and case 2, the latter not having a symmetric Φ-matrix.

The predicted bias of θ_1 from the asymptotic formula [Equation (12)] agrees with actual bias of θ_1 reasonably well. The approximation obviously becomes more accurate as size of test samples increases or as rules improve.

Biases would appear negligible in comparison with magnitude of variances of the estimators next considered. Absolute value of bias in the situations evaluated represents at most 3.1% of the parameter value, $\theta_1 = 0.6$. Random errors in estimation are the main concern.

Variances of the estimators ($\hat{\theta}_1$, $\hat{\theta}_2$, and $\hat{\theta}_3$) decrease as test samples become larger, agreeing in behavior with biases; in contrast to biases, variances also decrease as size of mixed samples increases. We computed variances under case 1 for the same test and mixed sample sizes described for bias evaluation (Table 3, lines 1 to 6). Although variance of any of the estimators (θ_1, θ_2, and θ_3) decreases with size of test or mixed samples, the rate decreases with size of either type when that of the other is fixed. For example, at test samples of

TABLE 3.—Variances (σ_{θ_1}, σ_{θ_2}, and σ_{θ_3}) of estimators and asymptotic variance ($\sigma_{\hat{\theta}_1}$) from Equation (11) for indicated Φ-matrices, indicated test and mixed sample sizes, and $\Theta = (0.6, 0.4)$

Φ	Test sample sizes	Mixed sample size	σ_{θ_1}	σ_{θ_2}	σ_{θ_3}	$\sigma_{\hat{\theta}_1}$
Case 1	20	120	0.11232	0.06741	0.86891	0.06900
		330	.08685	.05120	.66980	.05250
$\begin{bmatrix} 0.75 & 0.25 \\ 0.25 & 0.75 \end{bmatrix}$		540	.07417	.04311	.60199	.04425
	30	120	.07957	.06370	.23131	.06250
		330	.05904	.04686	.17620	.04600
		540	.04877	.03844	.14864	.03775
	40	540	.04051	.03538	.03518	.03450
Case 2	20	120	.04640	.04010	.04448	.03927
$\begin{bmatrix} 0.75 & 0.25 \\ 0.10 & 0.90 \end{bmatrix}$	30	330	.02892	.02668	.02658	.02618
	40	540	.02111	.01995	.01992	.01963
Case 3	20	120	.02425	.02293	.02290	.02269
$\begin{bmatrix} 0.90 & 0.10 \\ 0.10 & 0.90 \end{bmatrix}$	30	330	.01579	.01525	.01525	.01513

[1]Evaluated at all sample points except when $\Phi = 0$.
[2]Evaluated only at sample points for which probability of observing the outcomes of the test samples $< 10^{-6}$ and $\Phi \neq 0$.

20, variance of θ_1 decreases 24% when mixed samples increase from 20 to 30, but by only 16% when mixed samples increase further to 40. Similarly at a mixed sample of 40, variance of θ_1 decreases by 11% and 8% as test samples increase from 20 to 30 and 30 to 40, respectively. The return to sampling effort of precision of estimation by increase in mixed sample size with test sample sizes fixed diminishes and is limited by test sample sizes. Return of precision to increase in test sample sizes is similarly related to and limited by mixed sample size.

Overriding both test and mixed samples in determining ultimate precision of estimation are the rules characterized by the Φ-matrix. As rules of assignment improve and the Φ-matrix approaches the identity matrix, precision of estimation at fixed test and mixed sample sizes increases.

In our evaluations, variance of θ_1 is always less than that of θ_1. In this respect θ_1 also enjoys considerable advantage over θ_1 when rules are poor, case 1, and sample sizes are small. As test or mixed samples increase, the advantage diminishes until θ_1 has the smaller variance. However, differences among variances of the three estimators (θ_1, θ_1, and θ_1) become negligible either as rules improve or samples sizes become large.

Predicted variance of the estimators of θ_1 from the asymptotic formula [Equation (11)] describes variance of θ_1 remarkably well, even when rules are poor and sample sizes are small (Table 3, compare lines 1 to 7 of column $\sigma_{\theta_1}{}^2$ with column $\sigma_{\theta_1}{}^2$). With improved rules, variances of each of θ_1, θ_1, and θ_1 are well described by the asymptotic variance (Table 3, compare lines 8 to 12 of columns $\sigma_{\theta_1}{}^2$, $\sigma_{\theta_1}{}^2$, and $\sigma_{\theta_1}{}^2$ with column $\sigma_{\theta_1}{}^2$).

Two evaluations concerning adequacy of internal variance estimation by $\hat{\Sigma}_{\theta_1}$, $\hat{\Sigma}_{\theta_1}$, and $\hat{\Sigma}_{\theta_1}$ conclude our numerical studies. Computations are heavy so the range of these studies is restricted. First, we computed the mean of the internal variance estimator $\hat{\sigma}_{\theta_1}{}^2$ (i.e., of the element in the first row and first column of $\hat{\Sigma}_{\theta_1}$) for the cases of Φ and sample sizes used in the previous evaluations of bias and variance (Table 4). The mean of this internal variance estimator, $E(\hat{\sigma}_{\theta_1}{}^2)$, generally exceeds the actual variance of θ_1, $\sigma_{\theta_1}{}^2$. As rules improve with sample size fixed, percent bias changes from large positive values to small negative values.

Percent bias under case 1 decreases sharply with increase of test sample size, but increases slightly with increase of mixed sample size (Table 4, lines 1 to 7); conceivably omission of sample points in our evaluations underlies the slight increase with mixed sample size. Under any case of Φ, the internal estimator or variance of θ_1 becomes nearly unbiased at the largest sample sizes examined.

TABLE 4.—Variance, $\sigma_{\theta_1}{}^2$, of estimator, θ_1, mean, $E(\hat{\sigma}_{\theta_1}{}^2)$, of internal variance estimator, $\hat{\sigma}_{\theta_1}{}^2$, and percent bias for indicated Φ-matrices; for indicated test and mixed sample sizes, and $\mathbf{O}' = (0.6, 0.4)$.

	Φ	Test sample sizes	Mixed sample size	$\sigma_{\theta_1}{}^2$	$E(\hat{\sigma}_{\theta_1}{}^2)$	Percent bias
Case 1		20	[1]20	0.11232	0.24894	122
			[2]30	.08685	.19693	127
	$\begin{bmatrix} 0.75 & 0.25 \\ 0.25 & 0.75 \end{bmatrix}$		[2]40	.07417	.17096	130
		30	[2]20	.07957	.10171	28
			[2]30	.05904	.07707	31
			[2]40	.04877	.06450	32
		40	[2]40	.04051	.04289	5.9
Case 2		20	[2]20	.04640	.04894	5.5
	$\begin{bmatrix} 0.75 & 0.25 \\ 0.10 & 0.90 \end{bmatrix}$	30	[2]30	.02892	.02931	1.3
		40	[2]40	.02111	.02125	0.7
Case 3		20	[2]20	.02425	.02394	1.3
	$\begin{bmatrix} 0.90 & 0.10 \\ 0.10 & 0.90 \end{bmatrix}$	30	[2]30	.01579	.01562	1.1

[1]Evaluated at all sample points except when $\Phi = I$.
[2]Evaluated only at sample points for which probability of observing the outcomes of the test samples $> 10^{-6}$ and $\Phi \neq I$.

Our last computations are of the mean and variance of the internal variance estimators ($\hat{\sigma}_{\theta_1}{}^2$, $\hat{\sigma}_{\theta_1}{}^2$, and $\hat{\sigma}_{\theta_1}{}^2$) (i.e., of the elements in the first row and column of $\hat{\Sigma}_{\theta_1}$, $\hat{\Sigma}_{\theta_1}$, and $\hat{\Sigma}_{\theta_1}$, respectively) for the three cases of Φ with test and mixed samples all of size 20. Also we determined the actual probability that 90% and 95% simultaneous confidence intervals from Equation (16) using either $\hat{\theta}_1$, $\hat{\theta}_1$, or $\hat{\theta}_1$, each with its internal variance estimator, $\hat{\Sigma}_{\theta_1}$, $\hat{\Sigma}_{\theta_1}$, or $\hat{\Sigma}_{\theta_1}$, cover the actual composition vector $\mathbf{O}' = (0.6, 0.4)$ (Table 5).

Comparison of actual variances of the estimators (θ_1, θ_1, and θ_1) (Table 5, line 1) with the mean of the corresponding internal variance estimators (Table 5, line 2) shows the positive bias of each internal estimator diminishes as rules improve. Only the internal estimator of variance of θ_1 becomes negatively biased. Percent bias (Table 5, line 3) of each estimator decreases sharply with improvement of rules.

Variance of the internal variance estimators of θ_1 and θ_1 are manyfold greater than that of θ_1 under case 1 and case 2. With improved rules of case 3, all internal variance estimators have comparable variance.

Probabilities that simultaneous confidence intervals for each estimator ($\hat{\mathbf{O}}$, $\hat{\mathbf{O}}$, and $\hat{\mathbf{O}}$) cover the

TABLE 5.—Variances of the estimators (θ_1, θ_4, and θ_5), means of internal variance estimators, percent bias of internal variance estimators, variances of internal variance estimators, and probabilities of coverage of $\Theta' = (0.6, 0.4)$ by simultaneous 90 and 95% confidence intervals for three cases of Φ when test and mixed samples are all of size 20[1]

	Φ	$\begin{bmatrix} 0.75 & 0.25 \\ 0.25 & 0.75 \end{bmatrix}$			$\begin{bmatrix} 0.75 & 0.25 \\ 0.10 & 0.90 \end{bmatrix}$			$\begin{bmatrix} 0.90 & 0.10 \\ 0.10 & 0.90 \end{bmatrix}$		
Estimator		θ_1	θ_4	θ_5	θ_1	θ_4	θ_5	θ_1	θ_4	θ_5
Variance of estimator		0.11221	0.06740	0.86543	0.04634	0.04009	0.04259	0.02425	0.02293	0.02290
Mean of internal variance estimator		0.24824	0.12030	7.75453	0.04859	0.04683	0.07374	0.02394	0.02387	0.02386
Percent bias of internal variance estimator		121	78	796	4.9	16.8	73	-1.3	4.1	4.2
Variance of internal variance estimator		25.2471	0.10567	125.688	0.11388	0.00175	439.969	9.521×10^{-5}	9.166×10^{-5}	9.140×10^{-5}
Probability of coverage of Θ by 90% confidence intervals		0.733	0.949	0.950	0.906	0.917	0.917	0.890	0.897	0.897
Probability of coverage of Θ by 95% confidence intervals		0.976	0.981	0.981	0.956	0.960	0.960	0.947	0.950	0.950

[1]Evaluations only include sample points for which probability of observing the outcome of the test samples $> 10^{-5}$ and $\Phi > 0$

parameter vector $\Theta' = (0.6, 0.4)$ approach the intended levels of confidence as rules improve (Table 5, lines 5 and 6). For rules of case 1 or case 2, the level of confidence provided by any of the estimators exceeds that intended; such is preferable to the converse because the intervals provide at least the level of confidence the investigator intends. Our normality assumption used to construct confidence intervals will be better satisfied as mixed and test sample sizes increase. Apparently the internal variance estimators become less biased as test sample size increases. Therefore, we anticipate the level of confidence of intervals from any of the estimators will more closely approach the intended level as test sample size increases even when rules are poor.

Limited as these numerical studies are, they demonstrate that when sample sizes are small and rules are poor, $\tilde{\Theta}$ should be used to estimate composition of a mixture. We found then that $\tilde{\Theta}$ is least biased, has smallest variance, and its internal variance estimator itself has smallest variance. With larger sample sizes or good rules of assignment, the estimators $\hat{\Theta}$, $\bar{\Theta}$, and $\tilde{\Theta}$ appear more nearly equivalent.

Decisions on sample sizes depend on desired precision and the rules characterized by Φ. The closer Φ is to an identity matrix or, equivalently, the better the identification of stocks, the fewer required individuals in test and mixed samples to achieve desired precision of composition estimation. With an accurate initial estimate of Φ from the learning samples, the corresponding asymptotic variance-covariance matrix at Equation (11) can be used to estimate sample sizes needed to achieve required precision. We recall that variance of θ_1 is well described by the asymptotic variance-covariance matrix even when rules are poor and sample sizes are small, providing another reason for preferring $\tilde{\Theta}$ to $\hat{\Theta}$ or $\bar{\Theta}$ in that circumstance.

AFTERWORD

Withholding individuals of samples from the separate stocks to form test samples must result in less effective rules than if the learning and test samples were pooled for rule formation. Although the practice is repaid in part by the ability to evaluate precision of composition assessment, the penalty at rule development can be further alleviated. Roles of the two samples from each of the separate stocks can be interchanged; either can be the learning or test sample. If each of the samples from the segregated stocks is partitioned into two approximately equal sized subsamples, two sets of rules can be formed; two estimates of Φ obtained; two estimates of Θ computed by any of $\hat{\Theta}$, $\bar{\Theta}$, or $\tilde{\Theta}$; and two internal estimates of the variance-covariance matrices ($\hat{\Sigma}_{\theta\theta}$, $\bar{\Sigma}_{\theta\theta}$, or $\tilde{\Sigma}_{\theta\theta}$) calculated. The pairs of estimates are statistically dependent. Nonetheless, means of pairs of estimates of Θ and $\Sigma_{\theta\theta}$ have the same expectation and presumably greater precision than the individual members of the pairs. Exact evaluation of that enhanced precision for estimates of the composition vector Θ does not appear easy; however, use of the mean of internal estimates of the variance-covariance matrix in calculation of the confidence set Equation (15) provides an unknown but greater level of confidence than the indicated $100(1 - \alpha)\%$ value.

LITERATURE CITED

ANAS, R. E., AND S. MURAI
1969 Use of scale characters and a discriminant function

for classifying sockeye salmon (*Oncorhynchus nerka*) by continent of origin. Int. North Pac. Fish. Comm., Bull. 26:157-192.

COOK, R. C., AND G. E. LORD.
1978. Identification of stocks of Bristol Bay sockeye salmon, *Oncorhynchus nerka*, by evaluating scale patterns with a polynomial discriminant method. Fish. Bull., U.S. 76:415-423.

FUKUHARA, F. M., S. MURAI, J. J. LALANNE, AND A. SRIBHIBHADH.
1962. Continental origin of red salmon as determined from morphological characters. Int. North Pac. Fish. Comm., Bull. 8:15-109.

HILL, D. R.
1959. Some uses of statistical analysis in classifying races of American shad (*Alosa sapidissima*). U.S. Fish Wildl. Serv., Fish. Bull. 59:268-286.

KONOVALOV, S. M.
1975. Differentiation of local populations of sockeye salmon *Oncorhynchus nerka* (Walbaum). (Translated from Russ. by Leda V. Sagen.) Univ. Wash. Publ. Fish., New Ser., 6, 280 p.

MORRISON, D. F.
1967. Multivariate statistical methods. McGraw-Hill, N.Y., 338 p.

PARSONS, L. S.
1972. Use of meristic characters and a discriminant function for classifying spring- and autumn-spawning Atlantic herring. Int. Comm. Northwest Atl. Fish. Res. Bull. 9:5-9.

WORTUND, D. D., AND R. A. FREDIN.
1962. Differentiation of stocks. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 143-153. H.R. MacMillan Lectures in Fish., Univ. B.C., Vancouver, Can.

BEHAVIOR AND ECOLOGY OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN THE SOUTH ATLANTIC

BERND WÜRSIG AND MELANY WÜRSIG[1]

ABSTRACT

Bottlenose dolphins observed nearshore in Golfo San Jose, Argentina, spent 92% of their time in water less than 10 m deep. They moved into deeper water, up to 39 m depth, mainly during midday in nonsummer for brief (16 min) periods. They moved more rapidly in deeper water, and may have been feeding on schooling fish at that time. During summer they stayed in shallow water, 2-6 m deep.

Dolphins moved parallel to shore and in consistent depth of water at almost all times. They changed direction at predictable locations and patrolled certain nearshore waters for up to several hours. Their movement was influenced by tide and by nearshore rocks.

Slow movement and apparent resting occurred mainly during the morning, while most aerial behavior, apparent sexual and social behavior, and rapid-movement feeding occurred in the afternoon.

The Atlantic bottlenose dolphin, *Tursiops truncatus*, is undoubtedly the best studied of any of the toothed cetaceans. It was successfully kept in captivity over 60 yr ago (Townsend 1914), and has since that time served as the "white rat" of cetology, with a great deal known about its behavior in captivity, but until relatively recently practically nothing known about its behavior in the wild. Long-term behavioral studies of stable bottlenose dolphin colonies in captivity were mainly carried out at Marine Studios/Marineland of Florida from the mid-1930's to mid-1950's (McBride 1940; McBride and Hebb 1948; McBride and Kritzler 1951; Essapian 1953, 1963; Tavolga and Essapian 1957; Tavolga 1966). These studies showed that bottlenose dolphins have a complex social organization, often with a male-dominated social hierarchy. From some of these studies also developed the idea that bottlenose dolphins, and other odontocete species as well, use echolocation (McBride 1956). This concept was validated by numerous workers in the 1950's and 1960's (Schevill and Lawrence 1956; Kellogg 1961; Norris et al. 1961). Other research on captive bottlenose dolphins in general (including the species *T. gilli* and *T. aduncus*, as well as *T. truncatus*) was reported by Brown and Norris (1956), Caldwell et al. (1965), D. K. Caldwell and M. C. Caldwell (1972), M. C. Caldwell and D. K. Caldwell (1972), Tayler and Saayman (1972), and Saayman et al. (1973). The first reports of behavior in the wild consisted mainly of anecdotal information gathered opportunistically while capturing dolphins or pursuing other activities (Gunter 1942; Brown and Norris 1956; Norris and Prescott 1961; Brown et al. 1966). This led to more detailed field studies, most of which have been made within the past 10 yr, and all of which relied heavily on shore-based or small-boat operations close to shore (Saayman et al. 1972; Tayler and Saayman 1972; Irvine and Wells 1972; Saayman et al. 1973; Saayman and Tayler 1973; Shane 1977; Würsig and Würsig 1977; Castello and Pinedo 1977; Würsig 1978; Wells et al. in press; Irvine et al.[2]). At the same time, and also close to shore, behavioral investigations of other odontocete genera have been carried out. Thus, Norris and Dohl[3] studied the Hawaiian spinner dolphin, *Stenella longirostris*, Saayman and Tayler (in press) described Indian Ocean humpback dolphin, *Sousa* sp., behavior and social organization, and Würsig and Würsig[4] performed similar work on the South Atlantic dusky dolphin, *Lagenorhynchus obscurus*.

[1]State University of New York at Stony Brook, Program for Neurobiology and Behavior; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064

Manuscript accepted December 1978
FISHERY BULLETIN VOL. 77, NO. 2, 1979

[2]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1978. A study of the movements and activities of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Final report for U.S. Marine Mammal Commission Contracts MM4AC004 and MM5AC0018. 53 p.

[3]Norris, K. S., and T. P. Dohl. The behavior of the Hawaiian spinner porpoise, *Stenella longirostris* (Schlegel, 1841). Unpubl. manuscr., 66 p. Center for Coastal Marine Studies, University of California, Santa Cruz.

[4]Würsig, B. G., and M. A. Würsig. The behavior and ecology of the dusky dolphin, *Lagenorhychus obscurus*. Unpubl. manuscr., 64 p. Center for Coastal Marine Studies, University of California, Santa Cruz.

Detailed work on the social organization of bottlenose dolphins was carried out by Irvine et al. (see footnote 2) and Wells et al. (in press). They captured many animals for tagging, and thus gained size and sex information. They found that a resident herd in the Sarasota-Bradenton area of West Florida consisted of groups whose individual membership was constantly changing by influx and efflux in a "kaleidoscopic manner." Such changes were not random, however, and several patterns of association were observed. Within a relatively stable herd occupying a well defined home range, each age and sex class frequented particular regions and interacted with other classes to varying degrees. Females of all ages and adult males ranged through the northern portion of the home range and interacted more with each other than with subadult males, which formed bachelor groups or groups with one or more adult females in the southern portion. Females with young moved throughout the home range and interacted with adult males to a lesser extent than did other females. A given group generally remained intact for only a matter of hours or days.

At least superficially similar group instability was documented for Argentine bottlenose dolphins by Würsig and Würsig (1977) and Würsig (1978), for Texas bottlenose dolphins by Shane (1977), for Hawaiian spinner dolphins by Norris and Dohl (see footnote 3), and for humpback dolphins by Saayman and Tayler (in press). These studies present the first detailed accounts of some aspects of social organization of odontocete cetaceans, and make comparisons of these animals with terrestrial mammals such as bovids and primates possible.

The present analysis of South Atlantic bottlenose dolphins represents an attempt to describe the general movement patterns, aerial and social behavior, and ecology of this population. We made no attempt to capture animals for sex and size information as we were loathe to disturb their "natural" movement and social behavior. Instead, we observed them mainly from cliffs lining the shore. Earlier, we reported on some aspects of seasonal occurrence patterns, group stability, surfacing associations, and calving seasonality of the same population discussed here (Würsig and Würsig 1977; Würsig 1978). This paper presents additional information, with the primary purpose of providing background data on the natural history of bottlenose dolphins, and hopefully also with future application to other species as further studies unfold.

MATERIALS AND METHODS

Bottlenose dolphins were observed at Golfo San José (lat. 42°23′ S., long. 64°03′ W.) from July 1974 through March 1976. We made observations through binoculars and a 20-power transit monocular from two points, 14 m and 46 m high at mean low water ("Camp" and "Cliff Hut," respectively, Figures 1, 2).

To describe the movements of dolphin subgroups (averaging 15 animals) which were present near the observation point anywhere from several minutes to several hours, we plotted their positions with the help of a Kern[5] model DKM1 surveyor's theodolite. The theodolite had a 20-power monocular through which the animals were followed visually. A separate eyepiece showed horizontal degrees and vertical degrees which represented the location of the dolphins, and which we read at 15 s to several-minute intervals into a cassette recorder. In the laboratory, data from the theodolite were plotted on a depth map (Figure 2), by a Hewlett-Packard Model 9830A desk calculator and plotter. Besides plotting the animals' positions, the computer program also supplied their distance from the observer, their heading in degrees relative to true north, and their speed.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

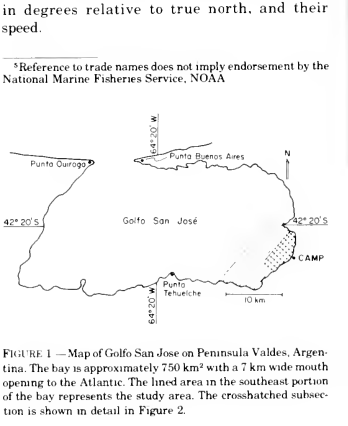


FIGURE 1.—Map of Golfo San Jose on Peninsula Valdes, Argentina. The bay is approximately 750 km² with a 7 km wide mouth opening to the Atlantic. The lined area in the southeast portion of the bay represents the study area. The crosshatched subsection is shown in detail in Figure 2.

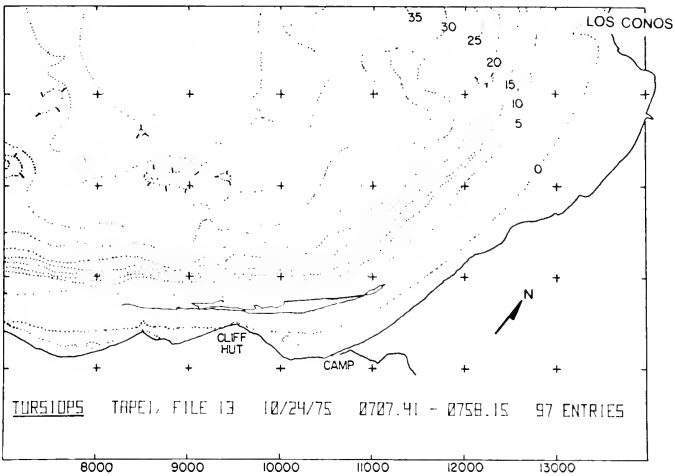


FIGURE 2.—Depth contour map of one-fourth of the study area. Margin numbers represent meter distances relative to a zero location on land. Crosses form 1 km squares. "Cliff Hut" and "Camp" are the locations from which most observations were made. Depth contours are in meters at mean low water (MLW). The usual distance for good observation of a moving dolphin group was at least 3 km. At a normal tide height of 5 m above MLW, water depth of 40 m was 1 km from Cliff Hut, and thus clearly visible. The solid line above Cliff Hut represents a sample track of a bottlenose dolphin group, and the printed information gives computer file location, date of track, time of day, and number of theodolite entries. About 200 such tracks were obtained of bottlenose dolphins during the 21-mo study. The map is from a larger area map which was by courtesy of Roger Payne, New York Zoological Society, Oliver Brazier, Woods Hole Oceanographic Institute, and Russ Charif, Harvard University.

Since dolphins often did not travel in straight line, speed information from theodolite readings separated by several minutes was lower than the actual speed traveled. To minimize errors in speed calculations, only readings made within 30 s of each other were used. The accuracy of the transit (±30″ of arc) allowed for placement of position within ±100 m at 5.5 km distance.

RESULTS

Preferred Depths

To determine whether dolphins prefer a specific depth of water, and to map their movement patterns, theodolite readings were obtained whenever bottlenose dolphins came within sighting range of shore (1-10 km, depending on visibility). Within that range, the depth of water varied from 1 to 65 m. Bottlenose dolphins occurred 92% of the time in water <10 m deep (2,655 of 2,883 theodolite readings), within 1 km of shore (Figure 3). None were ever sighted in water >39 m. Visibility at almost all times extended to at least 3 km from shore, where water depth was 45-50 m (see Figure 1), and we consistently tracked dusky dolphins in much deeper water (Würsig and Würsig see footnote 4). Furthermore, we traversed the study area by boat in waters 1 to 10 km from shore on 109 occasions and never saw bottlenose dolphins in water >39 m. For these reasons we believe that the data for shallow nearshore travel are not biased by sighting error. In general, dolphins moved in shallow water in the morning and

FIGURE 3.—The number of theodolite readings of dolphins found in different depths of water (a) and the total amount of area available in the study region at different depths of water, at a mean tide height of 5.0 m above mean low water (b). Most readings were obtained in shallow water despite the fact that more geographic area was covered by deeper water. The total area used for these calculations is represented by the lined and crosshatched sections of Figure 1.

afternoon, and in deeper water around noon (Figure 4a). When deepwater movement occurred, however, it was brief (16 min average per movement in water >10 m deep, SD = 7.1, $n = 230$) and was interspersed with longer shallow-water travel. As a result, the increase in mean depth around noon of Figure 4a and b was not because animals consistently traveled in deeper water at those times. Instead, they more often moved for brief periods into deep water, and therefore the mean depths increase at those times. When the data were divided into months (Figure 4b, c), the nonsummer months of March, July, October, and November account for the movement into deeper water shown in Figure 3a. This trend was particularly strong for July (midwinter in Argentina), with a peak of 23 m depth at 1300 h. On the other hand, no increase in depth of water during midday took place in summer (December and January, Figure 4c). It would appear that there are predictable seasonal and daily variations in depth of water in which the dolphins move.

Speed of Movement

The overall mean speed of the dolphins calculated from the 1,545 theodolite readings made within 30 s of each other was 6.1 km/h. Speed of travel was significantly correlated with depth of water; speed was 5.7 km/h in water <10 m deep, and 13.9 km/h in deeper water (Figure 5). But, was speed directly influenced by depth of water, or was it due to distance from shore, which in general increased with increasing depth? To solve this ambiguity, we took random samples of 10 readings each from 1) <600 m from shore and ≥ 10 m depth, 2) <600 m from shore and ≥ 10 m depth, and 3) <600 m from shore and <10 m depth, and compared their speeds (Table 1). If speed were influenced by distance from shore, we would expect speeds of 1) and 2) to be different. Instead, speeds of 2) and 3) were significantly different ($P < 0.005$, Wilcoxin two-sample test, Sokal and Rohlf 1969), indicating that depth of water, not distance from shore, was probably the prime determinant of speed increase.

TABLE 1.—Samples of bottlenose dolphin speeds (kilometers per hour) in three different water conditions, selected at random from the data.

	600 m from shore <10 m depth	600 m from shore >10 m depth	600 m from shore ≥ 10 m depth
	7.8	16.1	4.3
	15.3	21.8	2.5
	14.2	28.8	5.2
	13.7	20.4	7.0
	12.8	13.1	4.7
	14.2	12.0	4.5
	16.1	16.1	3.8
	11.4	13.7	5.6
	21.8	17.5	6.1
	21.4	14.3	5.9
Mean	11.4	17.4	5.0

Speed of travel appeared uniform throughout the day (Figure 6a), but a further subdivision into months (Figure 6b, c) shows that there was an increase around noon in nonsummer months, with the average speed over 14 km/h at 1300 h during October. During December and January, no such midday peak was evident, but instead animals traveled more rapidly during late afternoon than at other times of day.

Movement Patterns

In water <10 m deep, bottlenose dolphins almost always moved parallel to the depth lines; that is, they stayed in consistent depth (Figure 7). In deeper water, movement was more random and dolphins at times rapidly crossed into different depths. Nevertheless, a tendency to follow depth contours was still present.

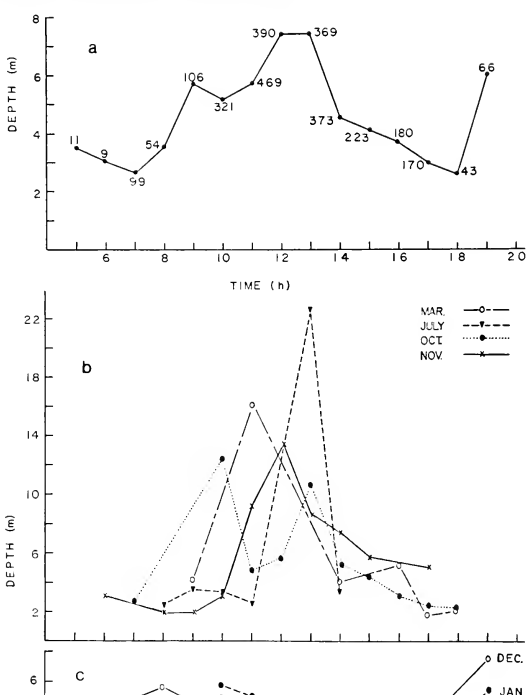


FIGURE 4.—Mean depth of water in which bottlenose dolphins were found during different times of day (a). The numbers near points represent number of theodolite readings gathered for that hour of day. The higher number of readings around midday is a result of increased work with the theodolite at that time; it does not represent an increase of dolphins in the area. Instead, the incidence of dolphin sightings was about equal for all daylight hours. These data were divided into different months (b, c). Average depths > 10 m are clumped toward midday (10-13 h, $P = 0.014$, Raleigh test, Greenwood and Durand 1955). These deeper water peaks are significantly different from shallow-water travel during the rest of the day for March, July, October, and November ($P < 0.01$ in all 4 mo, Kruskal-Wallis test in lieu of one-way ANOVA, Sokal and Rohlf 1969). In December and January, dolphins stayed in shallow water all day, and this trend is different from data in b ($P < 0.001$, Mann-Whitney U test, Sokal and Rohlf 1969).

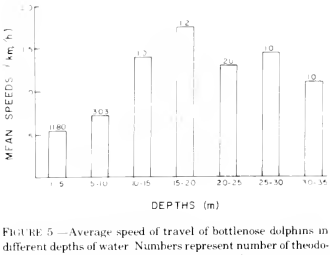


FIGURE 5.—Average speed of travel of bottlenose dolphins in different depths of water. Numbers represent number of theodolite readings per depth category for which speed information was available. Shallow-water (< 10 m) speeds are significantly different from those in deeper water ($P < 0.01$, Mann-Whitney U-test, Sokal and Rohlf 1969).

Movement of dolphins was also affected by tidal fluctuations. Animals were found in progressively shallower water as the tide ebbed. Thus, dolphins tended to remain the same distance from the high tide line. When the tide was 6 m above mean low water, dolphins were found in 9 m depth. At mean low water, they were found at a depth of 3 m (Figure 8a). At low water as the tide began to flood, the dolphins remained in shallow water (3 m) but as the tide continued to rise from 1 to 3 m, they moved into deeper water. At a tide height of 4-7 m, they moved into waters 5-10 m deep (Figure 8b). Depths over which dolphins were when flood tide was between 1 and 3 m were quite variable, indicating that the animals moved in all depths near shore at those times, and moved into deep water more often than at other tide heights. Thus, on a lowering tide, dolphins were found in progressively shallower water, while on a rising tide the reverse trend appeared, but with a dramatic interruption in this trend at tide heights of about 1-3 m. At those heights, dolphins more often moved into deep water for brief periods.

Bottlenose dolphin subgroups often moved back and forth longitudinally within a confined area near shore, thus at times staying within sight of our observation points all day. Within 0.5 km of shore, they turned (changed direction by $180° \pm 10°$) on the average every 673 m (SD = 980, n = 104), and farther than 0.5 km from shore they turned every 1,382 m (SD = 1,094 n = 11). Despite the large standard deviations in these readings, dolphins farther from shore traveled significantly longer distances before turning than when they

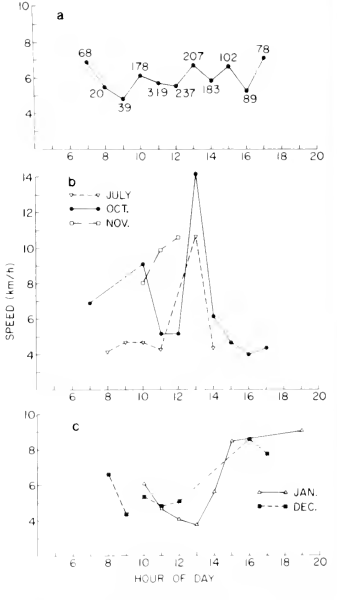


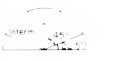
FIGURE 6.—Mean speed of travel at different times of day (a). The numbers near points represent number of theodolite readings with speed data gathered for that hour of day. These data were divided into months (b, c). In July and October, dolphins traveled faster at 1300 h than at other times, while in December and January, they traveled faster in late afternoon ($P < 0.01$, Kruskal-Wallis test in lieu of one-way ANOVA Sokal and Rohlf 1969).

were within 0.5 km of shore ($P = 0.05$, t-test). However, because they traveled faster when farther from shore (and in generally deeper water, see Figure 4), the time between turns was not significantly longer (mean time = 0.5 km from shore = 8.8 min, > 0.5 km = 10.0 min). Thus, dolphins changed direction about every 9 or 10 min. The increase in distance covered appeared to be a consequence of the greater speed in deeper water.

Changes in direction by $180° \pm 10°$ were often made at the same locations on different days, and

TYPE OF MOVEMENT IN WATER <10m DEEP

Movement	Observed	%	Expected	%
Parallel	796	77	258	25
Interm.	196	19	517	50
Perpend.	41	04	258	25
Total	1033	100	1033	100



TYPE OF MOVEMENT IN WATER ≥10m DEEP

Movement	Observed	%	Expected	%
Parallel	13	38	8.5	25
Interm.	19	56	17.0	50
Perpend.	2	06	8.5	25
Total	34	100	34	100

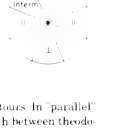


FIGURE 7.—Movement relative to depth contours. In "parallel" movement, dolphins stayed in the same depth between theodolite readings, in "intermediate" movement they crossed contour lines at an angle, and in "perpendicular" movement they moved perpendicular to depth contours, and therefore changed depths rapidly. In shallow (< 10 m) water, dolphins moved parallel to depth lines (±22.5°) significantly more than they moved perpendicular to them (±22.5°; $P < 0.001$, chi-square goodness of fit test) and in deeper (≥10 m) water this trend was weaker but still present ($P < 0.03$, test as above). The circles to the right show the divisions of movement, where parallel lines indicate movement parallel to depth lines, and an inverted T represents movement perpendicular to them. Only one-half circle is shown for shallow water because it is likely that animals near shore cannot travel into shallower water. However, the expected percentages of movement relative to depth contours remains the same in shallow and deep water.

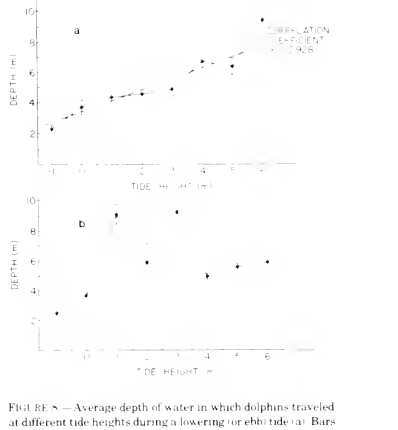


FIGURE 8.—Average depth of water in which dolphins traveled at different tide heights during a lowering (or ebb) tide (a). Bars above and below points represent 95% confidence limits. A least-squares regression line through the means shows that dolphins were found in progressively shallower water as the tide ebbed (correlation is statistically significant, $P < 0.01$). Average depth of water in which dolphins traveled at different tide heights during a rising (or flood) tide (b). The rising trend was interrupted between tides 1 and 3 m by animals more often moving into greater depth (shown by increase in mean depth and by larger 95% confidence limits, because variability increased).

therefore after a while could be predicted. Near camp there were three locations where subgroups turned more often than expected if turns were made at random ($P < 0.005$, chi-square goodness of fit test). All three of these locations were marked by rocks which were submerged during medium and high tides. When the tide was low enough to uncover these rocky areas, leaving only an even, sandy bottom covered, the preference for turning at those areas disappeared. It appears, therefore, that the animals used these rocks as underwater landmarks which, at least at times, stimulated them to change direction. It is unlikely that the dolphins turned at these locations simply to avoid bumping into the rocks, since one of the three areas was marked by rocks only 5-10 cm above the sandy substrate. All three areas formed distinct discontinuities in the bottom topography, however, and may have served as cues to turn at the boundary of the area traversed.

The tongue of land called Los Conos (Figure 2), 6 km north of camp, appeared to be the northward boundary of the present population's range. In 260 h of observation, dolphins were never observed traveling north of this point. When they were lost from sight, it was either due to bad visibility or because the animals traveled out of range in the southwest portion of the study area. In addition, when the animals were first spotted coming into the study area, they always came from the southwest, never from the north.

As was described earlier, bottlenose dolphins in the present study exhibited two distinct movements. Usually, they moved slowly and very close to shore, in shallow (< 10 m deep) water. They moved for brief (16 min) periods, mainly during midday in nonsummer seasons, into deeper (> 10

m) water, and moved more rapidly at that time. These two distinct movements were marked as well by a difference in group formation. While slowly traveling near shore, the dolphin subgroup was 87% of the time (226.2 h of 260 h) in a tight formation about 10-15 m wide and 50-75 m long. Because of this narrow formation, no individual was far from shore, and all were in similar depth. On the other hand, when dolphins moved into deeper water they advanced as a wider than long rank, with each animal separated from the next by as much as 25 m on its flank, yet the entire group presented one wide front. In this manner, the subgroup was able to cover a large swath of sea (up to about 300 m) as it rapidly moved ahead. During 13 of 134 times (9.7%) that rapid movement was observed, we noted 1-12 terns and at times gulls flying in front of this advancing dolphin line and diving into the water to pick up 10-15 cm long fish. We suspect that they may have been near parts of schools of southern anchovy, *Engraulis anchoita*, because of the abundance of this fish in the area. The wide front movement in deeper water may thus be a searching pattern by bottlenose dolphins for such schooling fish. When the subgroup slowed at the end of an individual-abreast run, the animals milled in different locations (122 of 134 times, 91%), giving us the impression that they were feeding in that location. However, such milling after rapid movement was usually short (60 s±30 s), and never lasted more than 5 min. At the end of milling, the subgroup usually (115 of 122 times, 94%) continued to move slowly in shallow water, but less often (7 of 122 times, 6%) began a new period of 16-min-long rapid movement in deep water.

Aerial Behavior

Aerial behavior was not as frequent in the bottlenose dolphin population we studied as in many other species of cetaceans (e.g., see Saayman and Tayler in press; Norris and Dohl see footnote 3, Würsig and Würsig see footnote 4). Individuals engaged in any form of aerial display <5% of the observed time. These displays were the 1) leap, 2) headslap, 3) noseout, 4) tailslap, and 5) kelp toss. For the sake of conformity, the aerial displays discussed below, except for 5), follow the names and descriptions of aerial behavior given for Hawaiian spinner dolphins by Norris and Dohl (see footnote 3):

1. Leaping either produced a loud sound when the animal fell back into the water onto its belly or side ("noisy leap"), or was relatively silent when the animal arched its body during the leap and reentered nose first ("clean leap"). Noisy and clean leaps occurred at any time of day when the animals were moving slowly close to shore. However, noisy leaps were most often performed by calves and subadults (calves leaped approximately 3 times as often as adults), and occurred more often in the afternoon (morning, 24 leaps in 117 h, mean = 0.21 h; afternoon, 70 leaps in 143 h, mean = 0.49 h; significant difference at $P < 0.001$, testing equality of percentages, Sokal and Rohlf 1969). Clean leaps were performed only by adults and usually occurred when the group was relatively stationary in medium-deep (10 m±5 m) water. At times (about 25%, not adequately quantified for exact numbers) such leaps were attended by terns diving in the vicinity and feeding on small fish, leading to the inference that such clean leaps, which allow animals to rapidly descend headfirst, may be food-related. No daily or seasonal pattern was evident for clean leaps.

2. The headslap was seen only twice in 260 h of observation, each time performed by a subadult while the subgroup slowly moved along shore.

3. Noseouts, when dolphins poked their heads out of the water to beyond at least one eye, were about as frequent as noisy leaps and usually occurred at the same time (i.e., more often in the afternoon).

4. Tailslaps were the most frequent form of aerial behavior. They also occurred at any time during the day, but were frequent only when some disturbance occurred. Thus tailslaps were noted a) when our outboard engine was started 300-500 m from the dolphins, b) 14 of 95 times (15%) our boat initially approached a subgroup of dolphins, c) when the subgroup had been split into two adjacent groupings for several hours and then rejoined (this happened five times), and d) once when a light plane flew overhead at low altitude. In these cases, the tailslapper was always an adult, and most of the time was a large, recognizable individual who was part of a stable subunit of five individuals which consistently stayed together (dolphin no. 1 in Würsig 1978). Unlike any of the other forms of aerial behavior, which usually were performed only once by one animal at a particular time, tailslapping occurred from 10 to 20 times during one bout.

5. "Kelp tossing" usually was accompanied by high incidences of noisy leaps and noseouts. Dur-

ing kelp tossing, an animal would balance a piece of *Macrocystis* sp. on its melon or forehead, flip it to its tail with a sudden head jerk, flip it to the dorsal fin with its tail, or any variation of the above. Kelp tossing was observed nine times during the study, and lasted an average of 15 min bout.

Social Behavior

Because most observations were done from a distance, and usually only dorsal fins were visible above the water, little insight was gained into social behavior. Nevertheless, a few major trends were apparent. When noisy leaps, noseouts, and kelp tossing occurred, animals were also often seen swimming side by side while touching, with at least one of the animals in an upside down position ("belly-up"). Viewed from directly overhead, as when the subgroup passed close beneath our observation cliff, individuals could be seen nudging each others' bodies with their snouts. As with leap frequency, most of this behavior was observed in the afternoon (12 of 17 times, 71%; significant difference from morning at $P < 0.02$, testing equality of percentages, Sokal and Rohlf 1969). It appeared as well that belly-up and rubbing behavior were more frequent when two subgroups which had moved separately for several hours joined again. However, this did not happen often enough (five times in total) for statistical analysis.

Five calves were observed during the study. Each stayed close to a particular adult (see Würsig 1978), and we assume that this adult was the mother. Calves and mothers were also observed engaging in rubbing behavior with other adults.

Bottlenose dolphins associated with the southern right whale, *Eubalaena glacialis*, which were seen near shore from June through November. While moving along shore, dolphins veered from their previous path by as much as 300 m to join one or more right whales. Once with the whales, they rapidly swam back and forth across the whales' head. Whales invariably became very active when dolphins were present, blowing and "snorting" loudly in air as well as underwater. Whales also rapidly surged or lunged ahead in the direction of dolphins crossing their heads. The dolphins then rode (or surfed) on the pressure waves created by these lunges, riding along the crest of either wave cascading to the side of the whales. This association appeared to us to be play, and occurred 24 of 26 times (92%) that whales were directly in front of the path of moving dolphins. It lasted an average of 15 min, after which the dolphins left the whales and continued in the direction in which they had been traveling before joining the whales.

Further interspecific associations occurred with the sea lion, *Otaria flavescens*, and, on one occasion, with a subadult male elephant seal, *Mirounga leonina*. The pinnipeds joined a subgroup of dolphins and traveled with it for up to 1 km, rapidly moving among the dolphins.

Dolphins also at times approached our 4.5 m rubber Zodiac boat and swam underneath the boat for brief (up to 5 min) periods. During 86 of 95 (91%) boat approaches, however, bottlenose dolphins appeared to ignore our boat, neither approaching nor avoiding it.

When winds rose above 20–30 km h, dolphins were often observed rapidly riding down the advancing crest of waves in the surfline. It appeared that they were surfing the waves much as human surfers do, and much as dolphins did with "bow" waves of whales.

Possible Predation

We saw no direct evidence for predation on bottlenose dolphins, but one of the animals, TS (for "tiger stripes," Würsig and Würsig 1977) appeared in January 1975 with a series of scratched lines along its left dorsum. From the regularity and spacing of the lines, we believe that they were made by killer whale, *Orcinus orca*, teeth. It seems possible that this individual narrowly escaped a killer whale. Furthermore, on two separate occasions, we observed killer whales approaching within 0.5 km of bottlenose dolphins. In each case, the bottlenose dolphins rapidly swam away and toward the open sea. Their swimming was so rapid at these times that the dolphins leaped clear of the water and covered 2 or 3 times their own length out of the water during low forward leaps. Hertel (1963) suggested from mathematical models that this type of movement is most efficient for rapid surface swimming. Theodolite readings taken at these times indicate that the dolphins were moving at speeds of at least 30 km h; however, no definitive upper limit speed information was obtained because it was difficult to follow rapidly moving animals accurately in a short-time period.

DISCUSSION

The bottlenose dolphin population studied here

spent 92% of its time in water <10 m deep, and was never seen in water >39 m during the 21-mo study. "Coastal dolphins" is therefore truly an appropriate label. Various investigators have mentioned the presence of bottlenose dolphins farther from shore and in deeper water populations distinct from the nearshore populations seen in the same general geographic area (e.g., Norris and Prescott 1961). We never saw *Tursiops* in offshore waters >3 km from land despite over 100 attempts to find them by boat in deeper water. Instead, a different animal, the dusky dolphin, *Lagenorhynchus obscurus*, was seen farther off shore during the entire year (Wursig in press; Wursig and Würsig see footnote 4).

The bottlenose dolphins studied here were almost always found in water <10 m deep; however, in autumn, winter, and spring they moved into deeper water for brief periods during midday. At that time, they sped up and moved as fast as 24 km/h. Because terns were seen feeding near such movement, and because of the wide swath of sea covered by the dolphins while rapidly advancing in this manner, we believe that during these times they were searching for and at times feeding on aggregations of schooling fish. Although adult southern anchovy are apparently not abundant in the area in winter (Brandhorst et al. 1971), juveniles are present near shore in small schools at this time (Brandhorst and Castello 1971). Similar group feeding by bottlenose dolphins has been reported on numerous occasions (Morozov 1970; Hoese 1971; Tayler and Saayman 1972; Saayman and Tayler 1973; Busnel 1973; Leatherwood 1975; Hamilton and Nishimoto 1977). We could not determine, however, whether the dolphins were actively herding fish into a tight unit against the surface of the water, as dusky dolphins are thought to do (Wursig and Wursig see footnote 4). The daily periodicity of deepwater movement during nonsummer indicates that the schooling prey of bottlenose dolphins may be more abundant in those waters during midday. However, this is at present only conjecture. At any rate, no such midday increase in speed and depth of water was evident in summer. During summer, southern anchovy are not found very often in coastal waters less than approximately 40 m deep (Ciechomski 1965; pers. obs.). Instead, these schooling fish are found in deeper (and cooler) offshore waters, where dusky dolphins feed on them. The present population, however, does not go into these deep waters in the southeast portion of Golfo San Jose, and thus does not appear to have this resource available in this area during summer. Whether or not there is active competitive exclusion between bottlenose dolphins and dusky dolphins is not known.

During summer afternoons, *Tursiops* moved more rapidly and in slightly deeper water than at other times of day. We do not know whether they were cooperatively hunting and feeding on schooling fish as in the manner described above. It is possible that the animals were moving into somewhat deeper water to avoid very warm water (up to 25° C, pers. obs.) present in 0–4 m depth during hot summer weather, but as bottlenose dolphins live in warmer water elsewhere, it is more probable that their daily movement pattern was food-related.

Average speed of travel by bottlenose dolphins was 6.1 km/h. This represents one of the first times that such a speed has been reported for an undisturbed group of wild dolphins. It is similar to speed estimates made for the Indian Ocean bottlenose dolphin, *Tursiops aduncus* (9.9 km/h) and for *Sousa* sp. (4.8 km/h) during normal progression (Saayman et al. 1972; Saayman and Tayler in press). As an interesting sidelight, which may be recognized as having general significance as more population studies of dolphins unfold, bottlenose dolphins studied by Saayman et al. (1972) were usually found in deeper water while humpback dolphins were almost always found in shallow waters. While moving near shore, south Atlantic bottlenose dolphins moved roughly as fast as did humpback dolphins, and while farther from shore, they moved roughly as fast or faster than the Indian Ocean bottlenose dolphin. The same trend is true for dusky dolphins in the south Atlantic waters (Wursig and Wursig see footnote 4). A possible explanation may be that nearshore searching for food and feeding are more often functions of individuals, while deeper water prey search appears often to utilize the combined sensory abilities of the entire group as it actively echolocates for whole schools of fish. A similar pattern of dispersed individual feeding near shore and group feeding offshore has been found by Irvine, et al. (see footnote 2). The nearshore search for food requires looking in detail at the prey possibilities near rocks, plants, and on the bottom, while most efficient search in open water is likely to be facilitated by covering as large an area as possible within a small space of time. Possibly more important intraspecifically is a recent suggestion that

coastal dolphins at times rest close to shore (and move slowly while resting) to avoid deeper water predators such as sharks and killer whales (Norris and Dohl see footnote 3; Würsig and Würsig see footnote 4). They more often feed farther from shore and in deeper water, and are more active at that time.

In this study there was evidence that bottlenose dolphins near shore paid attention to bottom topography. While they in general moved over consistent water depth for brief periods, they often moved back and forth over the same bottom topography during a falling tide. As a result, they traveled in progressively shallower water as the tide receded. Furthermore, they changed direction over particular underwater landmarks, usually consisting of groups of rocks. This type of movement associated with bottom topography may be strongest while the animals are searching for bottom-dwelling prey. However, we do not know what their food was at such times. The intertidal areas in which they were traveling had abundant snails, and part of the area was covered by mussels. Mussels were especially abundant on the rocky outcroppings where dolphins turned (and at times milled or lingered for several minutes), but we have no direct evidence for feeding on shellfish. Norris and Prescott (1961) reported that *Tursiops* in California waters feed at times on hermit crabs and shellfish. Also present in and around rocks were larger—up to 1 m long—fish, *Pinguipes fasciatus*. We observed individual dolphins shaking these fish in their mouths and repeatedly tossing them into the air on three separate occasions. Although this behavior at first looked like "play" before feeding on the fish, it is likely that the dolphins were tossing and shaking them to soften the fish and possibly to separate the head from the edible body (as reported by Brown and Norris 1956). It thus appears that this fish constitutes a nearshore prey item, and it may be part of the reason that bottlenose dolphins often turned and lingered near rocks.

During intermediate flood tides dolphins traveled more often into deep water than at other tide stages. Since deepwater movement appeared correlated with group feeding on schooling fish, feeding may have occurred more often during such intermediate rising tides. We therefore suspect that schooling fish were also more often present in nearshore waters during rising tides, perhaps brought into the area from deeper water by the tidal currents. Although we have no evidence for this postulated movement of bottlenose dolphin prey, it is a common behavior of many fish species to come in with the tide, and thus a reasonable possibility in the present case. Tide-related movements of *Tursiops* sp. have been described by McBride and Hebb (1948), Norris and Prescott (1961), D. K. Caldwell and M. C. Caldwell (1972), Irvine and Wells (1972), Shane (1977), and others. Most of these descriptions involved the movements of bottlenose dolphins into and out of coastal channels or canals and are therefore not strictly comparable with the present study. However, dolphin movement appeared often to be food-related in these studies. Saayman and Tayler (in press) found a peak in *Sousa* sp. feeding 2 h before high tide, presumably also because prey fish were being brought into their study area by the tide.

Near shore, dolphins changed direction by 180° approximately once every 700 m. This was the average distance between rocky outcroppings of cliffs. The turns often tended to keep the animals in a restricted area within sight of our observation points for several hours. When farther than 0.5 km from shore, dolphins traveled about twice the nearshore distance before turning, possibly because they encountered no rocks or outjuttings of cliffs in such deeper water. Nevertheless, because travel in one direction lasted on the average only 9 or 10 min whether near or far from shore, deeper water travel also usually kept the animals in a particular area.

Although we were able to describe the movements of bottlenose dolphins in some detail within an approximately 50 km^2 area, we do not know where the dolphins went when they moved out of our area. They did not travel beyond a certain point (Los Conos, Figure 2) within the study area, but at least once individuals traveled as far as 300 km away from the study site (Würsig and Würsig 1977; Würsig 1978). However, a more accurate definition of range awaits further data.

It was mentioned previously that slow movement near shore may at times be associated with feeding on large solitary fish as well as on smaller bottom-dwelling organisms. Dolphins also engaged in other activities while moving near shore. During the morning, we observed very little aerial behavior such as leaping, noseouts, belly-ups, and kelp tossing. As a result it appeared that their activity level was less during the morning than during the afternoon, and that much of the time the animals were resting as they moved back and forth close to shore. A similar pattern of rest dur-

ing morning has been reported for Hawaiian spinner dolphins by Norris (1974), Norris and Dohl (in press), and Norris and Dohl (see footnote 3) and for dusky dolphins by Würsig and Würsig (see footnote 4). Norris and Prescott (1961) also mentioned that *T. gilli* off California appears more active in the late afternoon than during the early part of the day. Why this period of rest should be concentrated in the forenoon in at least three different coastal species is not known. It contrasts in the present population with a greater amount of feeding activity in the afternoon, and it may be that schooling prey is more available in the deeper offshore waters in which these porpoises feed in the afternoon. As a result, they rest more frequently when prey is not available.

During the afternoon, activity level increased. Aerial displays were generally performed singly, however, and were often spaced in time, with only a few leaps or noseouts per hour. This amount of aerial displaying was less than for the spinner dolphins which spread out over large distances and for which the omnidirectional splashing sounds attendant to most aerial behavior is thought to serve a possible communication function (Norris 1974). Such communication would be most important when the animals are not close together as a tightly knit unit, which the present individuals were at almost all times. Nevertheless, it is still possible that noisy leaps, e.g., served to attract the attention of the rest of the subgroup in a highly efficient manner. The exact meaning, however, of these leaps is not clear.

Noseouts, belly-ups, kelp tossing, and clean leaps make little noise. These also occurred with higher frequency in the afternoon. Clean leaps, with individuals reentering the water headfirst, as has been mentioned previously, appeared to precede steep dives in intermediate and deep waters. They may be correlated with feeding on or near the bottom. Noseouts, belly-ups, and kelp tossing occurred when individuals were close together, often touching, and may be associated with "play" and copulatory activity. Especially during times when individuals moved upside down (belly-up) for 50 m or more, they were attended by one or more individuals rubbing along their flanks and dorsum. These close interpersonal associations need not necessarily indicate copulatory behavior, however. They were also performed on several occasions by adults and their small calves, and may represent a form of nonsexual social communication as has been proposed by several other works (Caldwell and Caldwell 1967; Bateson[6]; and others). Especially significant for this hypothesis may be the fact that we observed more of these behaviors when two subgroups which had been separated for several hours or longer rejoined. Rubbing behavior and attendant aerial displays may at least in part serve a greeting function, where individuals renew and strengthen social bonds in a manner analogous to many social terrestrial mammals (for a review, see Wilson 1975).

Belly-up movement was described by Leatherwood (1975) for *T. truncatus*, and by Saayman and Tayler (in press) for *Sousa* sp. as being performed by individuals while pursuing fish near the surface of the water. Although we saw belly-up behavior only in conjunction with other behavior which we assumed to be social, it may also occur for feeding in the present population.

A final form of aerial behavior which also made a loud sound was tailslapping. It was performed at any time that the group may have been disturbed, such as upon the approach of our boat. We therefore concur with other researchers (Norris and Prescott 1961; D. K. Caldwell and M. C. Caldwell 1972) who believe that tailslapping by dolphins in general serves as a warning signal or fright reaction. It was performed with highest frequency by a large adult who was part of a "core" of individuals present throughout the 21-mo study. We suggest that this individual may have been a "leader" of the subgroup of animals, possibly dominant over other individuals. This suggestion is based only on this one behavioral pattern, however, and must therefore be treated with caution.

Dolphins associated with whales by riding on the waves created by the larger cetaceans, and rode on wind-driven waves and the pressure wave of the boat. This type of behavior has been seen in many species, and was described for dolphins riding near whales by McBride and Kritzler (1951), for dolphins riding wind-driven waves by Woodcock and McBride (1951), and for dolphins riding boat bow waves by Matthews (1948) and Woodcock (1948). Especially insightful analyses of this behavior have been provided by Scholander (1959) and Norris and Prescott (1961). They showed that dolphins could travel with less muscle movement, and therefore presumably less expenditure of

[6]Bateson, G. The cetacean community in Whaler's Cove. Sea Life Park. Unpubl. manuscr., 16 p. Center for Coastal Marine Studies, University of California, Santa Cruz.

energy, by surfing in this manner. How much pure play (and perhaps play as a part of learning) is involved, and whether or not dolphins really ride waves to get a "free ride" to a different location are questions which remain unanswered.

In the present paper, we made an attempt to describe some of the behavior patterns which we saw most often from above the water surface, and suggested various possible functions for them. We realize, however, that most social interactions go on under water, and that dolphins probably communicate with sound at least as extensively as with observed movements. Tyack (1976) found differences in quality and quantity of sounds produced by the bottlenosed dolphins of the present study depending on whether they appeared to be feeding, socializing, or resting. Although this is a promising beginning, much more sound-behavior correlation is necessary before biological meaning can be ascribed to specific sounds.

In this paper, we have described certain movement patterns and behavior, and ascribed possible functions to them. However, the present analysis raises many more questions than it answers, and may be regarded as a first step in understanding the behavior of these animals.

ACKNOWLEDGMENTS

Jen and Des Bartlett, Peter Tyack, Marty Hyatt, and Russ Charif helped gather data. Jan J. Wolitzky wrote the computer program for analyzing theodolite track data, and Matt Lamishaw patiently worked at the computer. Roger and Katy Payne provided material and intellectual support. Kenneth Norris, Jay Quast, George C. Williams, J. L. McHugh, Randall Wells, William Perrin, Douglas Smith, and an anonymous reviewer for the *Fishery Bulletin* critically read the manuscript. Charles Walcott supported and encouraged all phases of the research. We are especially grateful to him.

This study was supported by the New York Zoological Society, the Committee for Research and Exploration of the National Geographic Society, and the Program for Neurobiology and Behavior of the State University of New York at Stony Brook.

LITERATURE CITED

BRANDHORST, W., AND J. P. CASTELLO.
1971. Evaluacion de los recursos de anchoita (*Engraulis anchoita*) frente a la Argentina y Uruguay. II. Abundancia relativa entre las latitudes 39° y 45° S en relación a las condiciones ambientales en febrero-marzo de 1970. Proyecto Desarrollo Pesq., Ser. Inf. Téc., Publ. 32, 47 p.

BRANDHORST, W., J. P. CASTELLO, R. PEREZ HABIAGA, AND B. H. ROA.
1971. Evaluacion de los recursos de anchoita (*Engraulis anchoita*) frente a la Argentina y Uruguay. III. Abundancia relativa entre las latitudes 34°40' S y 42°10' S en relación a las condiciones ambientales en may-junio de 1970. Proyecto Desarrollo Pesq., Ser. Inf. Tec., Publ. 34, 39 p.

BROWN, D. H., D. K. CALDWELL, AND M. C. CALDWELL.
1966. Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. Los Ang. Cty. Mus. Contrib. Sci. 95, 32 p.

BROWN, D. H., AND K. S. NORRIS.
1956. Observations of captive and wild cetaceans. J. Mammal. 37:311-326.

BUSNEL, R.-G.
1973. Symbiotic relationship between man and dolphins. Trans. N.Y. Acad. Sci., Ser. II, 35:112-131.

CALDWELL, D. K., AND M. C. CALDWELL.
1972. The world of the bottlenosed dolphin. J. B. Lippincott Co., Phila. and N.Y., 157 p.

CALDWELL, M. C., AND D. K. CALDWELL.
1967. Dolphin community life. Los Ang. Cty. Mus. Nat. Hist. Q. 5(4):12-15.
1972. Behavior of marine mammals. *In* S. H. Ridgway (editor), Mammals of the sea, p. 419-465. C. C. Thomas, Springfield, Ill.

CALDWELL, M. C., D. K. CALDWELL, AND J. B. SIEBENALER.
1965. Observations on captive and wild Atlantic bottlenosed dolphins, *Tursiops truncatus*, in the northeastern Gulf of Mexico. Los Ang. Cty. Mus. Contrib. Sci. 91, 10 p.

CASTELLO, H. P., AND M. C. PINEDO.
1977. Botos na Lagoa dos Patos. Fund. Zoobot. Rio Grande do Sul 2:46-49.

CIECHOMSKI, J. D. DE
1965. Observaciones sobre la reproduccion, desarrollo embrionario y larval de la anchoita argentina (*Engraulis anchoita*). Bol. Inst. Biol. Mar. Mar del Plata 9, 29 p.

ESSAPIAN, F. S.
1953. The birth and growth of a porpoise. Nat. Hist. 62:392-399.
1963. Observations on abnormalities of parturition in captive bottle-nosed dolphins, *Tursiops truncatus*, and concurrent behavior of other porpoises. J. Mammal. 44:405-414.

GREENWOOD, J. A., AND D. DURAND.
1955. The distribution of length and components of the sum of n random unit vectors. Ann. Math. Stat. 26:233-246.

GUNTER, G.
1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J. Mammal. 23:267-276.

HAMILTON, P. V., AND R. T. NISHIMOTO.
1977. Dolphin predation on mullet. Fla. Sci. 40:251-252.

HERTEL, H.
1963. Struktur-Form-Bewegung. Bd. 1, Biologie und Technik. Krausskopf-Verlag, Mainz, 244 p.

HOESE, H. D.
1971. Dolphin feeding out of water in a salt marsh. J. Mammal. 52:222-223.

IRVINE, B., AND R. S. WELLS.
1972. Results of attempts to tag Atlantic bottlenosed dolphins (*Tursiops truncatus*). Cetology 13:1-5.

KELLOGG, W. N.
1961. Porpoises and sonar. Univ. Chic. Press, Chic., Ill., 177 p.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gillii*) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.

MATTHEWS, L. H.
1948. The swimming of dolphins. Nature (Lond.) 161:731.

MCBRIDE, A. F.
1940. Meet mister porpoise. Nat. Hist. 45:16-29.
1956. Evidence for echolocation by cetaceans. Deep-Sea Res. 3:153-154.

MCBRIDE, A. F., AND D. O. HEBB.
1948. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. J. Comp. Physiol. Psychol. 41:111-123.

MCBRIDE, A. F., AND H. KRITZLER.
1951. Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. J. Mammal. 32:251-266.

MOROZOV, D. A.
1970. Del'finy okhotyatsya (Dolphin hunting). Rybn. Khoz. 46(5):16-17.

NORRIS, K. S.
1974. The porpoise watcher. W. W. Norton, N.Y., 250 p.

NORRIS, K. S., AND T. P. DOHL.
In press. The structure and functions of cetacean schools. *In* L. Herman (editor), The behavior of dolphins. Wiley Interscience, N.Y.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool. 63:291-401.

NORRIS, K. S., J. H. PRESCOTT, P. V. ASA-DORIAN, AND P. PERKINS.
1961. An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus* (Montagu). Biol. Bull. (Woods Hole) 120:163-176.

SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER.
1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. Koedoe 15:1-24.

SAAYMAN, G. S., AND C. K. TAYLER.
1973. Social organisation of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. J. Mammal. 54:993-996.
In press. The socioecology of humpback dolphins (*Sousa* sp.). *In* H. E. Winn and B. L. Olla (editors), The natural history of whales. Plenum Press, N.Y.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). Behaviour 44:212-233.

SCHEVILL, W. E., AND B. LAWRENCE.
1956. Food-finding by a captive porpoise (*Tursiops truncatus*). Breviora 53:1-15.

SCHOLANDER, P. F.
1959. Wave-riding dolphins: How do they do it? Science (Wash., D.C.) 129:1085-1087.

SHANE, S. H.
1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. Thesis, Texas A&M Univ., College Station, 239 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry; the principles and practice of statistics in biological research. Freeman, San Franc., 776 p.

TAVOLGA, M. C.
1966. Behavior of the bottlenose dolphin (*Tursiops truncatus*): social interactions in a captive colony. *In* K. S. Norris (editor), Whales, dolphins, and porpoises, p. 718-730. Univ. Calif. Press, Los Ang.

TAVOLGA, M. C., AND F. S. ESSAPIAN.
1957. The behavior of the Bottle-nosed Dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zoologica (N.Y.) 42:11-31.

TAYLER, C. K., AND G. S. SAAYMAN.
1972. The social organization and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Ann. Cape Prov. Mus. Nat. Hist. 9:11-49.

TOWNSEND, C. H.
1914. The porpoise in captivity. Zoologica (N.Y.) 1:289-299.

TYACK, P.
1976. Patterns of vocalization in wild *Tursiops truncatus*. Senior Thesis, Harv. Univ., Camb., Mass., 44 p.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
In press. The social ecology of bottlenosed dolphins off Florida's west coast: a comparison with other inshore odontocetes. *In* L. M. Herman (editor), The behavior of dolphins. Wiley-Interscience, N.Y.

WILSON, E. O.
1975. Sociobiology, the new synthesis. Harv. Univ. Press, Camb., Mass., 697 p.

WOODCOCK, A. H.
1948. The swimming of dolphins. Nature (Lond.) 161:602.

WOODCOCK, A. H., AND A. F. MCBRIDE.
1951. Wave-riding dolphins. J. Exp. Biol. 28:215-217.

WURSIG, B.
1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. Biol. Bull. (Woods Hole) 154:348-359.
In press. Radio tracking dusky porpoises (*Lagenorhynchus obscurus*) in the south Atlantic. FAO Fish. Ser. 5.

WURSIG, B., AND M. WURSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.

GROWTH OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA

RICHARD D. METHOT, JR. AND DAVID KRAMER[1]

ABSTRACT

Northern anchovy larvae from12 samples collected at 13.0°-16.2° C in the Southern California Bight were aged using daily growth increments in sagittal otoliths, and growth rates were calculated from size at age data. In nine samples, growth rate at 8 mm was very similar, ranging from 0.34 to 0.40 mm per day. Growth in the other three samples ranged from 0.47 to 0.55 mm per day. There was no correlation between growth rate and temperature within this set of field samples, but the range of growth rates was similar to the range expected from laboratory rearing experiments in this temperature domain. In no case was growth in the sea as slow as growth in the laboratory on severely limited rations. Anchovy larvae which obtain enough food to survive apparently obtain enough food to grow rapidly.

The presence of daily growth increments in some hard tissues of various plants and animals has been known for several decades (Neville 1967). Despite the fact that fish otoliths have been examined for annual growth marks throughout this century (Blacker 1974), daily growth increments were only recently identified in fish (Pannella 1971). The daily nature of these increments was verified in the laboratory by Brothers et al. (1976) using marine fish larvae. Taubert and Coble (1977) showed that increment formation in centrarchids is linked to the diel light cycle, not a feeding rhythm. Although studies have been conducted on the gross growth of otoliths (Degens et al. 1969; Mugiya 1974, 1977) the physiological mechanism responsible for daily growth increment formation in fish is unknown (Simkiss 1974). Regardless, daily growth increments provide the ecologist with a tool for determining age and growth of specimens from the field (Struhsaker and Uchiyama 1976).

The objective of this project was to estimate growth of larval northern anchovy, *Engraulis mordax*, in the sea. Many laboratory studies demonstrate that growth of young fish is limited by temperature and ration (Riley 1966; Brett et al. 1969; O'Connell and Raymond 1970; Houde 1975). Because food availability is frequently considered to be one of the major factors controlling larval survival (Cushing and Harris 1973; Jones 1973; May 1974; Lasker 1975; Arthur 1976), growth in the sea may frequently be limited by food. However, when collections of measured larvae are used for indices of spawner abundance or larval mortality studies, growth is assumed to be constant (Houde 1977) or a function solely of temperature (Bannister et al. 1974). Determining growth rates of larval fish in the sea should resolve this contradiction between theoretical and applied fishery science.

Anchovy larvae can be reared to metamorphosis and beyond in the laboratory (Kramer and Zweifel 1970; Hunter 1976; Sakagawa and Kimura 1976). Growth in these experiments was described best by the Gompertz growth equation, equation 1 (Kramer and Zweifel 1970; Zweifel and Lasker 1976). The effect of temperature on embryonic development and larval growth was incorporated by making the Gompertz growth parameters, A_0 and α, increasing functions of temperature (Zweifel and Lasker 1976; Zweifel and Hunter[2]). We compared the size at age of anchovy larvae in each field sample with that predicted by this temperature dependent model of anchovy growth in the laboratory, assuming that the temperature measured at the time of collection represented the temperature experienced by the larvae throughout their lifetimes.

[1]Southwest Fisheries Center LaJolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Zweifel, J. R., and J. R. Hunter. Temperature specific equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval states. (Manuscr. in prep.) Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted January 1979.
FISHERY BULLETIN: VOL. 77, NO. 2, 1979.

METHODS

Ichthyoplankton samples were collected from the Southern California Bight in March 1976, May 1976, and March 1977 with the NOAA ship *David Starr Jordan*. The sampling gear consisted of a CalCOFI (California Cooperative Oceanic Fisheries Investigations) ring net (1 m mouth diameter), MARMAP (Marine Resources, Monitoring, Assessment, and Prediction Program) Bongo net (60 cm mouth diameters), and a Manta neuston net; all with 505 μm mesh. Oblique tows were made from the depth indicated in Table 1 to the surface. Samples were drained of excess seawater and preserved in 85% ethanol. (Recently we found that preservation is greatly improved if the alcohol is changed at least once after initial preservation; the otoliths may dissolve in poorly preserved samples with large plankton volumes. We change it once within 24 h and again within a few weeks.) Surface temperatures were measured with a bucket thermometer, and vertical temperature profiles were obtained with expendable bathythermographs.

The 12 samples analyzed in this study are from a limited part of the spawning range of the northern anchovy, but the Southern California Bight in March is an important spawning area for the central population of the anchovy (Smith 1972). Samples A1-A3 and B1 were collected near Los Angeles and the Channel Islands in 1976 (Figure 1) and were selected because of the wide size range of anchovy larvae found in each. Samples C1 and C2 were collected in this same region in March 1977. They were selected to represent the widest temperature range possible. Samples D1-D6 were collected in March 1977 along a transect extending seaward from San Diego and were the only samples containing anchovy larvae on this transect. Additional station data are in Table 1.

All fish eggs and larvae were sorted from the plankton samples chosen for analysis and anchovy larvae were processed in a manner similar to that described by Brothers et al. (1976). The standard length, tip of snout to tip of notochord or hypural plates, of each larva was measured to the nearest 0.1 mm. Sagittae were removed and placed on a microscope slide with the lateral (flat) side up. A polarizing filter and analyzer in the dissecting microscope made the otoliths more visible during dissection. The slide was air-dried and the otoliths were mounted under a coverglass with a clear mounting medium (Pro-texx[3]). Daily growth increments were counted in otolith images on a video screen; the total magnification by the microscope and video camera was 600 · or 1,500 ·. Each otolith was counted by 1-3 observers until the range of accepted counts for the two otoliths was ≤ 2. Accepted counts were averaged over all observers and both otoliths.

The shrinkage of sea-caught larvae in preservative (Blaxter 1971) and the lag between hatching and first increment formation must be considered before comparing the size at age of sea-caught larave with laboratory-reared larvae. Shrinkage of anchovy larvae depends upon the elapsed time between death and preservation (Theilacker[4]). There is no shrinkage when live larvae are placed directly into ethanol but a 5-15 mm larva could shrink about 0.6 mm if dead throughout the 6 min duration of the net tow. No shrinkage correction was applied because the elapsed time between death and preservation probably was · 6 min and highly variable. Anchovy larvae tend to stay above the thermocline (Ahlstrom 1959) so are cap-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Theilacker, G. H. Preservative shrinkage of larval anchovy, *Engraulis mordax* laboratory versus field. Paper presented Nov. 1, 1978 at CalCOFI Conference, USC, Idyllwild, Calif.

TABLE 1.—Data on samples of larval northern anchovy taken from the Southern California Bight, spring 1976 and 1977.

Sample	Date	Time	Lat. N	Long. W	Gear	Depth (m)	Temperature (°C)	*N*
A1	29 Mar 1976	2150	33 35.9	117 56.6	Ring	10	15.8	196
A2	31 Mar	2205	33 43.5	118 28.0	Ring	5	15.0	38
A3	1 Apr	1850	33 42.0	118 20.5	Ring	5	15.0	29
B1	8 May	1835	33 27.5	118 40.0	Manta	0	16.2	146
C1	20 Mar 1977	1915	33 30.3	118 01.5	Bongo	70	15.1	35
C2	24 Mar	2320	33 29.4	117 54.1	Bongo	70	13.0	112
D6	27 Mar	0235	32 41.5	119 01.5	Ring	70	13.2	18
D1	27 Mar	1830	32 00.0	119 12.0	Ring	70	14.0	13
D2	27 Mar	2100	32 05.8	118 55.0	Ring	70	14.0	25
D3	28 Mar	0140	32 28.8	118 35.0	Ring	70	14.4	18
D4	28 Mar	0405	32 39.5	117 59.5	Ring	70	15.2	22
D5	28 Mar	0630	32 47.0	117 38.5	Ring	70	15.1	25

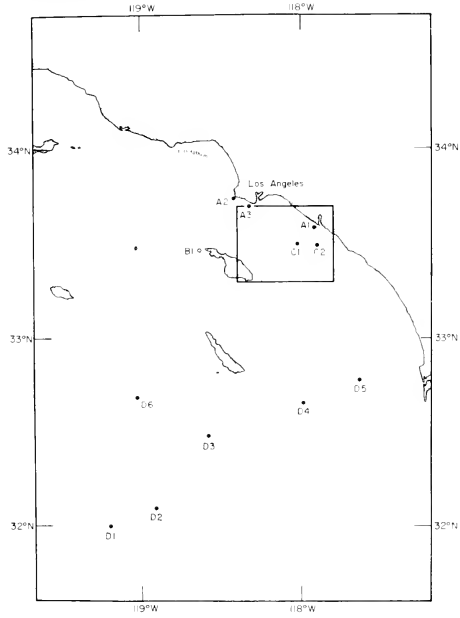


FIGURE 1.—Sampling sites for northern anchovy larvae off southern California. Box indicates the region shown in detail in Figure 4.

tured primarily during the last 1 or 2 min of an oblique tow, and some large larvae were still alive at the time of preservation.

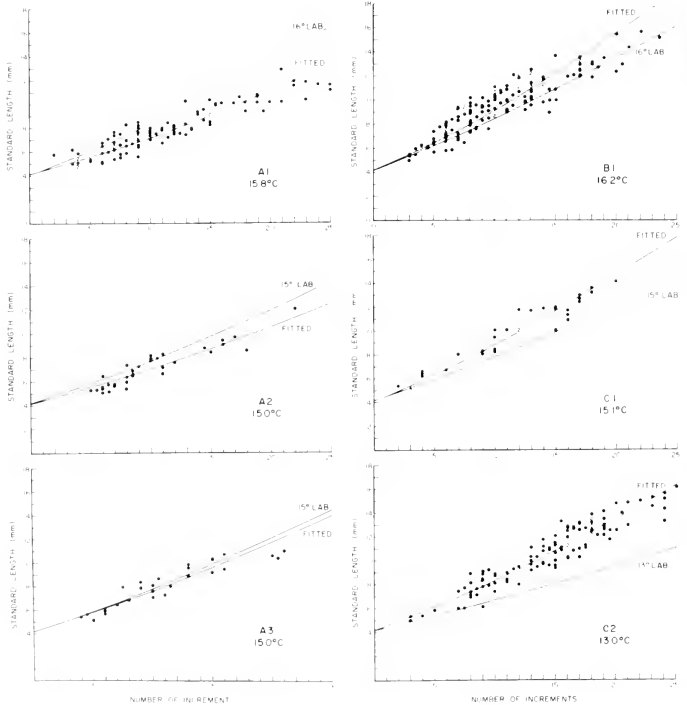
Brothers et al. (1976) found a 5-day difference between posthatch age and number of increments for anchovy larvae reared in the laboratory at 16 C. At 19 C the lag is 3 days and at 12.5 C it is about 9 days (Methot unpubl. data). These lags are very close to the age at completion of yolk absorption (19 C, 2.9 days; 16 C, 4.7 days; 12.5 C, 8 days—Zweifel and Hunter (see footnote 2)); the larvae are about 4.2 mm at this age. Since developmental events, such as a functional jaw, occur at a constant size at all temperatures in this range (Zweifel and Lasker 1976), we assume that increment formation also begins at a constant size of 4.2 mm at all temperatures. The number of increments represents the age in days after yolk absorption.

RESULTS

Standard length of each larvae in a sample was plotted against the mean number of increments (Figure 2). Each data point represents the integral of the growth rate of an individual larva over its lifetime, and a trend line through these points estimates the average growth history of larvae in the region sampled. Possible biases in this estimate of growth rate are discussed below.

According to the null hypothesis, the laboratory growth curve corresponding to the temperature at which the sample was taken should provide the best fit to the data. A suitable parametric procedure for testing this goodness of fit was not available. The nonlinear least-squares method for fitting the Gompertz growth function to size at age data (Zweifel and Lasker 1976) does provide estimates of confidence intervals on the parameters, but the probability levels associated with these intervals are only approximate (Conway et al. 1970). We found these confidence intervals to be rather broad.

We tested the goodness of fit by using a modification of the median regression procedure of Tate and Clelland (1957), replacing their estimated regression line by the laboratory derived Gompertz growth curve specified by our null hypothesis. Only curves at 1° C intervals were considered. Each larva in a sample was classified into a 2 × 2 contingency table, according to whether it was to the left or right of the median age of larvae in the



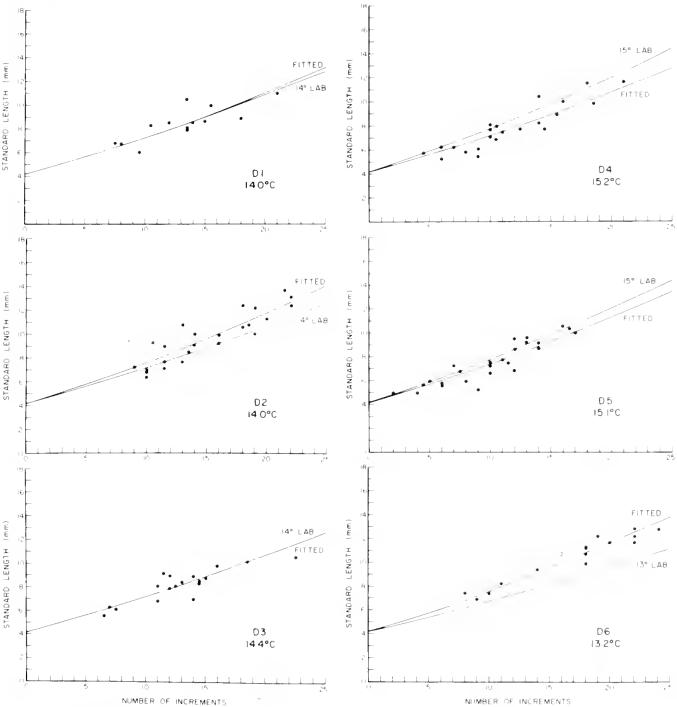


FIGURE 2.—Relationship between standard length of northern anchovy larvae and the number of daily growth increments (age postyolk absorption) in their otoliths. Two growth curves are shown. One (LAB) is the laboratory growth curve which was expected to fit the data because of the temperature at which the sample was collected. The other (FITTED) was fit to the data using a nonlinear least-squares method.

sample and whether it was above or below the laboratory growth curve (line labelled LAB in Figure 2). Points which fell on lines were split equally between the cells on either side of the line. A chi-square statistic with 2 degrees of freedom was calculated using the expectation of equal numbers of larvae in each cell of the table. The results of these tests are in Table 2.

In general, larvae collected between Los Angeles and the Channel Islands in March 1976 (samples A1-A3) grew slower than expected while those collected there in March 1977 (C1, C2) grew

TABLE 2.—Results of chi-square test of the hypothesis (see text) that temperature-specific growth in the northern anchovy is the same in sea and laboratory (A-E) and the parameters of the Gompertz growth curve fit to the data in each sample (F-I). A, sample size; B, surface temperature in degrees Celsius; C, growth curve compared with data; D, probability that growth curve fits data; E, sign of significant deviations (0.05 level) from laboratory curve; F and G, Gompertz parameters, A_0 and α; H, standard error of regression; I, growth rate at 8 mm (in millimeters/day). Last row shows results for combined data (samples with *).

Sample	A	B	C	D	E	F	G	H	I
A1*	106	15 8	16	0 001		0 060	0 024	0 094	0 356
A2*	38	15 0	15	0 01		0 059	0 025	0 089	0 341
A3*	29	15 0	15	0 25	0	0 067	0 029	0 086	0 387
B1	146	16 2	16	0 001	-	0 093	0 037	0 111	0 552
C1	35	15 1	15	0 001	-	0 089	0 038	0 074	0 515
C2	112	13 0	13	0 001	-	0 080	0 033	0 083	0 471
D6*	18	13 2	13	0 001	-	0 067	0 029	0 059	0 389
D1*	13	14 0	14	0 25	0	0 061	0 024	0 109	0 358
D2*	25	14 0	14	0 025	-	0 068	0 029	0 120	0 397
D3*	18	14 4	14	0 25	0	0 059	0 025	0 092	0 348
D4*	22	15 2	15	0 10	0	0 061	0 027	0 105	0 348
D5*	25	15 1	15	0 25	0	0 064	0 027	0 103	0 371
*						0 063	0 027	0 097	0 370

faster than expected. The larvae collected in March 1977 along the transect extending seaward from San Diego (D1-D6) grew about as fast as expected, given the surface temperature at which the sample was collected.

Since the data in 7 of 12 samples deviated significantly from the predicted Gompertz growth curve, we fit the Gompertz growth function (Zweifel and Lasker 1976)

$$\log_e (SL) = \log_e (SL_0) + \frac{A_0}{\alpha}(1 - e^{-\alpha t}) \quad (1)$$

where SL = standard length in millimeters
t = number of increments = age in days postyolk absorption
SL_0 = initial size, fixed at 4.2 mm
A_0, α = parameters to be estimated

to each using a nonlinear least-squares method (Conway et al. 1970).

The parameters of the fitted curves (Table 2) were used to calculate a linear approximation of the growth rate of 7.5-8.5 mm anchovy larvae (Figure 3). The range of growth rates among the 12 samples collected at 13°-16.2° C was bounded by the growth rates of anchovy larvae grown in the laboratory at 14° and 17.5° C. Growth was very similar in all but three samples (B1, C1, C2) although the temperatures associated with these nine samples spanned a range of 2.5° C. The growth rate of 8 mm larvae calculated from a Gompertz curve fit to the combined data of the nine similar samples was 0.37 mm day. The mean

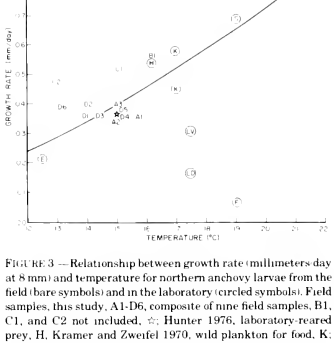


FIGURE 3.—Relationship between growth rate (millimeters/day at 8 mm) and temperature for northern anchovy larvae from the field (bare symbols) and in the laboratory (circled symbols). Field samples, this study, A1-D6, composite of nine field samples, B1, C1, and C2 not included, ☆; Hunter 1976, laboratory-reared prey, H, Kramer and Zweifel 1970, wild plankton for food, K; Lasker et al. 1970, dinoflagellates only, LD, dinoflagellates plus veliger, LV, Sakagawa and Kimura 1976, S, unpubl. data available at Southwest Fisheries Center, low temperature experiment, E, periodic starvation experiment, F. Curve was derived from the model of Zweifel and Hunter (see text footnote 2), it was not fit to the growth rate data presented here.

temperature of these nine samples (weighted by number of larvae) was 15.04° C. The model of Zweifel and Hunter (see footnote 2) predicts that 8 mm larvae reared at 15° C would grow at 0.395 mm day.

Standard deviation of $\log_e$ (size) at age, calculated from the set of combined data, ranged from 0.045 at 4 increments to 0.144 at 19 increments with a mean of 0.0904. The standard error of regression (standard deviation of residuals) of the Gompertz curves fit to the data (Table 2) were similar to these estimates of standard deviation of size at age. Any difference in growth rate between these samples, small scale environmental heterogeneity integrated by our nets, or random error in the aging of the larvae causes the standard error of regression to overestimate variability in the growth process. Over the same age range in a laboratory experiment (Hunter 1976), standard deviation ranged from 0.064 to 0.153 with a mean of 0.115.

EVALUATION OF POTENTIAL BIASES

The conditions under which larvae are reared and growth is measured in the laboratory may differ sufficiently from conditions in the sea to bias the comparison of growth in the sea with growth in the laboratory. In the laboratory, growth is estimated from a time series of samples from a cohort. The exact age of each larva is known; temperature rarely varies >1°C; prey concentration is rather constant; and mortality is low (about 3% /day in Hunter 1976) and except for cannibalistic species, not influenced by size-selective predation. Growth of sea-caught larvae is estimated from one sample containing larvae of several ages. The age of each is estimated from the number of daily growth increments in its otoliths, the environmental conditions are measured only when the sample is taken, mortality is over 10% /day (Smith and Lasker 1978) and probably size selective, and large larvae avoid the net disproportionately.

Age Determination

Anchovy larvae deprived of food at the normal time of first feeding may delay deposition of daily growth increments until food is provided and growth resumes (Theilacker[5]), but if larvae are still about 4.2 mm when the first increment appears, estimates of the growth rate of larger larvae will be unaffected. Taubert and Coble (1977) found that increment formation in late larval and juvenile centrarchids stopped if growth was slowed sufficiently by low temperature. We examined the otoliths of some anchovy larvae whose growth was drastically retarded by a reduction in rations (Methot unpubl. data) (F in Figure 3). The slowest growing of these larvae had fewer increments than expected, so increment formation can stop before the point of no return is reached. However, if we use number of increments rather than known age to estimate growth rate of these laboratory-reared larvae, the resulting overestimated growth rate is still slower than that observed in any field samples used in this study. We conclude that the sea-caught larvae were growing fast enough to deposit a growth increment every day.

Temperature Determination

Anchovy larvae usually remain above the thermocline (Ahlstrom 1959), so surface temperature probably accurately represents the temperature they experience. Growth was slower than expected in March 1976, but it is unlikely that the surface temperature overestimated the temperature experienced by the larvae because these samples were all collected shallower than 10 m (Table 1). Positive deviations in growth rate, equivalent to a temperature change of up to 3° C, were observed in March 1977, but additional temperature data collected at that time indicate that the measured surface temperature accurately represented the temperature experienced by the larvae throughout their lifetimes. The relative surface temperature field determined from satellite observations of infrared radiation (Bernstein et al. 1977), taken just before and after this 2-wk cruise, was entirely consistent with the temperature field measured during the cruise; there was no cooling trend. The resolution of the satellite observations was insufficient to distinguish details of the eddy structure in the region of samples C1 and C2, but here the greater intensity of surface temperature determinations allowed contouring of isotherms for the first 4 days of the cruise and the next 5 days (Figure 4). Samples C1 and C2 were taken within persistent water masses of about 10 km width, not in regions with steep horizontal gradients in temperature. Because of the shallow thermocline in this region (<5 m at some stations), we may have overestimated the temperature experienced by the larvae but this would cause a negative deviation from the model, not the observed positive deviations.

[5]G. H. Theilacker, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1978.

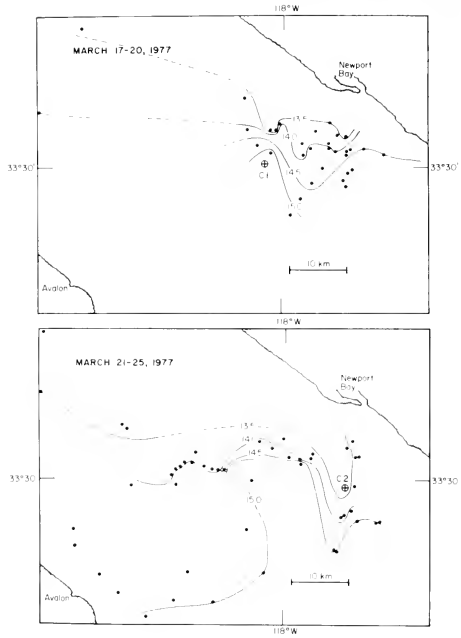


FIGURE 4.—Surface isotherms in degrees Celsius between Los Angeles and Santa Catalina Island, Calif., in March 1977

Selective Mortality

If mortality rate is a function of size, then growth rates determined from size at age data will provide a biased estimate of the true growth rate of the survivors which are sampled (Ricker 1969). The effect of size selective mortality on our estimates of growth is difficult to assess. Few sets of data are extensive enough to even consider the question of ontogenetic changes in mortality rate of larval fish. All available estimates are based upon sized but not aged specimens. They depend upon an assumed growth curve (Farris 1960) and are susceptible to bias by size selective avoidance of the sampler. Smith (1973) found a difference in mortality rate between sardine eggs and young sardine larvae, but mortality in plaice was essentially constant through the egg and larval stages (Bannister et al. 1974). Laboratory experiments show that older, more active yolk-sac anchovy larvae are less susceptible than newly hatched larvae to some invertebrate predators (Lillelund and Lasker 1971; Theilacker and Lasker 1974). As a rough estimate of the magnitude of the maximum effect of size selective mortality on our growth estimates, we examined the interaction between variable growth and size selective mortality and determined the effect of this mortality on mean size of anchovy larvae at 25 days after yolk absorption.

Suppose variation in growth is such that individuals of age 25 days range in size from 11.4 to 16.6 mm and that the exponential growth rate parameter which gives rise to this variation has an uniform statistical distribution. If mortality during this 25-day period is random with respect to size, the mean size of individuals which survive to age 25 days will be 13.86 mm. However, if the instantaneous daily mortality rate is related to size by $M = 3.5\,L^{-2}$ (this is consistent with current estimates of egg, young larvae, and adult mortality rates for anchovy (MacCall 1974; Smith and Lasker 1978)), the mean size of individuals which survive to age 25 days will increase only slightly to 14.08 mm. We conclude that an overestimate of growth because of size selective mortality is unlikely to occur.

Another possibility is that mortality is related to growth rate rather than size, the mortal fraction being that portion of the population which is slow growing and weak and therefore more susceptible to predators (Isaacs 1964). If we make the extreme assumption that the daily mortal fraction is the slowest growing 10% of the cohort, the survivors at age 25 days will be the fastest growing 7% of the original cohort, but this extreme model unrealistically predicts that variations in size at age would decline as the slow growing larvae die. Some intermediate degree of growth rate selective mortality could affect estimates of growth rate in the sea, especially if mean growth rate is slow and the slower growing individuals are near starvation.

Net Avoidance

Avoidance of the ring net by anchovy larvae in daylight begins at a length of about 5 mm and increases with size (Lenarz 1973; Murphy and Clutter 1972). The Bongo net catches larvae more effectively but avoidance still occurs in the larger size classes. The degree to which we underestimated mean size at age depends upon how rapidly avoidance increases with increasing size. We attempted to minimize this bias by only considering larvae with fewer than 25 increments (lengths less than about 15 mm) and samples taken at twilight or dark. There was no difference in size at age between the twilight samples (D1, D5) and the night samples (D2-D4) along the transect. Although fast growth was observed only in samples taken with the Bongo or neuston net (B1, C1, C2), we do not believe this was an artifact caused by size-selective avoidance of the ring net. If this were an artifact, then ranges in size at age in samples taken by the less selective gear would have been broader and overlapped the distribution of size at age in samples taken with gear which allowed larger larvae to escape. This was not observed.

DISCUSSION

Growth rates of larval northern anchovy < 1 mo old were determined with size at age data. In 9 of 12 samples, growth rates at 8 mm were very similar, ranging from 0.34 to 0.40 mm/day. The growth rate estimated from the combined data of these samples was 0.37 mm/day. Growth in the three other samples was faster, 0.47-0.55 mm/day. Variation in size at age between individuals was small. A typical 95% confidence interval for larvae with 12 daily growth increments was 6.5-9.5 mm.

When the trend of growth rate on temperature, obtained from several rearing experiments, was compared with the field results (Figure 3) it was obvious that growth in the sea was similar to growth in the laboratory. The range in growth rate between field samples at the same temperature was similar to the range in growth rate between laboratory rearing experiments conducted at the same temperature (Kramer and Zweifel 1970). Variation of size at age was also similar in the sea and the laboratory. In no case were sea-caught larvae growing as slowly as larvae reared in the laboratory on inadequate rations (LV, LD, F in Figure 3). At 17.5° C (Lasker et al. 1970) anchovy larvae fed only a dinoflagellate grew at about 0.15 mm/day (LD) and larvae fed dinoflagellate and veligers (LV) grew still slower than larvae fed wild plankton (K) (Kramer and Zweifel 1970). Although the availability of suitable prey may limit the feeding success rate of first feeding anchovy larvae (Lasker 1975), larvae which get enough food to survive apparently get enough food to grow rapidly.

There was no obvious relationship between growth rate and temperature. This is not surprising considering the narrow temperature range considered, the variation in growth rate between laboratory experiments at the same temperature, and the uncertainty in our measurement of the temperature experienced by the larvae in the sea. The samples we examined came from near the center of distribution of northern anchovy larvae with respect to space, time, and temperature. As samples from the periphery of this species range

become available, we expect to find increased variation in growth rate.

Correlations between the spatial-temperature pattern of variation in growth rate and environmental parameters may provide clues to the events which control larval survival. This analysis will require that the measured growth rates reflect the larvae's response to the environmental factors measured at the time the sample was collected. We estimated the growth rate of larvae in a sample by determining the relationship between size (L) and age (T). This technique is susceptible to several biases discussed above and is not sensitive to changes in growth conditions occurring a few days before the sample is taken. If the instantaneous growth rate of each individual could be measured, then the same growth rate parameters could be estimated from the relationship between dL/dT and L. This alternative method would reflect growth conditions at the time of sampling and would be independent of changes in growth conditions during the lifetime of the older larvae in the sample. Ottaway and Simkiss (1977) developed a relative measure of the instantaneous growth rate of adult fish using the in vitro rate of incorporation of ^{14}C labelled glycine into scales, but this technique may not be adaptable to larval fish. Another approach is to correlate the width of a daily growth increment with the growth of the fish on that day. A measurement of the width of the outer increments could provide an absolute measure of growth rate during the few days before capture.

In addition, the radius of each increment in an individual's otoliths could be used to back calculate its growth history (Ricker 1969). The difference between the back calculated growth histories of older individuals, the survivors captured with nonselective gear, and the distribution of size at age of all younger individuals supplies information on differential mortality and size dependent net avoidance by the larvae. Ultimately, analysis of daily growth increments in the otoliths of larval fish may provide a means of determining whether larval survival is limited primarily by predation or food and how these two factors interact.

ACKNOWLEDGMENTS

David Kramer passed away in December 1977 during the early stages of this paper's preparation. The personnel at the Southwest Fisheries Center are indebted to him for his contributions to the CalCOFI program, in particular for his early work on the taxonomy and rearing of larval fish and for his devotion to this project on the aging of larval fish. We will miss him. He was a friend and a model to many of us.

I want to thank Ken Plummer for his assistance in the preparation of many of the otoliths used in this study. Special thanks are due John Hunter for his helpful comments on early versions of this manuscript.

LITERATURE CITED

AHLSTROM, E. H.
1959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BANNISTER, R. C. A., D. HARDING, AND S. J. LOCKWOOD.
1974. Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 21-37. Springer-Verlag, Berl.

BERNSTEIN, R. L., L. BREAKER, AND R. WHRITNER.
1977. California Current eddy formation: ship, air, and satellite results. Science (Wash., D.C.) 195:353-359.

BLACKER, R. W.
1974. Recent advances in otolith studies. *In* F. R. Harden Jones (editor), Sea fisheries research, p. 67-90. John Wiley and Sons, N.Y.

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:128-136.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

CUSHING, D. H., AND J. G. K. HARRIS.
1973. Stock and recruitment and the problem of density dependence. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:142-155.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

FARRIS, D. A.
1960. The effect of three different types of growth curves on estimates of larval fish survival. J. Cons. 25:294-306.

HOUDE, E. D.
1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea

bream, *Archosargus rhomboidalis* (L.) (Sparidae). J. Fish. Biol. 7:115-127.

1977. Abundance and potential yield of the round herring, *Etrumeus teres*, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull., U.S. 75:61-90.

HUNTER, J. R.

1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

ISAACS, J. D.

1964. Night-caught and day-caught larvae of the California sardine. Science (Wash., D.C.) 144:1132-1133.

JONES, R.

1973. Density dependent regulation of the numbers of cod and haddock. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:156-173.

KRAMER, D., AND J. R. ZWEIFEL.

1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

LASKER, R.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.

1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LENARZ, W. H.

1973. Dependence of catch rates on size of fish larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:270-275.

LILLELUND, K., AND R. LASKER.

1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S. 69:655-667.

MACCALL, A.

1974. The mortality rate of *Engraulis mordax* in southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 17:131-135.

MAY, R. C.

1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.

MUGIYA, Y.

1974. Calcium-45 behavior at the level of the otolithic organs of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 40:457-463.

1977. Effect of acetazolamide on the otolith growth of goldfish. Bull. Jpn. Soc. Sci. Fish. 43:1053-1058.

MURPHY, G. I., AND R. I. CLUTTER.

1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

NEVILLE, A. C.

1967. Daily growth layers in animals and plants. Biol. Rev. (Camb.) 42:421-441.

O'CONNELL, C. P., AND L. P. RAYMOND.

1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

OTTAWAY, E. M., AND K. SIMKISS.

1977. "Instantaneous" growth rates of fish scales and their use in studies of fish populations. J. Zool. (Lond.) 181:407-419.

PANNELLA, G.

1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

RICKER, W. E.

1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479-541.

RILEY, J. D.

1966. Marine fish culture in Britain. VII. Plaice (*Pleuronectes platessa* L.) post-larval feeding on *Artemia salina* L. nauplii and the effects of varying feeding levels. J. Cons. 30:204-221.

SAKAGAWA, G. T., AND M. KIMURA.

1976. Growth of laboratory-reared northern anchovy, *Engraulis mordax*, from southern California. Fish. Bull., U.S. 74:271-279.

SIMKISS, K.

1974. Calcium metabolism of fish in relation to ageing. *In* T. B. Bagenal (editor), Ageing of fish, p. 1-12. Unwin Bros. Ltd., Old Woking, Surrey.

SMITH, P. E.

1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:282-292.

SMITH, P. E., AND R. LASKER.

1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

STRUHSAKER, P., AND J. H. UCHIYAMA.

1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

TATE, M. W., AND R. C. CLELLAND.

1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

TAUBERT, B. D., AND D. W. COBLE.

1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.

THEILACKER, G. H., AND R. LASKER.

1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer-Verlag, Berl.

ZWEIFEL, J. R., AND R. LASKER.

1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

A LINEAR PROGRAMMING APPROACH TO DETERMINING HARVESTING CAPACITY: A MULTIPLE SPECIES FISHERY

ROBERT A. SIEGEL,[1] JOSEPH J. MUELLER,[2] AND BRIAN J. ROTHSCHILD[3]

ABSTRACT

The U.S. Fishery Conservation and Management Act of 1976 (P.L. 94-265) requires that fishery management plans specify the capacity of a fishing fleet. However, the Act does not provide a definition of capacity. This paper considers some of the problems of defining and measuring capacity in the harvesting sector of the fishing industry and suggests an estimation procedure. A linear programming model is used to estimate the economic capacity of a fishing fleet. The model provides estimates of the expected output in a multiple species fishery.

Measurement of capacity in the U.S. fishing industry has become of increasing importance as a result of the passage of the Fishery Conservation and Management Act of 1976 (FCMA). The FCMA requires (Section 303 (a) (4) (A)) fishery management plans prepared by Regional Fishery Management Councils or the Secretary of Commerce to: "assess and specify . . . the capacity and the extent to which fishing vessels of the United States, on an annual basis, will harvest the optimum yield . . . ."

The FCMA, however, does not provide a functional definition of capacity that can be used in the preparation of fishery management plans. This raises operational difficulties since "capacity" can be based on economic or physical concepts. For example, physical capacity can be measured in terms of the hold space of a fishing vessel, although this generally exceeds the catch. An economic measure would simply be past catches (assuming these reflect equilibrium conditions), but this does not necessarily provide an accurate indication of future catches.

It is apparent that the hold space or past catches are only "first" approximations to "capacity" and that better indicators are needed in order to have meaningful estimates of the expected catch of the fleet. Since estimates of capacity are of obvious importance in determining U.S.-foreign allocations, it is essential that the measurements of capacity and expected catch be accurate. Thus, a major effort must be made to develop meaningful estimates of capacity that are consistent and to indicate what these measures are designed to represent.

Analysis of the capacity problem must address four issues:

1) development of a definition and measure of capacity, at least initially, relevant to the harvesting sector of the fishing industry;
2) development of appropriate methods of estimating capacity;
3) estimation of what the fleet will catch under a set of economic and environmental conditions (it will be suggested that the expected domestic catch is indeed the appropriate notion of "capacity" in the short run); and
4) the time frame for the analysis.

This paper will consider some of the problems of measuring capacity in the harvesting sector of the fishing industry and suggest possible estimation procedures. Section I focuses on economic and technical concepts of capacity. Section II presents a linear programming model which can be used to estimate the output of a fishing fleet in a multispecies fishery. Section III contains an example problem which shows the applicability of this model to a multispecies fishery such as the New England otter trawl fleet. Section IV provides a summary of the paper and briefly describes areas of further research.

[1]National Marine Fisheries Service, Office of Resource Conservation and Management, Washington, DC 20235.
[2]National Marine Fisheries Service, Federal Building, 14 Elm Street, Gloucester, MA 01930.
[3]National Oceanic and Atmospheric Administration, Office of the Administrator, Washington, DC 20230

Manuscript accepted October 1978.
FISHERY BULLETIN: VOL. 77, NO. 2, 1979

CONCEPT OF CAPACITY: FISHING INDUSTRY

General Capacity Characteristics

In general, a firm's productive capacity refers to the quantity of output that can be produced during a given time with existing plant and equipment. This definition is characterized by physical and time dimensions. The physical dimension requires that output be specified in terms of a measurable quantity. The time dimension reflects what "can be produced" during the period of operation of the plant. An important aspect of the time dimension centers on the interpretation of "what can be produced." For example, plant and equipment can be used to produce a certain quantity of output if operated continuously 24 h a day, for 7 days a week, assuming no resource input constraints; and another quantity of output if operated 8 h a day, 5 days a week, taking into account the most economical combination of inputs. Because of these characteristics and the variability of output given different economic and environmental conditions, there does not appear to be a unique number for capacity.

Fishing Fleet Capacity Measures

Technical Capacity

While it may not be possible to define the concept of capacity in precise detail, a distinction can be made between technical and economic capacity. A technical interpretation can be formulated in terms of the following question: how much fish can be caught by a given vessel on each trip, utilizing the entire physical hold space and with no constraints on resource abundance? Capacity in this context is associated with the physical hold space of a fishing vessel. It represents an upper limit on the physical capabilities of the vessel, assuming no input constraints. However, a technical definition of capacity as described above has limited applicability under the FCMA because the capacity problem is to determine the amount of fish the fleet can be expected to catch during a given time period. In other words, the physical notion relates to "assess the capacity" but does not provide any guidance on the "extent to which" this capacity will be utilized.

Economic Capacity of a Fishing Fleet

Economic theory contains several different concepts of capacity. These are briefly described as follows:

1) the output that can be produced at minimum average cost in a competitive model (Klein and Preston 1967);
2) the production flow associated with the input of fully utilized manpower, capital, and labor, and other relevant factors of production (Klein 1960);
3) the maximum sustainable level of output the industry can attain within a very short time if the demand for its product were not a constraining factor, when the industry is operating its existing stock of capital at its customary level of intensity (Klein and Summers 1966);
4) the greatest level of output that a plant can achieve within the framework of a realistic work pattern (U.S. Bureau of the Census 1976).

The first concept has generally been used in theoretical discussions about capacity. The other concepts have been applied in the measurement of capacity in the manufacturing sectors of the economy. In addition, there are several concepts pertaining to agricultural capacity, although none of these have gained universal acceptance (Spielmann and Weeks 1975). After reviewing these concepts and taking into account the specific requirements of the FCMA, it is nevertheless possible to develop a concept of capacity applicable to the harvesting sector of the fishing industry.

Harvesting Capacity Under the FCMA

The FCMA requires that estimates be made of U.S. harvesting capacity which are clearly short run in nature. This is due to the fact that, in a particular year, total allowable catch constraints are established, and the problem then is to determine the catch of the U.S. fleet under different economic conditions. In the short run, economic capacity is related to the quantity of fish that can be caught with a fishing vessel in order to maximize profits or other objectives during a specified period of time. The concept of capacity in this context reflects the behavior of the vessel in the

short run corresponding to the level of output that can be produced as determined by market conditions, input prices, technology, vessel hold space, and a normal fishing pattern. In effect, economic capacity, other things being equal, moves with price. If prices rise, capacity or output of those vessels already in the fishery will be expected to increase. If prices drop, it will fall.[4]

Conversely, if the catch per unit effort increases, and factor costs and output prices remain unchanged, then capacity rises. The important point to note about the economic concept of capacity is that it is not necessarily the full utilization of the hold space of a fishing vessel. If there are changes in cost conditions, market prices, and stock abundance, then capacity output will also change. Thus, the technical notion of capacity described what can be produced based on the physical characteristics of a fishing vessel and the fleet. This concept, however, does not incorporate constraints on output or the quantity of landings because of economic or environmental factors. In contrast, the economic concept of capacity describes what will be produced given technical relationships, factor prices, and product price information, and it is essentially what is implied in the FCMA regarding the "extent to which the (physical) capacity will be utilized."

The definition of fleet capacity used hereafter in this report is as follows: Capacity is the amount of fish that the fleet is expected to harvest during a specified period with the existing stock of capital (vessels and gear) and technology, given catch quotas, processing capabilities, and market conditions. Clearly, the expected domestic catch is synonymous with the "extent to which" notion contained in the Act, and both of these are synonymous with the notion of short run economic capacity as defined above.

SPECIES ALLOCATION OF CAPACITY USING A LINEAR PROGRAMMING (LP) FRAMEWORK

This section outlines an approach that can be used to estimate short-run capacity (output) in a multispecies fishery.

[4]This assumes that there is no entry or exit in a fishery during a given fishing season. If prices rise, vessels may shift from other fisheries; but it is not clear whether the shift will occur in the current or following season.

The LP Problem for a Multispecies Fishing Fleet

A complete generalization of the problem of estimating the "extent" or the expected catch of the fleet is to determine the allocation of resources (over species, vessel category, fleet capacity, fishing area, and time period) that maximizes a stated objective. The following LP model is based on a model formulated by Mueller.[5]

The statement of the objective function and the associated constraints of the model are presented below:

$$\text{Maximize } Z = \sum_{i,j,t} P_{ijt}L_{ijt} - \sum_{i,j,t} C_{ijt}L_{ijt} \qquad (1)$$

or

$$Z = \sum_{i,j,t} L_{ijt}\,(P_{ijt} - C_{ijt})$$

where Z = net revenue received at the harvesting level

L_{ijt} = pounds of species i in area j landed in a directed fishery for that species during period t

P_{ijt} = revenue realized per pound of species i landed in a directed fishery for species i in area j during period t (includes value of bycatch)

C_{ijt} = cost associated with catching a pound of species i (and its associated bycatch) in area j during period t in a directed fishery for species i.

Equation (1) is the objective function to be maximized. It shows the number of pounds of each species that should be caught in a directed U.S. fishery in each area during a particular time period in order to maximize net revenues. These net revenues include the value of the target species and the associated bycatch. In this LP problem formulation, the price per pound landed and cost per pound landed are invariant with the quantity of output.[6] However, these can be allowed to vary.

[5]Mueller, J. J. 1976. A linear programming discussion model for maximizing the net revenues from a multiple species fishery. Unpubl. manuscr., 13 p. National Marine Fisheries Service, Federal Building, 14 Elm Street, Gloucester, MA 01930.

[6]An alternative formulation of the objective function could involve substitution of a demand function for a given price in each time period. In addition, instead of the assumption of a constant average cost per pound of fish landed, costs could be allowed to vary with the quantity of fish landed and with the

Total Allowable Catch Constraint

Presumably there will be a year's total allowable catch (TAC) set for each species for each area. However, because of the bycatch problem, if the number of pounds of each species taken in a directed fishery equaled the TAC for each species, then all of the TAC's would be exceeded. To deal with this problem the following constraint is formulated:

$$\sum_{i,t} A_{mijt} L_{ijt} \leq T_{mj} \qquad (2)$$

where A_{mijt} = number of pounds of species m caught per pound of species i in a directed fishery for species i in area j during period t. It is assumed that these A_{mijt} are the same for all vessel categories.

T_{mj} = TAC for species m in area j for all periods.

Processing Capacity

Generally there exists an upper bound on the total amount of species processing capacity available during a particular time period. To reflect this situation the following constraint was formulated:

$$\sum_{i,j} b_{ijt} L_{ijt} \leq B_t \qquad (3)$$

where b_{ijt} = the number of pounds of processing capacity required when a pound of species i is caught in a directed fishery for species i in area j during period t

B_t = the number of pounds of processing capacity available during period t.

Harvesting Capacity

The final restriction used in this model is a physical upper limit on the amount of fish that can be caught by the fleet in a particular time period or season. To address this problem, the following constraint was formulated:

$$\sum_{i} d_{ijt} L_{ijt} \leq FC_{jt} \qquad (4)$$

where d_{ijt} = the number of units of physical harvesting capacity required when a pound of species i is caught in a directed fishery for species i in area j during period t.

FC_{jt} = the total number of pounds of fish that a fleet consisting of a specified number of vessels (given technology and gear) is physically capable of catching in area j during a particular time period t.

AN APPLICATION TO THE NEW ENGLAND OTTER TRAWL FLEET

New England Otter Trawl Fishery

The fishery to be studied is the otter trawl fishery in New England. The output consists of landings by vessels using otter trawls in Maine, Massachusetts, and Rhode Island during the 1955-74 period (Table 1). In the late 1950's landings in this fishery averaged more than 304,000 metric tons (t). However, by 1972 landings had declined sharply to about 126.8 thousand t.

The catch per gross registered ton (CGRT) reached a maximum value of 9.03 t in 1957 (Table 2). The total associated catch in 1957 also peaked at 318.5 thousand t. By 1973 both CGRT and landings sharply declined to 3.45 t and 127.4 thousand t, respectively. This decrease can be generally attributed to a lower stock abundance of target

TABLE 1.—Landings (metric tons) of fish by otter trawl vessels in Maine, Massachusetts, and Rhode Island. (Sources: U.S. Department of Commerce 1971-77, U.S. Fish and Wildlife Service 1957-69.)

Year	Maine	Massachusetts	Rhode Island	Total
1955	51,341	208,495	39,470	299,306
1956	49,920	207,514	53,281	310,715
1957	44,200	224,436	49,827	318,463
1958	49,525	213,007	42,066	304,598
1959	50,769	198,544	40,846	290,159
1960	46,438	179,805	15,417	241,660
1961	46,094	180,201	23,151	249,446
1962	43,473	190,430	26,550	260,453
1963	40,454	184,294	25,837	250,585
1964	42,167	180,006	11,090	233,263
1965	42,788	177,877	15,435	236,100
1966	45,634	162,307	25,361	233,302
1967	41,716	136,194	29,648	207,558
1968	42,709	127,465	27,494	197,668
1969	34,774	105,859	35,644	176,277
1970	31,872	103,152	26,288	161,312
1971	29,154	96,984	24,838	150,976
1972	24,485	79,457	22,954	126,896
1973	22,049	77,309	28,044	127,402
1974	17,766	72,263	27,051	117,080

fishing area. If these changes were incorporated into the LP model, they would certainly make the problem more realistic. However, the purpose of this was to initially formulate a simple problem and then to develop more complex models in future research. A drawback to this assumption of a given price in each time period is that the quantity landed would be expected to influence price. At the time of this analysis, appropriate demand functions had not been estimated.

TABLE 2.—Estimates of potential output (capacity) based on prices, costs, and stock abundance.

Year	Gross registered tons (GRT)	Catch per gross registered ton (t)	Potential capacity (t) 1957 abundance	Abundance index (Clark and Brown 1977)	Potential capacity (t) adjusted for abundance
1955	37 472	6 93	338,820	1 000	338,820
1956	36,362	8 42	323,335	1 000	323,335
1957	35,269	9 03	318,463	1 000	318,463
1958	35,192	8 66	317,762	1 000	317,762
1959	34,786	8 34	314,099	1 000	314,099
1960	39,280	6 15	354,469	1 000	354,469
1961	36 833	6 77	332,571	1 000	332,571
1962	38,677	6 73	349,226	1 000	349,266
1963	38,839	6 45	350,691	1 000	350,691
1964	39 155	5 96	353,557	1 000	353,557
1965	39,256	6 01	354,503	0 3639	128,984
1966	42,216	5 53	381,212	0 7315	278,848
1967	42,237	4 91	381,316	1 0561	402,787
1968	37,698	5 24	340,217	0 8741	297,548
1969	40,629	4 38	363,456	0 5761	211,353
1970	40,093	4 02	361,734	0 7011	253,818
1971	39,452	3 83	356,071	0 3844	136,936
1972	39,383	3 43	333,933	0 3739	132,957
1973	36,918	3 45	333,512	0 4923	164,116
1974	39,016	3 00	352 283	0 3693	130,098
[1]1975	38,972	3 54	351,901	0 2693	94 767
[1]1976	38,972	3 54	351,901	0 4041	142,203

[1]Based on 1970-74 average

species in the otter trawl fishery resulting from the entry of foreign effort in these fisheries in the late 1950's and early 1960's.

The LP model formulated in the previous section required data on species, prices, harvesting costs, bycatch ratios, and physical capacity estimates for both the harvesting and processing sectors. Data are generally available for these items except for harvesting costs. In the absence of harvesting cost data, the objective function in the model was specified to only maximize gross revenues. Because of this, the solution variables would probably be overestimates of actual expected catches.

In this report the method of incorporating cost factors is to deflate the peak CGRT by an index of relative species abundance (Clark and Brown 1977). The index of stock abundance is being used to adjust the expected level of catch for changes in cost conditions for the 1955-77 period. Since the level of catch is, among other factors, a function of abundance, any declines in abundance would be expected to result in a lower level of catch (other things being equal). Reductions in abundance, therefore, would be expected to result in declining CGRT and increased costs per unit of output. A more realistic measure of factor productivity would be catch per unit of effort; this information is not available.

Data in Table 2 indicate that GRT has not changed significantly since 1955 for this otter trawl fishery. The assumption was made that the number of days fished per GRT has not changed.[7] The year 1957 was chosen as the base year because CGRT reached a maximum value and stock abundance was probably relatively high. Table 2 also shows an index of stock abundance for the International Commission for the Northwest Atlantic Fisheries (ICNAF) designated subarea 5 and statistical area 6 for finfishes and squids.

In order to develop a measure of expected output relative to 1957, it is noted that catch in subsequent years will vary as a function of fishing effort and stock abundance. If the catchability coefficient relative to GRT can be assumed to be the same, at least as a first approximation for each year, then the catch in any year is:

$$\frac{T_i}{T_0} \times C_0$$

where T_i is the GRT in the ith year, and T_0 and C_0 are, respectively, the GRT and catch for the year 1957.[8] Furthermore, it is assumed that catch would depend on the abundance of the stock and, therefore, the catch in any year should be modified by:

$$A_i/A_0$$

where A_i denotes the abundance in the ith year and A_0 the abundance in the base year (1957).

Thus, an estimate of expected output relative to the base year is:

[7]Data are not available to verify this assumption.

[8]Using this approach, it is necessary to choose a base year. As a result, physical capacity and economic capacity were identical for 1957.

$$\frac{T_1}{T_0} \times \frac{A_i}{A_0} \times C_0 .$$

An underlying feature of this simple index (A_i/A_0) is that while catches should rise and fall with effort (T_i's), they should also increase and decrease with abundance. Consequently, abundance is a factor influencing output or capacity when the other inputs, except for effort (GRT), are fixed.

Example Problem

An example problem is presented below utilizing the model formulations in the previous section. In this problem it is assumed that there are: 1) 11 species, 2) 1 vessel category (all otter trawlers), 3) 1 time period (1 yr), and 4) 1 area. The objective of the problem is to maximize the gross revenues to the otter trawl fleet assuming the 1977 catch restrictions, the most recent bycatch ratios, and an estimated U.S. deflated harvesting capacity as developed in the previous section.[9]

The species that were used and their associated bycatch ratios are in Table 3. The interpretation of the entries in the table is as follows: when a pound of cod is sought in a directed fishery for cod, 1 lb of cod, 0.059 lb of haddock, 0.012 lb of redfish, etc., are caught.[10] The total pounds caught when seeking to catch a pound of cod in a directed fishery for cod is 1.344.

Table 4 presents the total gross revenue realized for each species when attempting to catch that species in a directed fishery. For example, when attempting to catch a pound of cod in a directed fishery, the total of 1.344 lb of fish actually caught is worth a total of 35.2 cents and includes the value of the cod and the value of the bycatch. Table 5 presents the amount of processing capacity required per pound of each species caught in a directed fishery and includes the bycatch requirement. Cod, haddock, and pollock are the only species of those listed that are landed drawn and a loss of 15% by weight is assumed. A total processing capacity of 500 million pounds (226,796 t) was assumed.

Estimates of Landings Adjusted for Abundance

Estimates of adjusted landings (incorporating cost factors) were made (Table 2) using the ap-

[9]For the purpose of this problem, gross revenues were used in the objective function since the separable costs of catching these species has not yet been determined. The costs of traveling to and from the fishing grounds should also be included in the objective, but these are not available at present.

[10]The bycatch ratios used in the LP problem were not converted from pounds to metric tons. The basic data for the computations in the LP problem were specified in pounds

TABLE 4.—Gross revenue per pound in a directed fishery. (Source: U.S. Department of Commerce 1976.)

Species	Total revenue per pound caught in a directed fishery (includes value of bycatch) (¢/lb)
Atlantic cod	35.2
Haddock	52.7
Redfish	16.6
Silver hake	16.2
Red hake	20.3
Pollock	22.6
Yellowtail flounder	46.4
Other flounders	55.6
Other finfish	28.7
Atlantic mackerel	13.3
Squid	10.0

TABLE 3.—United States otter trawl bycatch ratios in 1974 for ICNAF areas. (Source: Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass.)

Species sought	Species caught (pounds)											
	Atlantic cod	Haddock	Redfish	Silver hake	Red hake	Pollock	Yellowtail flounder	Other flounders	Other finfish	Atlantic mackerel	Squid	Total
Atlantic cod	1.0	0.059	0.012	0.002	0	0.07	0.041	0.108	0.052	0	0	1.344
Haddock	0.214	1.00	0.022	0.027	0	0.027	0.038	0.049	0	0	0	1.377
Redfish	0.04	0.011	1.0	0.002	0	0.059	0	0.001	0.046	0	0	1.159
Silver hake	0.051	0.003	0.004	1.0	0.081	0.005	0.061	0.073	0.106	0.009	0.04	1.433
Red hake	0.021	0	0	0.496	1.0	0	0.054	0.082	0.360	0.001	0.098	2.112
Pollock	0.213	0.032	0.035	0.009	0.022	1.0	0.003	0.003	0.073	0.001	0.085	1.476
Yellowtail flounder	0.101	0.015	0	0.001	0	0.003	1.00	0.058	0.004	0	0.004	1.186
Other flounders	0.266	0.036	0	0.054	0.005	0.007	0.296	1.0	0.170	0.002	0.112	1.948
Other finfish	0.313	0.078	0.06	0.152	0.048	0.153	0.07	0.124	1.0	0.019	0.046	2.063
Atlantic mackerel	0.009	0	0	0.024	0	0.012	0	0	0.042	1.0	0.051	1.138
Squid	0	0	0	0	0	0	0	0.001	0.002	0	1.0	1.003

TABLE 5.—Processing requirements per pound of each species in a directed fishery. (Source: National Marine Fisheries Service, Statistics Branch, Gloucester, MA 01930.)

Species	Processing requirement
Atlantic cod	1.1745
Haddock	1.19085
Redfish	1.1425
Silver hake	1.42415
Red hake	2.10885
Pollock	1.2895
Yellowtail flounder	1.1911
Other flounders	1.8935
Other finfish	1.98135
Mackerel	1.3485
Squid	1.003

proach outlined in the previous section.[11] In 1976, for example, the deflated estimate of landings was 142,000 t under current conditions of abundance. Another way of explaining this figure is as follows: if we assume that the relationship between aggregate production prices and aggregate factor costs have been unchanged since 1957, then we would expect that 142,000 t of fish would be landed by the otter trawl fleet (given the current level of abundance). It should be noted that in 1965 and 1971 the actual catch was larger than the estimated potential catch adjusted for abundance. These discrepancies could be due to reasons such as increased fishing intensity or possibly large sampling errors given the stochastic nature of the stocks.

Estimates of undeflated catch are also provided in Table 2. These indicate what could be caught if 1957 productivity conditions prevailed. However, these estimates are not particularly meaningful since they do not reflect changes in stock abundance and cost conditions.

[11]Data on catch per gross registered ton were not available for 1975-76. The estimates of deflated capacity in 1976 for this example were based on 1973 data on catch per GRT and the 1976 index of abundance (A_t/A_0). It is interesting to note that the 1974 forecast was within 5% of the actual 1974 catch by otter trawls.

The estimate of 142,000 t for 1976 also could be modified to take into consideration the changes in technology of the fleet. The changes include, among others, the utilization of stern trawlers, pair trawls, improved loran, and increase in horsepower. It is assumed for this example that these changes account for an estimated 5,000 t of additional harvesting capacity under current conditions of abundance. Table 6 shows the simplex tableau for the LP calculations for the base model.

RESULTS

The base model computations are presented in Table 7. Column 2 (Directed catch) shows the catches of each of the species in the directed fisheries. Column 3 (Bycatch) presents the resultant incidental catches of each of the species that are implied by the directed catches in column 2. The total gross revenues that would accrue to the otter trawl fleet by employing this fishing strategy, as predicated on the optimal LP solution, would be $68.5 million. This is the maximum gross revenue that the fleet could obtain given the assumptions of the LP model. In other words, there is no other fishing strategy (allocation of harvesting capacity) that would result in a larger level of gross revenues.

The FCMA requires that foreign fishing be allowed on those stocks for which surpluses have been identified. This LP model can be used to estimate foreign surpluses. Column 4 (Total catch) presents the estimated total U.S. catches of each of the species. Column 5 (Quota) indicates the recommended quotas for 1977. Column 6 (Estimated surplus) shows the resultant surplus or the excess of each species quota over the probable U.S. catch of the particular species as identified by the model.

TABLE 6.—Basic computational form or simplex tableau for LP calculations

Decision variables											
X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	Constraints
1.0	0.214	0.04	0.051	0.021	0.213	0.101	0.266	0.313	0.009	0	55,125,000
0.059	1.0	0.011	0.003	0.0	0.032	0.015	0.036	0.078	0	0	13,230,000
0.012	0.022	1.0	0.004	0	0.035	0	0	0.060	0	0	19,845,000
0.022	0.027	0.002	1.0	0.496	0.009	0.001	0.054	0.152	0.024	0.0	264,600,000
0	0	0	0.081	1.0	0.022	0	0.005	0.048	0	0	97,020,000
0.070	0.027	0.059	0.005	0	1.0	0.003	0.007	0.153	0.012	0	66,150,000
0.041	0.038	0	0.061	0.054	0.003	1.0	0.296	0.07	0	0	30,870,000
0.108	0.049	0.001	0.073	0.082	0.003	0.058	1.0	0.124	0	0.001	44,100,000
0.052	0	0.046	0.106	0.360	0.073	0.004	0.170	1.0	0.042	0.002	269,000,000
0	0	0	0.009	0.001	0.001	0	0.002	0.019	1.0	0	165,375,000
0	0	0	0.040	0.098	0.085	0.004	0.112	0.046	0.051	1.0	174,195,000
1.344	1.377	1.159	1.433	2.112	1.476	1.186	1.948	2.063	1.138	1.003	325,000,000
1.1745	1.19085	1.1425	1.42415	2.10885	1.2895	1.1687	1.8935	1.98135	1.150	1.003	500,000,000
0.352	0.527	0.166	0.162	0.203	0.226	0.464	0.556	0.287	0.133	0.1004	Objective function

TABLE 7.—Results of the base model showing estimated U.S. catches and surpluses in the otter trawl fisheries in ICNAF Areas 5 and 6. Harvesting capacity = 325 million pounds (147,565 t); gross revenues = $68,605,600.

Species	Directed catch	Bycatch	Total catch	Quota	Estimated surplus	Actual surplus
			Millions of pounds			
Atlantic cod	27	28	55	55	—	0
Haddock	8	5	13	13	—	0
Redfish	17	3	20	20	—	0
Silver hake	—	4	4	265	261	188
Red hake	—	2	2	97	95	77
Pollock	62	4	66	66	—	0
Yellowtail flounder	18	13	31	31	—	0
Other flounders	40	4	44	44	—	0
Other finfish	—	16	16	269	253	132
Atlantic mackerel	61		61	165	104	152
Squid	—	13	13	174	161	94
Total	233	92	325	1,199	874	643

The results of the model (Table 7) indicate that all of the cod, haddock, redfish, pollock, yellowtail flounder, and other flounders be allocated for exclusive U.S. exploitation since the sum of the directed catches and the bycatches for these species are equal to the quotas.

The results from the model did identify the existence of surpluses for silver and red hake, Atlantic mackerel, squid, and other finfish. Coincidentally, the species or species groupings for which surpluses were identified in the Preliminary Management Plans (PMP's) for the Fishery Conservation Zone in the northwest Atlantic were for these same species identified by the model. All of the surpluses, except for Atlantic mackerel, are larger than the actual surpluses specified in the PMP's. (These surpluses appear in column 7 of Table 7.) This would be expected since the model only considered the otter trawl fleet capacity in New England and did not include harvesting capacity by other gear types in New England and in the Mid-Atlantic area.

An important implication of the optimal solution for the LP model was the calculation of shadow prices for certain species for which the constraints were binding (i.e., there were zero surpluses).[12] The optimal solution indicates that the quotas for Atlantic cod, haddock, redfish, pollock, yellowtail flounder, and other flounders were harvested. In addition, the entire harvesting capacity was utilized. Therefore, all of these species quotas were binding constraints and the resources had positive shadow prices in the optimal solution. Furthermore, harvesting capacity was also a binding constraint. Shadow prices are shown in Table 8. For the species in excess supply

TABLE 8.—Shadow prices for binding constraints.

Resource	Shadow price ($ lb)
Atlantic cod	0.14
Haddock	0.32
Redfish	0.02
Pollock	0.01
Yellowtail flounder	0.30
Other flounders	0.19
Harvesting capacity	0.12

(as evidenced by surpluses) there are no shadow prices. This is to be expected since the corresponding shadow price is zero because the excess supply is of no value to the U.S. fleet if it cannot be harvested and sold.

In this particular problem, the shadow price for cod can be interpreted as follows: if the Atlantic cod quota was increased by 1 lb, the objective function would increase by 14 cents. This 14 cents includes the imputed value of Atlantic cod (shadow price) and the other species caught as bycatches with cod less the value of a pound of lower valued species that the new mix replaces. As can be seen from Table 8, the shadow prices vary since the exvessel prices shown in the simplex tableau (Table 6) are different. In the optimal solution, the shadow price for harvesting capacity is lower than most of the other species in Table 8. This is because if the harvesting capacity was increased by 1 lb, the only species available to harvest are the lower valued species.

Shadow prices play an important role in the development of resource management strategies. For example, a decision to rebuild the stock for a particular species could be based on the shadow price that indicates the greatest return when a constraint is increased by one unit. The LP model in this paper, given the shadow prices from the optimal solution, shows that in the multispecies otter trawl fishery, cod, haddock, and yellowtail

[12]Shadow prices show the changes in the objective function for a unit change in the constraint (see column RHS in Table 6).

flounders would be likely candidates for rebuilding.

An area of further interest in this model is to determine how sensitive the optimal solution (Table 7) is to changes in the prices, bycatch ratios, and quotas. If the optimal solution is not particularly sensitive to changes in these parameters, this means that it may not be necessary to be overly concerned with very precise estimates of technical parameters. Consequently, the bounds on the technical parameters in the LP model may not result in a large impact on changes in the objective function. A sensitivity analysis was not performed for this LP model, but the implication for future research is that estimates of certain technical parameters may not have to be as precise as researchers believe before there is a significant change in the optimal solution to the LP problem.

SUMMARY

The purpose of this paper was to discuss alternative approaches used to measure capacity, to develop a definition of capacity for the harvesting sector of the commercial fishing industry, and to present a model that could be used to estimate this capacity in a multispecies fishery. We have argued that the concept of capacity contained in the FCMA is identical to short-run economic output. We feel the suggested methodology and the model presented in this paper can be used to address the issue of capacity in a multispecies fishery. The model can be used to examine other scenarios than presented here, by incorporating seasonal quotas, alternative mesh sizes, and stock rebuilding considerations.

ACKNOWLEDGMENTS

The authors express their appreciation for the helpful suggestions and comments on the work to Darrel Hueth, Joel Dirlam, and Ivar Strand. All omissions and errors are, of course, the responsibility of the authors.

REFERENCES

CLARK, S. H., AND B. E. BROWN
1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull., U.S. 75:1-21.

DELEEUW, F.
1961. The concept of capacity. American Statistical Association. Proc. Bus. Econ. Stat. Sect., p. 320-329.
1966. A revised index of manufacturing capacity. Fed. Reserve Bull. 52:1605-1615.

HERTZBERG, M. P., A. I. JACOBS, AND J. E. TREVATHAN
1974. The utilization of manufacturing capacity, 1965-1973. Surv. Curr. Bus. 54(7):47-57.

KLEIN, L. R.
1960. Some theoretical issues in the measurement of capacity. Econometrica 28:272-286.

KLEIN, L. R., AND R. S. PRESTON.
1967. Some new results in the measurement of capacity utilization. Am. Econ. Rev. 57(1):34-58.

KLEIN, L. R., AND R. SUMMERS.
1966. The Wharton index of capacity utilization. Univ. Pennsylvania, Wharton School of Finance, Dep. Econ., Philadelphia, Pa., 94 p.

PERRY, G. L.
1973. Capacity in manufacturing. Brookings Papers on Economic Activity 3:701-742.

PHILLIPS, A.
1963. Industrial capacity: an appraisal of measures of capacity. Am. Econ. Rev. 53(2):275-292.

QUANCE, L., AND L. TWEETEN.
1972. Excess capacity and adjustment potential in U.S. agriculture. Agric. Econ. Res. (U.S. Dep. Agric.) 24(3):57-66.

RADDOCK, R. D., AND L. R. FOREST.
1976. New estimates of capacity utilization: manufacturing and materials. Fed. Reserve Bull. 62:892-905.

ROTHSCHILD, B. J.
1972. An exposition on the definition of fishing effort. *In* Economic aspects of fish production, p. 257-271. Organization for Economic Cooperation and Development, Paris.

ROTHSCHILD, B. J., AND J. W. BALSIGER
1971. A linear-programming solution to salmon management. Fish. Bull., U.S. 69:117-140.

SPIELMANN, H., AND E. WEEKS.
1975. Inventory and critique of estimates of U.S. agricultural capacity. Am. J. Agric. Econ. 57:922-928.

U.S. BUREAU OF THE CENSUS.
1976. Survey of plant capacity, 1975-MQ-C1(75)-2. U.S. Gov. Print. Off., Wash., D.C.

U.S. DEPARTMENT OF COMMERCE.
1971-77. Fishery statistics of the United States 1968 [to 1974]. (Various editors and pagination.) National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Wash., DC 20235.

U.S. FISH AND WILDLIFE SERVICE.
1957-1969. Fishery statistics of the United States 1955 [to 1967]. (Various editors and pagination.)

YEH, C. J., L. G. TWEETEN, AND C. L. QUANCE.
1977. U.S. agricultural production capacity. Am. J. Agric. Econ. 59:37-48.

SOME ASPECTS OF THE BIOLOGY OF DEEP-SEA LOBSTERS OF THE FAMILY POLYCHELIDAE (CRUSTACEA, DECAPODA) FROM THE WESTERN NORTH ATLANTIC [1,2]

ELIZABETH LEWIS WENNER[3]

ABSTRACT

Stereomastis nana was the most abundant species of Polychelidae collected by otter trawl on the continental slope of the Middle Atlantic Bight, off the eastern United States. Total catches were almost four times greater than those of its congener, *S. sculpta*. Other polychelid species, *Polycheles validus* and *P. granulatus*, were caught infrequently. *Stereomastis nana* was abundant at depths of 1,400-2,599 m, and *S. sculpta* occurred at 486-2,257 m. *Stereomastis nana* and *S. sculpta* appear to spawn year round, and both may be deep-sea scavengers.

The Polychelidae are the only extant members of the superfamily Eryonoidea, a group represented in fossil records from the mid-Triassic period (Glaessner 1969; Firth and Pequegnat[4]). The family is currently placed by Glaessner (1969) within the infraorder Macrura, along with the spiny lobsters (Palinuridae) and the shovel-nosed lobsters (Scyllaridae). Although the Polychelidae are not of commercial importance, interest in these lobsters dates back when Bate (1888) discussed uniqueness of the family because its members lack eyes and are related to forms thought to be extinct since the Mesozoic. In addition, some species live at extreme depths. Since that time, Andrews (1911) indicated the occurrence of external spermatophores and discussed sperm transfer among male and female polychelids; Santucci (1933) and Bernard (1953) suggested that *Polycheles typhlops* performs reproductive migrations up slope; and Firth and Pequegnat (see footnote 4) investigated taxonomic relationships of the entire family Polychelidae as well as certain aspects of its biology.

Otter trawl collections of Polychelidae have been made by the Virginia Institute of Marine Science on the continental slope near Norfolk Canyon, off the eastern United States from 1973 to 1976, which confirmed their importance as benthic slope crustaceans. In this paper, I give new biological information on this interesting group of decapods that has come to light as a result of these collections. Species from the western North Atlantic which are discussed include *Polycheles validus*, *P. granulatus*, *Stereomastis nana*, and *S. sculpta sculpta* (distinguished from the Pacific form, *S. sculpta pacifia*, by Firth and Pequegnat (see footnote 4), but referred to in this paper, for simplicity, as *S. sculpta*).

METHODS AND MATERIALS

Polychelidae were collected during eight seasonal cruises from June 1973 to January 1976 in the Middle Atlantic Bight (lat. 33°33′-38°52′ N). Tows were made either with a 13.7 m or 9.1 m (headrope) semiballon four-seam otter trawl for 0.5 h at depths shallower than 2,000 m and 1 h in water deeper than 2,000 m (see Musick et al.[5] for detailed gear description). A precision depth recorder determined mean depth of trawl every 3 min after the trawl hit bottom for 0.5-h tows and every 6 min for 1-h tows. Bathythermographs or reversing thermometers recorded bottom temperatures. Analyses of relative abundance did not include samples from tows in which the net tore, failed to reach bottom, or became twisted during a

[1]Based on part of a dissertation to be presented to the School of Marine Science, College of William and Mary, Williamsburg, Va.

[2]Contribution No. 881, Virginia Institute of Marine Science, Gloucester Point, Va.

[3]Virginia Institute of Marine Science, Gloucester Point, Va.; present address: South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

[4]Firth, R.W., Jr., and W.E. Pequegnat. 1971. Deep-sea lobsters of the families Polychelidae and Nephropidae (Crustacea, Decapoda) in the Gulf of Mexico and Caribbean Sea. Texas A&M Res. Found. Ref. 71-11T, College Station, 106 p.

[5]Musick, J. A., C. A. Wenner, and G. R. Sedberry. 1975. Archibenthic and abyssobenthic fishes. *In* May 1974 baseline investigation of Deepwater Dumpsite 106, p. 229-269. NOAA Dumpsite Eval. Rep. 75-1, 388 p.

Manuscript accepted December 1978
FISHERY BULLETIN VOL 77, NO 2, 1979

tow, but these samples were used in length-frequency distributions and reproduction analyses.

All specimens were identified by me from Firth and Pequegnat's (see footnote 4) key to the Polychelidae. Short carapace length (SCL), i.e., the distance from the median posterior margin of the carapace to the orbit, was measured to the nearest millimeter.

Sex and gonad condition were recorded for all polychelids, and gonads representative of stages of development were obtained for histological examination and placed in Davidson's fixative (Humason 1972). Validity of female gonad stages was determined by gross ovarian morphology, ovarian histology, and oocyte diameter. The longest horizontal diameter of 15 oocytes randomly chosen from excised ovaries of each lobster was measured with an ocular micrometer.

Fecundity was estimated from total external egg number. I stripped eggs from the pleopods, placed them in a graduated tube, and adjusted the volume to 10 ml with water. After mixing, I took three 0.5 ml aliquots and counted eggs from the aliquots on a gridded Petri dish. I then noted the degree of embryological development of eggs, similar to descriptions by Meredith (1952) and Allen (1966), and measured the longest horizontal diameter of 15 randomly chosen eggs.

I also removed stomachs from preserved lobsters and sorted and identified their contents where possible. The importance of food taxa was then determined from their numerical abundance.

RESULTS

Stereomastis nana (Smith)

Stereomastis nana is found in the three major oceans but not in the Mediterranean and Caribbean Seas or the Gulf of Mexico (Firth and Pequegnat see footnote 4). Its bathymetric distribution within the western North Atlantic off the east coast of the United States was reported to be 1,289-3,506 m (Smith 1884, 1887); off Greenland and Iceland, specimens have been taken from 1,271 to 2,271 m (Hansen 1908).

Abundance data based on our 13.7 m otter trawl catches show that *S. nana* constitutes 20% by number of the total benthic decapod fauna at depths below 1,200 m. Its importance within the benthic decapod community diminishes to 0.3% at depths between 400 and 1,199 m. Trawls within the Middle Atlantic Bight collected 459 *S. nana* from depths of approximately 613-2,642 m and temperatures of 2.4 -5.0° C. Analysis of variance showed a significant difference (Table 1) between abundance of *S. nana* for depth intervals shown in Figure 1. Scheffé's multiple mean comparison test (Snedecor and Cochran 1967) showed the mean catch rate, expressed as $\log_{10}(x + 1)$ 0.5 h tow, to be significantly higher at depths of 1,400-2,599 m. There was no discernible change in depth distribution of this species with season.

There was also no apparent segregation of sex with depth since both male and female *S. nana* occurred throughout the depth range. Chi-square analysis using Yates correction (Woolf 1968) showed females and ovigerous females to be significantly more numerous than males at arbitrarily chosen depth strata of 1,200-1,999 and 2,000-2,800 m (Tables 2, 3). There was no significant relationship between average size of *S. nana* and depth of capture ($F = 0.056$, df = 1,460).

Males (mean = 22 mm SCL), females (mean = 25 mm SCL), and ovigerous females (mean = 28 mm SCL) differed significantly from each other in size by analysis of variance (Table 4) and Scheffé's multiple mean comparison test. Sex ratios varied significantly with size, with females predominating at lengths ~26 mm SCL and males at lengths < 22 mm SCL (Table 5).

Among the Polychelidae, sperm transfer is accomplished by attachment of spermatophores to the surface of the posterior sterna of the females (Andrews 1911). Most ovigerous and nonovigerous females >23 mm had externally attached spermatophores (Figure 2). All ovigerous females except five damaged individuals had spermatophores attached. It is probable that spermato-

TABLE 1.—One-way analysis of variance on abundance, expressed as $\log_{10}(x + 1)$ per 0.5 h tow, of *Stereomastis nana* and *S. sculpta* by depth interval (see Figure 1 for description of depth intervals)

Source of variation	df	SS[1]	MS[2]	*F*
S. nana				
Among groups (depth interval)	10	13 3	1 3	16 23**
Within groups	126	10 4	0 1	
Total	136	23 7		
S. sculpta				
Among groups (depth interval)	9	1 5	0 17	2 88
Within groups	129	7 6	0 06	
Total	138	9 1		

[1]SS = sum of squares
[2]MS = mean squares
**P < 0.01

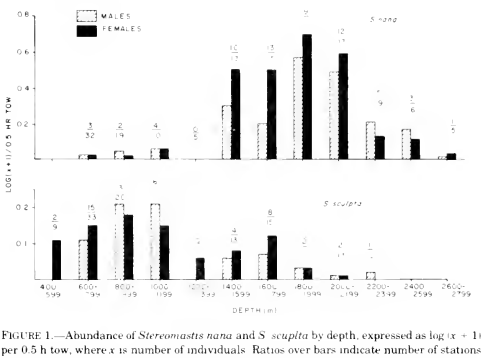


FIGURE 1.—Abundance of *Stereomastis nana* and *S. sculpta* by depth, expressed as log $(x + 1)$ per 0.5 h tow, where x is number of individuals. Ratios over bars indicate number of stations where *Stereomastis* spp. were captured to total number of stations within depth intervals.

TABLE 2.—Summaries for three depth strata of morphological and reproductive data on *Stereomastis nana* and *S. sculpta* from the continental slope. $\bar{x}$ = arithmetic mean; SCL = short carapace length in millimeters, 95% confidence limits (CL) follow the means. Percent ovigerous females is based on total female samples only.

	400-1,199 m		1,200-1,999 m		2,000-2,800 m	
Item	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*
No. successful tows	9	36	32	15	21	3
Temperature (°C)	4.5	4.8	3.7	3.8	3.1	2.9
No. individuals	14	107	239	20	209	3
N (Percent) males	5(35.7)	48(45.1)	73(30.5)	12(60.0)	79(37.8)	1(33.3)
N (Percent) females	9(64.3)	59(54.9)	166(69.5)	8(40.0)	130(62.2)	2(66.7)
N (Percent) ovigerous females	3(33.3)	8(14.0)	92(55.4)	0	36(27.7)	0
$\bar{x}$ (CL) SCL all individuals	24(18.29)	34(31.37)	26(26.27)	30(24.35)	24(23.25)	35(0.78)
Size range	18-34	16-69	17-37	19-72	16-38	19-54
$\bar{x}$ (CL) SCL males	21(15.27)	33(31.36)	22(22.23)	27(24.31)	22(22.23)	20(ND[1])
Size range	18-26	16-52	17-28	19-37	18-26	ND
$\bar{x}$ (CL) SCL females	27(20.33)	35(32.38)	27(26.28)	33(29.47)	25(24.25)	42(0.192)
Size range	19-34	18-55	18-37	22-72	16-38	30-54
$\bar{x}$ (CL) SCL ovigerous females	29(16.41)	52(48.56)	29(28.29)	ND	29(28.30)	ND
Size range	25-34	45-58	25-35	ND	24-38	ND

[1]ND = no data.

TABLE 3.—Chi-square test for goodness of fit, using Yates correction for continuity of male: female ratios of *Stereomastis nana* and *S. sculpta* by depth interval.

Depth interval (m)	Sex	Frequency		χ^2	
		S. nana	*S. sculpta*	*S. nana*	*S. sculpta*
400-1,199	M	5	48	0.64	0.93
	F	9	59		
1,200-1,999	M	73	12	36.18**	0.45
	F	166	8		
2,000-2,800	M	79	1	11.96	ND[1]
	F	130	2		

**P < 0.01.
[1]ND = no data.

phores from these individuals were dislodged during capture. Thirty-seven male *S. nana* > 19 mm were also found with a hardened secretion of spermatophores projecting out of the gonopore at the base of the fifth pereopod (Figure 2). Ovigerous females, nonovigerous females, and males with external spermatophores occurred at all depths, with maximum numbers at 1,400-2,199 m. No males or females with external spermatophores, and only one ovigerous female occurred deeper than 2,400 m.

By examination of ovaries, I defined six stages of ovarian development in *Stereomastis* spp. (Figure

TABLE 4.—One-way analysis of variance on short carapace length of *Stereomastis nana* and *S. sculpta* by sex (male, female, and ovigerous female).

Source of variation	df	SS[1]	MS[2]	F
S. nana				
Among groups (sexes)	2	3 010	1,505.2	74.25**
Within groups	459	9 304	20.3	
Total	461	12,314		
S. sculpta				
Among groups (sexes)	2	3 592	1 796.2	16.90**
Within groups	122	12 964	106.3	
Total	124	16 556		

[1]SS = sum of squares.
[2]MS = mean squares.
**$P < 0.01$.

TABLE 5.—Percent of male *Stereomastis nana* by size interval. Size groupings result from chi-square analysis of male and female frequencies by 2 mm size intervals.

SCL (mm)	Males	Females	Males (%)	χ^2
16-21.9	69	23	75	22.01**
22-25.9	72	67	52	0.11
26-39.9	14	210	6	171.50**
Total	155	300	34	45.57**

**$P < 0.01$.

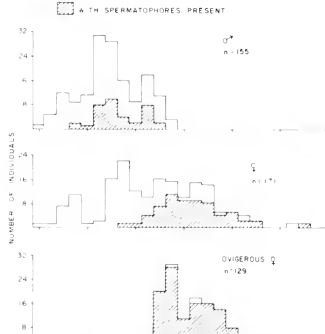


FIGURE 2.—Length-frequency distribution of *Stereomastis nana* pooled for all months of collection.

3). Immature ovaries were threadlike and difficult to remove from the specimens because of their adherence to the dorsal portion of the digestive gland. In cross section, the oocytes appeared very small (0.05-0.2 mm, mean = 0.1 mm) with the nucleus composing most of the oocyte. Resting ovaries had oocytes (0.1-0.3 mm, mean = 0.2 mm) with a large nucleus and no yolk granules (Figure 4A). The intermediate ovary had fewer densely packed oocytes (0.1-0.4 mm, mean = 0.3 mm). A distinct basophilic nucleus with condensed chromosomes was visible in cross section. Yolk granules partially filled the cytoplasm. The germinative zone was well developed and filled with developing, basophilic oocytes (Figure 4B). In the ripening ovary, the oocytes were irregularly shaped (0.3-0.8 mm, mean = 0.5 mm), with the cytoplasm partially filled with yolk granules. There was a visible nucleus. The germinative area within the ovary was larger than in ripe individuals. In gravid individuals, the ovary occupied much of the thoracic cavity, with anterior and posterior horns extending laterally. The oocytes (0.5-0.9 mm in diameter, mean = 0.7 mm) were tightly packed and irregularly shaped, yet they were easily dislodged from the ovary with slight probing. Histological sectioning revealed oocytes to be filled with yolk granules. The nucleus was generally not visible and the central germinative zone of the ovary was compressed (Figure 4C). Individuals with ovaries judged to be spent were usually ovigerous females. The ovaries contained a few atresic (0.3-0.4 mm) oocytes, but much of the ovary was filled with resting stage basophilic oocytes (0.1-0.2 mm (Figure 4D)).

Most nonovigerous females > 26 mm had immature and resting ovaries (Figure 5). Individuals with ripening and gravid ovaries first appeared at 21 mm, and the percentage of females in these stages increased with increasing size. Approximately 58% of the 65 nonovigerous females with external spermatophores were ripe. The remaining individuals had immature (6%), resting (9%), intermediate (11%), ripening (8%), or spent (8%) ovaries. A large percentage of ovigerous *S. nana* 21 mm or larger were spent, but there were some ovigerous individuals with ovaries in each stage of development (Figure 5). In most cases, ovigerous females with ripening or gravid ovaries had advanced eggs (eyes and a discernible abdomen), corresponding to C or C+ stage designated by Meredith (1952). Spent individuals had eggs that were newly deposited (stages A-A+) or gastrulated (stage B+).

Ovigerous and other female *S. nana* with external spermatophores attached were found during

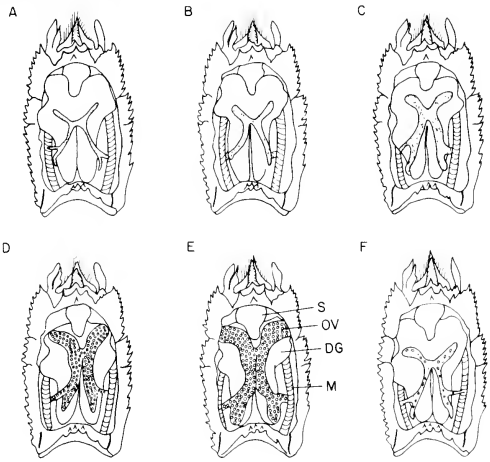


FIGURE 3.—Cephalothoracic position and relative size of the ovary of Polychelidae during ovarian development stages (dorsal view). A. Immature; B. Resting; C. Intermediate; D. Ripening; E. Gravid; and F. Spent. OV = ovary, DG = digestive gland, M = muscle, and S = stomach.

every month of collection (Table 6). Individuals with advanced eyed (stages C-C+) eggs and egg remnants (stage D), indicative of imminent or recent hatching, were also collected each month. Similarly, there were gravid and ripening females and spent ovigerous females present throughout the year (Figure 6), but there was no indication that seasonal peaks in oviposition occurred.

The estimated number of eggs on the pleopods ranged from 1,015 to 7,580 (mean = 3,392, n = 10) with a mean diameter of 0.7 mm. There was no apparent relation between body size and fecundity for 10 individuals examined.

I examined 127 males (17-36 mm SCL) for presence of external (protruding from gonopores) and internal (present in vas deferens) spermatophores.

TABLE 6.—Summary of data on reproductively mature individuals and advanced egg development in *Stereomastis nana* and *S. sculpta* by month of collection.

	September		November		January		April		May-June		July	
Item	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*	*S. nana*	*S. sculpta*
Males												
Sample size	10	15	58	16	19	8	23	5	13	13	34	2
Percent total catch	20	45	35	53	26	50	39	28	36	59	42	33
Percent with spermatophores exuding	40	13	5	6	5	0	26	20	46	31	50	0
Nonovigerous females												
Sample size	13	17	70	11	30	7	24	11	10	8	27	4
Percent with spermatophores attached	77	29	37	9	17	29	46	9	40	12	37	25
Ovigerous females												
Sample size	26	1	37	3	24	1	12	2	13	1	19	0
Percent of total females	67	5	35	21	44	12	33	15	57	11	41	0

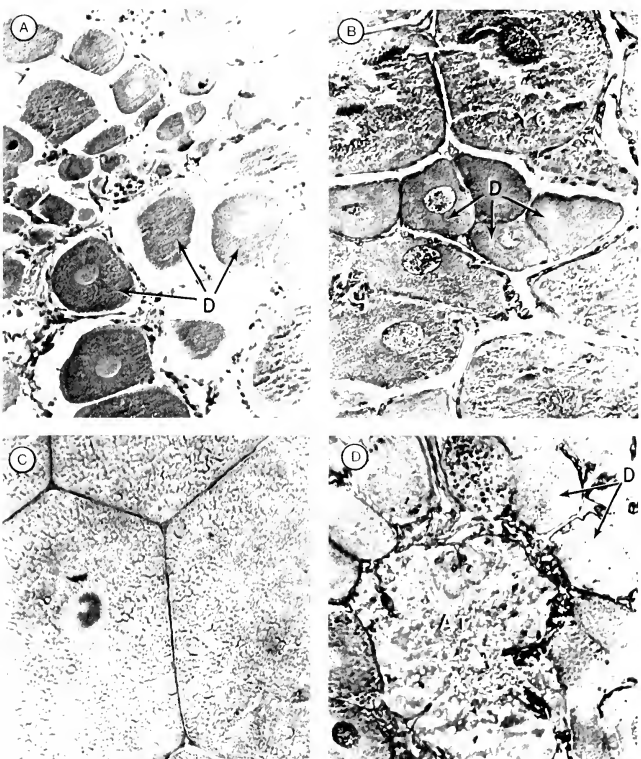


FIGURE 4.—Photomicrographs of four ovarian stages of *Stereomastis sculpta* and *S. nana*. Harris hematoxylin-eosin stain. A. Resting ovary from *S. nana* showing preponderance of developing (D) oocytes. ×165. B. Intermediate stage ovary from *S. nana*. Note presence of developing (D) oocytes among more advanced oocytes with yolk granules (YG) present. ×52. C. Gravid ovary from *S. sculpta* showing compacted yolk filled oocytes. ×52. D. Spent condition of *S. nana* showing atretic (AT) oocyte surrounded by developing (D) oocytes. ×52.

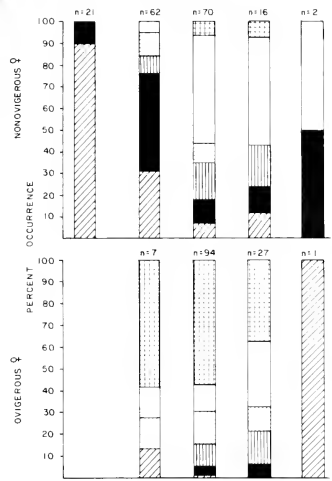


FIGURE 5.—Percent occurrence of ovigerous and nonovigerous *Stereomastis nana* in ovarian development stages for five length intervals.

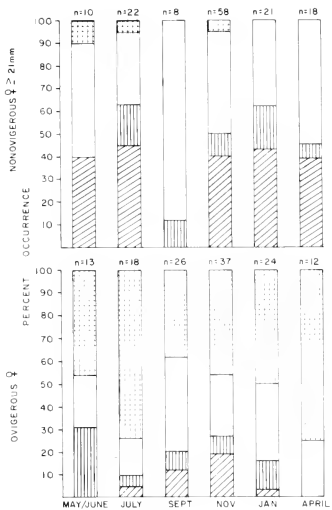


FIGURE 6.—Percent occurrence of ovigerous and nonovigerous *Stereomastis nana* in designated ovarian development stages by month of collection.

All individuals were sexually mature with spermatophores present within the vas deferens, and there were also some males at each season with spermatophores protruding from the gonopores (Table 6).

Analysis of stomachs from 438 *S. nana* showed 89% of them were empty. Among the remainder, 3% contained sediment with some Foraminifera, 2% contained either polychaete fragments or crustacean body parts, and 3% had unrecognizable paste. Single occurrences of fish scales (1%), shell fragments (1%), and one entire fish (Myctophidae?) (1%) were also noted.

Stereomastis sculpta (Smith)

Stereomastis sculpta has a wide geographic distribution, captures having been reported from the Atlantic and Indian Oceans, the Arabian, Mediterranean, and Caribbean Seas, and the Gulf of Mexico. It has been reported off the east coast of North America from lat. 35°49'-43°10' N at depths of 460-1,568 m. It has not been reported from the Pacific Ocean, where it is replaced by the subspecies *S. sculpta pacifica* (Firth and Pequegnat see footnote 4). Roberts (1977) found *S. sculpta* to

be the most abundant polychelid collected by benthic skimmer in the Gulf of Mexico, and Firth and Pequegnat confirmed it as the most commonly caught polychelid both in that region and in the Caribbean Sea. Although Firth and Pequegnat stated that *S. sculpta* is one of the most commonly reported species in the Polychelidae and probably one of the most important polychelid species numerically on the continental slope, it was much less abundant than *S. nana* in my Middle Atlantic Bight collections (Figure 1). Abundance data based on 13.7 m otter trawl catches showed *S. sculpta* constituted 6.5% of the total benthic decapod catch. Its importance diminishes at lesser and greater depths within its bathymetric range of 486 (5.7 C) to 2,257 m (2.9 C). Analysis of variance showed no significant difference in abundance by depth intervals for 115 *S. sculpta* (Table 1).

The overall ♀:♂ ratio (1:1.1) and sex ratios for depths of capture did not differ significantly from 1:1 (Tables 2, 3). There was also no apparent relationship between average size of *S. sculpta* and depth of capture ($F = 2.321$, df = 2,122, $P = 0.05$).

Ovigerous females (mean = 54 mm) were significantly larger (Table 4) than males (mean = 32 mm) and other females (mean = 35 mm), based on analysis of variance and Scheffé's multiple mean comparison.

Spermatophores occurred only on females 45 mm and larger and were found protruding from the gonopores of males 32 mm and larger. Ovigerous females were 45 mm and larger, and all had attached spermatophores (Figure 7). Ovigerous females and most males and females with externally located spermatophores were found at the shoaler depths sampled; none were obtained below 1,199 m.

Ovarian development stages of *S. sculpta* were similar to those described for *S. nana*. Immature gonads were found in all nonovigerous females ($n = 36$) 36 mm and larger. Ripening and gravid individuals occurred only at sizes 38 mm and larger. Seven ovigerous females were spent, and one 54 mm individual was ripening.

Since ovigerous females were obtained each month, except July (Table 6), I conclude there was no clearly defined spawning season. Nonovigerous females with spermatophores attached occurred at all months. There was no relation between ovarian stage and month of capture.

Fecundity of four *S. sculpta* varied from 10,093 to 19,080 with a mean of 15,541. Eggs had a mean diameter of 0.6 mm.

All males were found to have spermatophores in the vas deferens. Males with external spermatophores were present during all months except January and July (Table 6).

Sixty-eight percent of 114 *S. sculpta* stomachs were empty. Stomachs of other individuals contained sediment with Foraminifera (13%), fish body parts (5%), polychaete parts (3%), crustacean parts (5%), and unidentifiable gurry (6%).

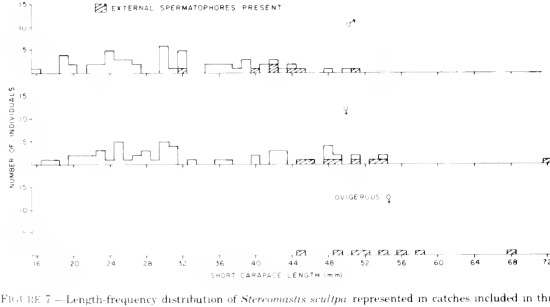


FIGURE 7.—Length-frequency distribution of *Stereomastis sculpta* represented in catches included in this study

Other Polychelid Species

Polycheles validus (A. Milne-Edwards) is found in the eastern and western Atlantic, the Mediterranean and Caribbean Seas, and the Gulf of Mexico. Its distribution in the western North Atlantic extends northward to lat. 42° N at 2,211-2,393 m (Firth and Pequegnat see footnote 4). My Middle Atlantic Bight collections recovered 10 *P. validus* at depths between 1,698 and 2,337 m and temperatures of 3.8°-2.9° C. Males ranged from 21 to 48 mm with spermatophores present in gonopores of two individuals, 32 and 44 mm SCL. Two females were collected, 21 and 28 mm SCL, and both were immature. Small catches of *P. validus* are best attributed to its deep-living existence, having never been reported shallower than 1,280 m.

Polycheles granulatus (Faxon) has been reported from the Atlantic, Pacific, and Indian Oceans at depths of 347-2,505 m (Firth and Pequegnat see footnote 4). Captures of this species were reported at 349-799 m in the western North Atlantic by Squires.[6] I collected 11 individuals from the Middle Atlantic Bight at depths between 932 (4.4° C) and 2,068 m (3.4° C). Nine males, none with external spermatophores, were 16-22 mm SCL. Two immature females 18-28 mm were also captured. The presence of ovigerous female *P. granulatus* off the Nova Scotian Shelf at 350-440 m (Squires see footnote 6) and the fact that this species has not been reported from the Gulf of Mexico or the Carribbean Sea (Firth and Pequegnat see footnote 4) is evidence that reproducing populations of this species occur in the northerly reaches of the western Atlantic.

DISCUSSION

Although *Stereomastis nana* and *S. sculpta* were both represented in catches from the Middle Atlantic Bight, it is evident that relative abundance and bathymetric distribution of the two species are markedly different. *Stereomastis nana* was the most abundant species collected, total catches being almost four times greater than those of *S. sculpta*. Haedrich et al. (1975) collected only *S. nana* during trawling with a 4.9 m (16-ft) net on the continental slope south of New England. From further trawls in this location, they obtained 92 *S. nana* at 24 stations between 828 and 3,642 m, and only 2 *S. sculpta* at 2 stations between 1,328 and 1,938 m (Haedrich et al.[7]). Farther north, Squires (see footnote 6) collected 15 *S. sculpta* off the slope of the Grand Banks at depths of 420-810 m (4.1°-4.5° C). The lack of *S. nana* in his samples probably resulted from confinement of trawls to depths shallower than 800 m. *Stereomastis sculpta* is the most commonly caught polychelid in the Gulf of Mexico (Firth and Pequegnat see footnote 4). Roberts (1977) reported density estimates of 394 individuals/ha (565-918 m), 343 individuals/ha (1,061-1,829 m), and 88 individuals/ha (2,744-3,256 m) for the northeastern Gulf of Mexico. It appears, therefore, that *S. nana* is more abundant in the Middle Atlantic Bight while *S. sculpta* is more plentiful in southern latitudes.

Bathymetric distributions of the two species also differ, with *S. nana* found deeper on the continental slope than *S. sculpta*. Separate bathymetric distributions of these species as proposed by Barnard (1950) formed the basis for rejection of Smith's (1884) hypothesis that *S. nana* was a dwarf deep-sea form of *S. sculpta*.

Stereomastis nana and *S. sculpta* appear to spawn year round, producing large numbers of small eggs. There is no indication that increased numbers of ovigerous females occur at certain months, as suggested by Santucci (1933) and Squires (see footnote 6). Santucci (1933) found the greatest number of ovigerous female *Polycheles typhlops* were taken between April and July, while most *S. sculpta* were ovigerous in May, October, and November (Squires see footnote 6). Squires (see footnote 6) concluded from a study of 15 individuals that annual breeding occurs in *S. sculpta*. Collections of *S. nana* from my study indicate spawning occurs year round. Reproduction in *S. sculpta* appears also to be year round, but the small sample size limits interpretation of reproduction in this species.

There is also no evidence to indicate that the reproductively mature females perform upslope migrations similar to those Santucci (1933) and Bernard (1953) suggested for *P. typhlops*. These investigators found that ovigerous females and other females with well-developed ovaries ascend to shallower depths where their eggs are released.

[6]Squires, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern Arctic. Fish. Res. Board Can. Manuscr. Rep. Ser. 810, 212 p.

[7]R. L. Haedrich, G. T. Rowe, and P. T. Polloni, Biological Oceangraphers, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. October 1977.

Firth and Pequegnat (see footnote 4) suggested a similar pattern for *P. crucifer* and *S. sculpta* but cautioned that other polychelid species may not perform migrations to shallow waters. There was no evidence to support this hypothesis among *S. nana* or *S. sculpta* since ovigerous and reproductively mature females occurred within depths of maximum abundance for the species. Lack of support for the hypothesis is also indicated by failure to find any correlation between size of individuals and their depth range. If such migrations occur, larger individuals, such as ovigerous and sexually mature females, would have been found at shallower depths.

Size at sexual maturity for *Stereomastis* spp. examined in my study agrees with Firth and Pequegnat's (see footnote 4) observations. However, they found *S. sculpta* as small as 18 mm with spermatophores protruding from the genital pores. In the present study, the smallest male in this condition was 32 mm.

Feeding habits among the Polychelidae are also not resolved. Firth and Pequegnat (see footnote 4) indicated the polychelids are detritus scavengers but Lagardere (1976) found *P. typhlops* exists by almost exclusive predation on mobile crustacean prey, such as mysids, euphausiids, and pelagic amphipods. He did note, however, presence of benthic polychaetes (Aphroditidae) in several stomachs. Stomach content analysis from the present study is most inconclusive since sediment, detritus, polychaetes, and fish body parts were found. Since polychelids have seldom been seen in bottom photographs and are thought to bury in sediment (Firth and Pequegnat see footnote 4), it appears that a scavenging mode of existence along the bottom is likely for *S. nana* and *S. sculpta*.

ACKNOWLEDGMENTS

I would like to thank J. Musick for providing ship time through National Science Foundation (NSF) Grants GS-37561 and GS-27725. Special thanks go to F. Perkins and P. Berry for providing histological sections. Information on catches of *Stereomastis* from the slope off New England were provided by R. Haedrich, G. Rowe, and P. Polloni (Woods Hole Oceanographic Institution) under NSF Grant OCE-74-22339.

This research was completed while the author was recipient of an NSF award (OCE-77-05698) for support of doctoral dissertation research in biological oceanography.

LITERATURE CITED

ALLEN, J. A.
1966. The dynamics and interrelationships of mixed populations of Caridea found off the north-east coast of England. In H. Barnes (editor), Some contemporary studies in marine science, p. 45-66. Hafner Publ. Co., N.Y.

ANDREWS, E. A.
1911. Sperm transfer in certain decapods. Proc. U.S. Natl. Mus. 39:419-434.

BARNARD, K. H.
1950. Descriptive catalogue of South African decapod Crustacea. Ann. S. Afr. Mus. 38:1-837.

BATE, C. S.
1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873-76. Rep. Sci. Res. Voyage H.M.S. Challenger, 1873-76, Zool. 24, 942 p.

BERNARD, F.
1953. Decapoda Eryonidae (*Eryonicus* et *Willemoesia*). Dana Rep. Carlsberg Found. 37, 93 p.

GLAESSNER, M. F.
1969. Decapoda. In R.C. Moore (editor), Treatise on invertebrate paleontology, Part R, Arthropoda 4, Vol. 2, p. 399-533. Geol. Soc. Am., Inc., and Univ. Kans.

HAEDRICH, R. L., G. T. ROWE, AND P. T. POLLONI.
1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.

HANSEN, H. J.
1908. Crustacea Malacostraca. I. Dan. Ingolf-Exped. 3(2), 120 p.

HUMASON, G. L.
1972. Animal tissue techniques. 3d ed. W. H. Freeman and Co., San Franc., Calif., 641 p.

LAGARDERE, J. P.
1976. Recherches sur la distribution verticale et sur l'alimentation des crustacés décapodes de la pente continentale de l'Atlantique nord-oriental. These, l'Université d'Aix-Marseille, France, 188 p.

MEREDITH, S. S.
1952. A study of *Crangon crangon* L. in the Liverpool Bay area. Proc. Trans. Liverp. Biol. Soc. 58:75-109.

ROBERTS, T. W.
1977. An analysis of deep-sea benthic communities in the northeast Gulf of Mexico. Ph.D. Thesis, Texas A&M Univ. College Station, 270 p.

SANTUCCI, R.
1933. Biologia del fondo a "Scampi" nel mare Ligure. I. *Polycheles typhlops*. Heller R. Comit. Talassograf. Ital. Mem. 199, 48 p.

SMITH, S. I.
1884. XV. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States in 1883. U.S. Comm. Fish. Fish. Rep. Comm. for 1882 10:345-426.
1887. XXI. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States during the summer and autumn of 1884. U.S. Comm. Fish. Fish. Rep. Comm. for 1885 13:605-705.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

WOOLF, C. M.
1968. Principles of biometry. D. Van Nostrand Co., Inc., Princeton, N.J., 359 p.

REPRODUCTION IN THE BLUE SHARK, *PRIONACE GLAUCA*

HAROLD L. PRATT, JR.[1]

ABSTRACT

In the male blue shark, *Prionace glauca*, paired testes produce spermatozoa year round which are stored first in the epididymides, then as spermatophores in the lower ductus deferentia. Spermatozoa are transferred to the female through paired claspers employed singly. Spermatozoa are injected into the upper vagina and pass through the uterus and isthmus into the shell (oviducal) gland, where they are stored until the female is ready for fertilization. Male blue sharks reach maturity at 183 cm fork length when 50% possess spermatophores. Females pass through a subadult phase (145-185 cm), when the organs for copulation and sperm storage are developed but the ova are undeveloped. During this phase females receive numerous toothcuts in their thickened dermis as a prelude to mating and frequently copulate

I examined reproductive organs from 160 subadult female blue sharks, caught in shelf waters off southern New England during summer months, by histological sectioning to determine if spermatozoa were present. Of these females, 79 had spermatozoa in the oviducal gland, establishing successful copulation. Inseminated females then emigrate offshore where fertilization occurs the following spring during ovulation. Blue sharks are viviparous and bear young after 9 to 12 months gestation. Thirty-eight new or unpublished accounts of gravid females are investigated, as well as one 192 cm hermaphroditic blue shark.

In shelf waters during the summer the sex ratio for subadults is nearly equal while males dominate the adult sizes due to the emigration of inseminated females.

The blue shark, *Prionace glauca*, is the most abundant of the larger oceanic sharks in the Atlantic (Bigelow and Schroeder 1948). It is frequently among the incidental catch of tuna and swordfish longliners in temperate, subtemperate, and tropical parts of the world ocean. Nichols and Murphy (1916) reported seeing "hundreds, even thousands" of them swimming free and attracted by the activity of the sperm whale fishery in the tropical Atlantic. Longline fishing operations conducted by National Marine Fisheries Service biologists in the offshore areas between Cape Cod, Mass., and Cape Hatteras, N.C., reveal the blue shark to be more numerous in this area than any other large shark or big game fish (Casey and Hoenig[2]).

Like other elasmobranchs, blue sharks have a complex reproductive cycle which contributes to their success as a species. Suda (1953), Strasburg (1958), Aasen (1966), and Stevens (1974) have all contributed information about blue shark reproduction, but many of the details concerning anatomy, maturity, and the sexual cycle were incomplete. New information is presented on the mechanism of spermatozoa storage in the male and female blue sharks and adaptations for mating in the female.

In this study, the reproductive systems of western North Atlantic blue sharks have been investigated to better understand the life history of this important apex predator.

MATERIALS AND METHODS

Blue sharks sampled from October 1969 to April 1977 came from two sources: 1) longline catches made by research and commercial vessels and 2) anglers' catches landed during shark fishing tournaments. The area sampled extended from Cape Hatteras to east of Georges Bank, both on the continental shelf and in the Gulf Stream. Three fish were also collected north of St. Thomas, V.I.

Throughout this paper I use fork length (FL), a straight line measurement from the tip of the snout to the fork of the tail. Measurements involving the upper caudal (such as total length, TL) are variable due to its flexibility. Fork length is an easier and more accurate measurement for one person to make at sea. Many authors cited use

[1]Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882.

[2]Casey, J. G., and J. M. Hoenig. 1977. Apex predators in deepwater dumpsite 106. *In* Baseline report of environmental conditions in deepwater dumpsite 106. NOAA Dumpsite Evaluation Report 77-1, p. 309-376.

Manuscript accepted November 1978
FISHERY BULLETIN VOL. 77, NO. 2, 1979

total length, defined by Bigelow and Schroeder (1948) as a caliper measurement along the body axis from the snout to a perpendicular extended from the upper caudal. I have converted all references to blue shark total lengths in the literature to fork lengths in centimeters using a regression[3] derived from a sample of 554 males and females between 93 and 282 cm FL ($r = 0.995$).

Clasper length (posterior free tip to the free trailing edge of the pelvic fin lateral to each clasper) and internal organs were measured with calipers to the nearest millimeter.

Sharks were dissected as soon as possible after being caught. Several adults were frozen whole and dissected in detail at the laboratory. Specimens for analysis and anatomical description ranged in size from 1.1 to 264 cm and included 210 females and 114 males.

A single ventral incision from cloaca to pectoral girdle permits access to the body cavity. The size and condition of internal organs of both sexes were noted. To determine maturity and insemination, both oviducal glands were excised carefully, without squeezing, with several centimeters of adjacent oviduct. Oviducal glands and other histological samples were preserved in Bouin's fixative because it is compatible with the primary stain (Mallory's Triple Stain). Larger organs were preserved in 10% Formalin.[4] Tissues were prepared by the paraffin method and sectioned to 10-15 μm. In the latter part of the study a smear technique was developed to quickly determine insemination. This new technique, which obviates the need for histological sectioning, is discussed in a later section.

RESULTS AND DISCUSSION

Male Anatomy

Testes and Epigonal Organ

The male blue shark has two equally developed testes each embedded in the anterior portion of a long irregular epigonal organ which has no known reproductive function other than to support the testes (Figures 1, 2). Dissected from the epigonal organ, the testis is cylindrical with rounded ends. It is packed with tiny spheres averaging 0.3 mm in

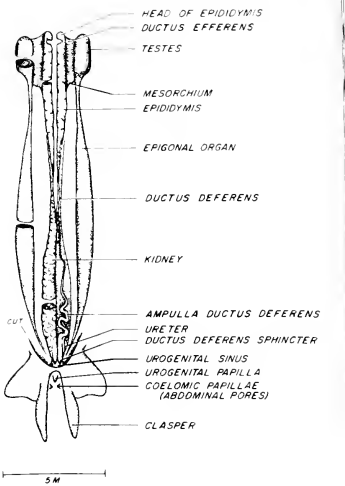


FIGURE 1.—Male reproductive system in the adult blue shark, general ventral view.

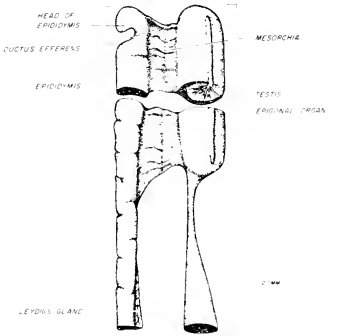


FIGURE 2.—Testes, epididymis, and epigonal organ of the adult male blue shark

[3]Computed regression FL = 1.73872 + 0.82995 TL.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

diameter, the seminiferous ampullae (Figure 3). The only other macroscopic structures are supportive partitions of connective tissue radiating internally from a band on the mediolateral surface of the testes. A double mesorchia suspends the testes from the midline of the dorsal body wall. The ductus efferens is a series of fine tubules which crosses the mesorchium at its anterior edge and communicates with the head of the epididymis.

Epididymis

Above the testes on the dorsal abdominal wall lie the paired epididymides. They are attached on either side of the dorsal aorta in the hollow of the ventrolateral processes of the vertebral column. In the adult blue shark the epididymis is approximately 3 cm wide, 30 cm long, and 0.5 cm thick. In sharks captured from March to November it is turgid with spermatozoa in a matrix of supportive tissue secreted by accessory glands on the dorsal surface. The epididymis originates just forward of and adjacent to the testes as a firm subspherical "head" which narrows to a short "neck" and then expands to form a long straplike organ (Figure 2). The tubules of this organ describe a path of convolutions so complex that its surface appears cerebriform. Tubule diameters range from 1.5 to 1.75 mm adjacent to the testes, expanding to >2 mm at the junction of the ductus deferens. Here it enters Leydig's gland, the modified anterior section of the mesonephric kidney. At this level the function of the ductus changes from spermatozoa storage to spermatophore formation and storage.

Ductus Deferens

The ductus deferens (Figure 4) is the storage organ for male seminal products. The ductus gradually increases in diameter as it penetrates the kidney, finally enlarging in strong convolutions to form the ampulla ductus deferens which is 10-15 mm in diameter in the adult blue shark. The ampullae are lined with partitions or septa similar to those noted by Matthews (1950) in the basking shark, *Cetorhinus maximus*. The thin-walled ureter becomes entwined with the ductus deferens in the last 20 cm of its length and roughly parallels its sinuous course. The ureter and ductus deferens terminate in a common double papilla which projects into the anterior wall of the urogenital sinus. The ductus occupies the central orifice of the papilla and is closed by a sphincter muscle. The ureter has a crescent-shaped sphincterless duct on the dorsal edge of the cone of the papilla. The urogenital sinus vents into the common cloaca by means of a single large (2 cm) papilla that projects from the dorsal body wall.

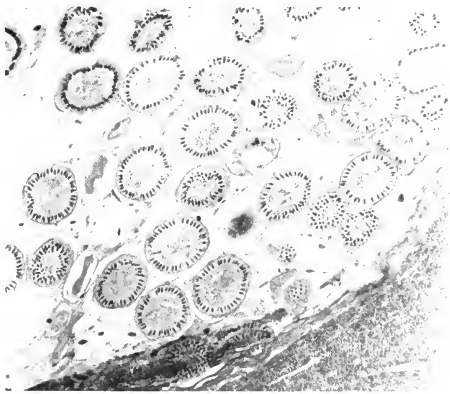


FIGURE 3.—Seminiferous ampullae of mature testes in the blue shark (× 160). Spermatozoa arranged radially inside spheres (seen in cross section).

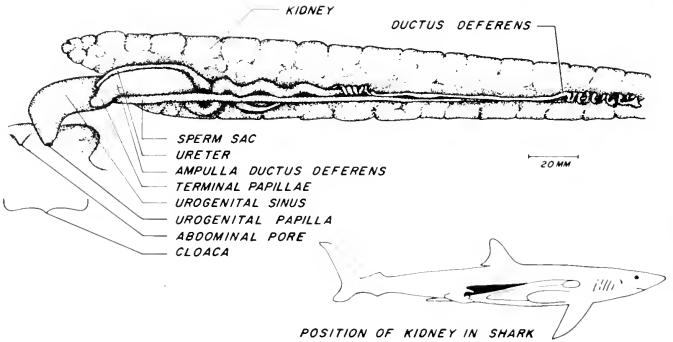


FIGURE 4.—Male urogenital complex in the blue shark

Sperm Sac

The sperm sac (Figure 4) is not well developed in the blue shark. This paired organ communicates with the anterior end of the urogenital sinus through an opening between the paired terminal papillae of the ductus deferens. The diameter in a mature 200 cm male was 16 mm at the sinus. The sperm sacs lie along the dorsal midline of the body cavity and extend anteriorly into the kidney approximately 15 cm, where the tubes taper down to threads and end blindly.

Siphon Sacs and Clasper

In the adult blue shark the paired claspers are heavily calcified scroll-shaped appendages which transfer sperm from the lower ductus through the urogenital papilla to the vagina of the female during copulation. Propulsive force is provided by a water piston driven by the muscular subdermal siphon sac associated with each clasper. An accurate description of clasper morphology and function is given by Leigh-Sharpe (1920). The clasper is similar in form to that of the basking shark, which has been described in detail by Matthews (1950) and to the tope, *Galeorhinus galeus* (Leigh-Sharpe 1921). The blue shark lacks a distinct spur or clasper hook and uses instead the sharpened edges of the terminal parts, which are splayed open after insertion to secure the clasper in the

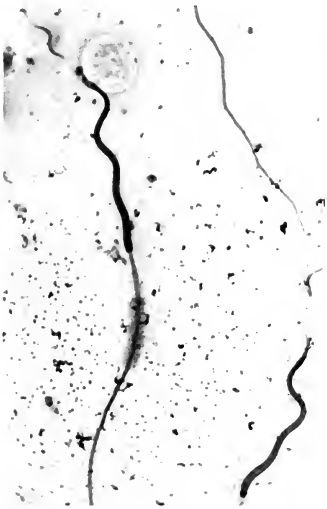


FIGURE 5.—Spermatozoa of the blue shark (×1,600).

vagina during copulation. The siphon sacs originate on the surface of the pelvic fin at the proximal end of the clasper and extend anteriorly under the dermis to end blindly just short of the pectoral girdle. They are approximately 25 mm in diameter and 60 cm long.

Spermatozoa

Sperm cells (Figure 5) develop in expendable spheres of germinal tissue, the seminiferous ampullae described by Romer (1962). They form radially, then clump together in groups of 60-70 (Figure 6). When the sperm mature the ampullae disintegrate, liberating individual spermatozoa into the interstitial spaces of the testis. They pass through the ductus efferens (Figure 2) and into the epididymis. Secretions from the accessory glands flow into the epididymis and form a matrix which supports the individual spermatozoa. Spermatozoa are stored in the epididymis which usually appears swollen in adult males. This is the most convenient location to obtain a sperm smear. In the lower epididymis the spermatozoa again aggregate, with heads aligned parallel until groups of 60-70 are formed in the anterior section of the ductus deferens. Hundreds of these packets then aggregate into spermatophores (Figure 7), which are stored in the expanded terminal ampulla of the ductus deferens.

Spermatophores

In mature males the entire lumen of the lower ductus deferens is usually turgid with seminal products. Most noticeable macroscopically are snow-white clumps of a gelatinous substance 3-4 mm in diameter and containing no spermatozoa. This evidently is a supportive and possibly nutritive material for the smaller spermatophores. The blue shark spermatophore (Figure 7) is an ivory white ovoid, 0.5-2.0 mm across its largest diameter. When the ampulla is cut at midkidney, spermatophores flow freely and copiously from the incision and are interspersed with the white gelatinous clumps. Several hundred milliliters may be expressed from the two ductus deferens of an adult male.

Matthews (1950) gave a good account of the structures and functions involved in spermato-

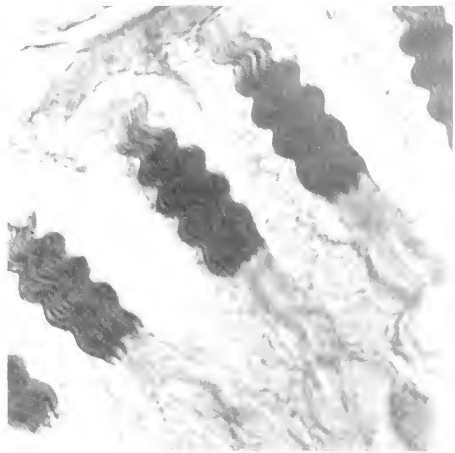


FIGURE 6.—Spermatozoa in seminiferous ampullae of the blue shark (×1,600).

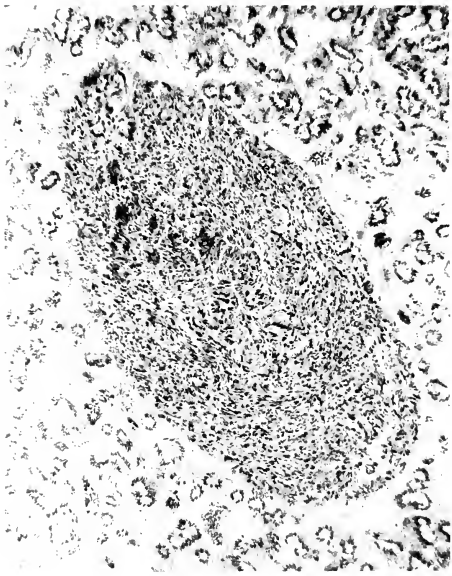


FIGURE 7.—Spermatophore of the blue shark (×100).

phore formation in the basking shark. He speculated that spermatophores preserve the sperm from loss in leakage to the surrounding water during copulation. Blue shark spermatophores break down in seawater, liberating individual spermatozoa, so rapid transfer is necessary. The spermatophore may simply be an efficient way to store spermatozoa in the male's ductus deferens.

Indicators of Sexual Maturity in Males

The simplest technique to determine maturity is to compare external secondary sexually dimorphic characteristics that occur in large animals with those same characters as they appear in less developed members of the species. In male elasmobranchs changes in relative size, hardness, and development of the claspers is the most frequently employed method for determining sexual maturity. Clark and von Schmidt (1965) considered a male mature when: 1) the distal end of the clasper and rhipidion are fully formed and can be spread open on a fresh specimen, 2) the clasper proximal to the head is rigid due to calcification of the supporting cartilage, 3) the base of the clasper rotates easily and the clasper can be directed anteriorly, and 4) the siphon sacs are fully elongated. Aasen (1966, footnote 5) used clasper length exclusively as a maturity index in his work on blue and porbeagle sharks. Springer (1960) noted that the claspers of the sandbar shark become hardened or calcified at about the same time that the testes enlarge.

[5]Aasen, O. 1961. Some observations on the biology of the porbeagle shark *Lamna nasus*, Bonnaterre. Int. Counc. Explor. Sea, C.M. 1961, 109:1-7.

Blue shark claspers exhibit these characteristics (Figure 8) in a gradual transition with body growth rather than the abruptness noted by Clark and von Schmidt (1965) for the carcharhinids. It is therefore difficult to distinguish maturity in subadult blue sharks based on external organs.

Another valid index of sexual maturity is the presence or absence of sex products such as eggs and sperm. Several authors have used the presence of male sexual products as indicators of maturity. Kauffman (1950) working on the tiger shark observed "... the release of milt from the gonoduct when pressure was applied." Matthews (1950) stated that a basking shark of 622 cm "... was just approaching sexual maturity, for though the testis was showing incipient activity, the ampullae of the ductus deferentia were rather small, completely empty of spermatophores and showing no signs of having contained any." Olsen (1954) recognized that maturity took place over a fairly extensive size range. He noted that in the school shark, *Galeorhinus australis*, seminal fluid flows freely from the cut surface of the enlarged testes and the seminal vesicles contain active spermatozoa in early summer. In borderline cases Olsen histologically sectioned the testis. He considered those fish to be mature that had "... enlarged seminiferous tubules [sic] which carried bundles of ripe spermatozoa ...." Bonham et al. (1949) and Templeman (1944) working on the spiny dogfish, *Squalus acanthias*, combined clasper length with the presence of spermatozoa in the seminal vesicles to determine maturity.

In the blue shark, two organs which enlarge as the male matures are the testes and the epididymides. Unfortunately, testes length (Figure 9) and epididymis width (Figure 10) follow the same gradual size increase as the claspers (Figure 8). Because they do not exhibit major inflections, these relationships are of little use for determining the onset of sexual maturity.

The most reliable method that I have found for determining maturity in the difficult subadult to adult sizes is to assess the ability of a shark to produce spermatophores. Many sharks with claspers that appear mature lack spermatophores and have small ductus deferentia. The spermatophore is the last tissue to mature and it develops abruptly in blue sharks.

Of 193 male blue sharks examined, 74 (38.3%) contained some quantity of spermatophores. The sharp increase in spermatophore occurrence between 175 and 205 cm body length is the transition

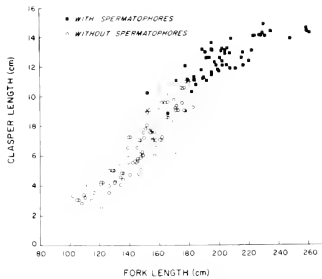


FIGURE 8.—Clasper-body length relationship compared with spermatophore development in the blue shark.

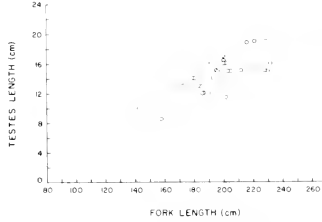


FIGURE 9.—Testes length-body length relationship in the blue shark.

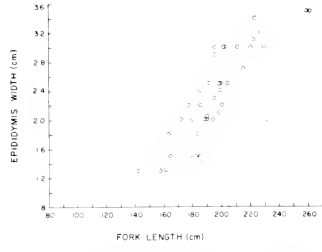


FIGURE 10.—Epididymis width-body length relationship in the blue shark.

zone between immaturity and maturity (Figure 11).

By this definition, the smallest mature blue shark (with spermatophores) in my sample was 153 cm and at 183 cm, 50% were mature. Judging from the radii of male tooth cuts on females (discussed below) and the condition of the clasper, 183 cm is the average size at which male sexual maturity is attained. Ninety-five percent of the males 205 cm and 100% 235 cm were mature.

These data agree well with Aasen's (1966) length at sexual maturity for the male blue shark. He cited 196.6 cm as the point of maturity as determined by an analysis of clasper length and my observations show 80% of the males contain spermatophores at this size. Stevens' (1974) sample contained only one mature male blue shark. He drew no conclusions regarding male maturity. Stevens speculated that all of his blue sharks were either immature or in a resting stage, except the largest one which was in poor condition. By my criteria, all of his sharks were immature except this individual. Bigelow and Schroeder (1948) suggested that both sexes mature in the range of 177-203 cm which agrees well with my finding of 183 cm.

A field test for the presence of spermatophores is accomplished by making a cross-sectional cut through the kidney at its thickest part. Four large (10-15 mm) ducts are visible ventral to the kidney at this level. Two of these are the thin-walled ureters, usually filled with a clear fluid. The thicker walled pair are the ampullae ductus deferens containing several hundred cubic centimeters of spermatophores, 0.5-2.0 mm in diameter, and their associated white flocculent supportive tissue. The presence or absence of spermatophores provides a positive answer to the question of sexual maturity in an individual male blue shark.

I observed no obvious seasonal fluctuations of sperm production in the blue shark as have been noted by Olsen (1954) and other authors for different species of sharks.

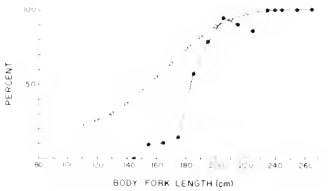


FIGURE 11.—Comparison of clasper length and spermatophore presence with body length. Circles are clasper growth as percent of largest clasper. Dots are percent of blue sharks with spermatophores. Dotted lines indicate coordinates for 50% maturity.

Female Anatomy

Ovary and Epigonal Organ

Only the right ovary of the blue shark is present and functional. It lies at the anterior end of the abdominal cavity adjacent to the liver and gall bladder (Figure 12). The ovary is a large organ (25 cm × 6 cm) adnate to the forward lateral surface of the right epigonal organ. It is roughly teardrop shaped, corresponding to the expansion of the epigonal organ as it reaches its forward terminus.

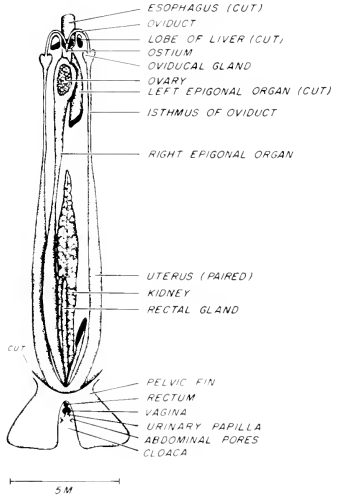


FIGURE 12.—Female reproductive system in the blue shark, general ventral view.

The ovary is composed of hundreds of follicles in a dense stroma of connective tissue. In the blue shark, follicles are contained in a single layer of generative tissue which blankets the ova as they develop.

The ovary of a full-term 243 cm gravid female, with 60 embryos "in utero," contained over 1,000 follicles (Figure 13). Although the average number of embryos seldom exceeds 54 (Bigelow and Schroeder 1948), this ovary contained 123 ripe eggs from 6 to 20 mm in diameter. Also present was a similar number of corpora lutea of various sizes, ranging from 1.2 to 7.5 mm in diameter, presumably from the generation then contained in the uterus. So-called corpora lutea are also found in the developing ovaries of immature blue sharks. It is likely that the 123 large ova constitute the next generation of 50-60 embryos, and that the balance would be reabsorbed. This would explain the presence of 120 corpora lutea found in the ovary of this female which, as determined by her size, was at the end of her first pregnancy. The next generation is recruited from those follicles currently in the 0.3-3.5 mm size class. No follicles were present between 3.5 and 6.9 mm diameter.

The epigonal organ is a paired straplike organ that extends the length of the peritoneal cavity. The anterior end is suspended from the dorsal body wall just behind the heart cavity near the origin of the liver and extends caudally, supported by a thin mesentery, to the insertion of the rectal gland. The organ is 3 cm in diameter in the central body cavity and gradually expands and flattens to 10-15 cm wide and 2-3 cm thick at each end. Matthews (1950) speculated that this is the site of erythrocyte production in elasmobranchs. It serves no reproductive function other than supporting the ovary.

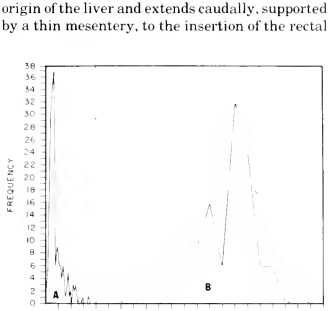


FIGURE 13.—Size-frequency population of ovarian follicles in a 243 cm gravid blue shark. A. 202 follicle subsample of an estimated 1,000 follicles in the ovary, grouped in 1.0 mm intervals. B. 124 maturing ova grouped in 10 mm intervals.

Ostium

The ostium is the anterior opening of the oviduct located at the forward end of the peritoneal cavity. It is a 10 mm long membranous funnel which bifurcates into the right and left oviducts. Lying between the ostium and the oviducal gland, the oviducts are firm white cylindrical tubes 10 mm in diameter. They traverse the curved mesentery that supports the liver to become attached to the dorsal peritoneal wall where the oviduct joins the oviducal gland.

Oviducal Gland and Isthmus

Approximately 80 cm from the ostium the oviduct expands to form the oviducal gland. It is heart-shaped, 3-4 cm in diameter, and 4-5 cm long. The oviducal glands of the adult female blue shark are small relative to other elasmobranchs. Externally, each is a symmetrical snow-white organ, with two short horns on the lateral anterior surfaces. The structure and function of this gland are discussed in a later section.

As it leaves the oviducal gland, the oviduct resumes its original diameter of 10 mm, but is now lined with longitudinal furrows and folds of tissue. This part of the oviduct is termed the isthmus (Figure 12) and runs for 15-20 cm from the oviducal gland to the uterus.

Uterus and Vagina

At the end of the isthmus the oviducts expand in diameter to 2 or 3 cm in nongravid adults and join the paired uteri (Figure 12). Each uterus is 50-60 cm long and supported by a mesometrium. In fish that have pupped recently the uterus is flaccid and much larger (5-15 cm diameter). Even at its smallest diameter the uterus of adult females is always thick-walled and oval in cross section. The uteri unite at their posterior end to form the common vagina. The length of the vagina is about 15 cm. Its distal end is demarcated by the hymen, a circular transverse fold. The hymen separates the vagina

from the cloaca. In young females 82-120 cm the vagina is sealed or nearly sealed by a thin circular membrane originating from the hymen.

Cloaca

The rectum opens into the cloaca ventrally and forward of the vagina. A single urinary papilla is located on the dorsal wall of the cloaca just posterior to the hymen. Paired abdominal pores are found on the dorsal wall of the cloaca (Figure 12).

Copulation

During copulation spermatophores pass from the male ductus deferens to the urogenital sinus and sperm sac. They exit from the sinus through the common urogenital papilla which is positioned over the apopyle of the clasper and partially fill the clasper groove. The paired muscular siphon sacs drive a water piston past the apopyle to force the spermatophores through the clasper and into the common vagina of the female through the uterus and into the oviducal gland. Many females have been observed to contain spermatozoa packed in the greatly distended tubules of the oviducal gland (Figures 14, 15). The motility of individual spermatozoa may play a part in entering the inner tubules of the oviducal gland.

From the presence of vaginal scars, Matthews (1950) determined that the basking shark employs one clasper at a time in copulation. Leigh-Sharpe (1920) killed two tope "in copula" and observed both claspers inserted. I have found unpaired vaginal scars in female blue sharks caused by the employment of a single clasper. Judging from the size of the organs involved, the use of both claspers simultaneously may be an option only for young male blue sharks.

Mating Injuries

Wounds resulting from mating in large sharks have been described by several authors. Springer (1960) noted bite marks between the first and second dorsal fins of the female sandbar shark, *Carcharhinus milberti*. He stated, "These are never present on males or immature females and are obviously produced during courtship." Suda (1953) was the first to record tooth cuts on blue sharks. In the Pacific, tooth cuts appear as early as March and are most numerous from June to August. Stevens (1974) conducted a study of tooth cuts on blue sharks in British waters. He divided wounds into three types, semicircular impressions, tooth slashes, and individual tooth nicks, and recorded their distribution on the female. He found tooth cuts only on female sharks >150 cm and suggests that this is the size at sexual maturity for the blue shark.

Northwest Atlantic blue sharks bear dermal wounds similar to those described as courtship scars by Stevens (1974). Distinct tooth cuts have been observed on females of 134 cm. (The smallest female carrying sperm is 136.5 cm.) Occasionally slashes and wounds resembling mating marks occur on females as small 118 cm. External tooth cuts are most extensive in female blue sharks from 145 to 200 cm long (Figure 16). Pregnant females generally bear only older healed scars. Males of all sizes are usually free of cuts. Wounds are so consistently present on females that the fish being tagged during longline or sportfishing operations may be sexed from the dorsal surface without examination of the pelvic appendages.

To accommodate the male's aggressive mating behavior, the skin over most of the body of the mature female is more than twice as thick as that of the male (Figure 17). The skin is thicker than the males' teeth are long and only occasionally do the wounds penetrate the dermis and involve the musculature. Tooth cuts are generally punctures or slashes made by the upper jaw only. Resistance to infection and healing rates are apparently high in the blue shark. Despite injuries that seem very serious, evidence of infection and necrotic tissue are notably absent.

Matthews (1950) noted internal lacerations on the thick vaginal pads of female basking sharks. They are caused by the male's clasper claw, a structure common to several families of elasmobranchs.

The blue shark clasper does not bear a claw. After insertion, the terminal end of the clasper is flexed about 45°, unfolding and expanding the sharp-edged rhipidion to form an anchor in the vagina. The female often bears hematose abrasions on the otherwise light colored walls of the vagina as a result of copulation. Specimens from the Middle Atlantic Bight possess vaginal wounds during all seasons examined (March-October). Fresh marks are more frequent in summer months while older dark purple scars are observed in spring and fall. Spermatozoa have been found in young females lacking vaginal wounds indicating

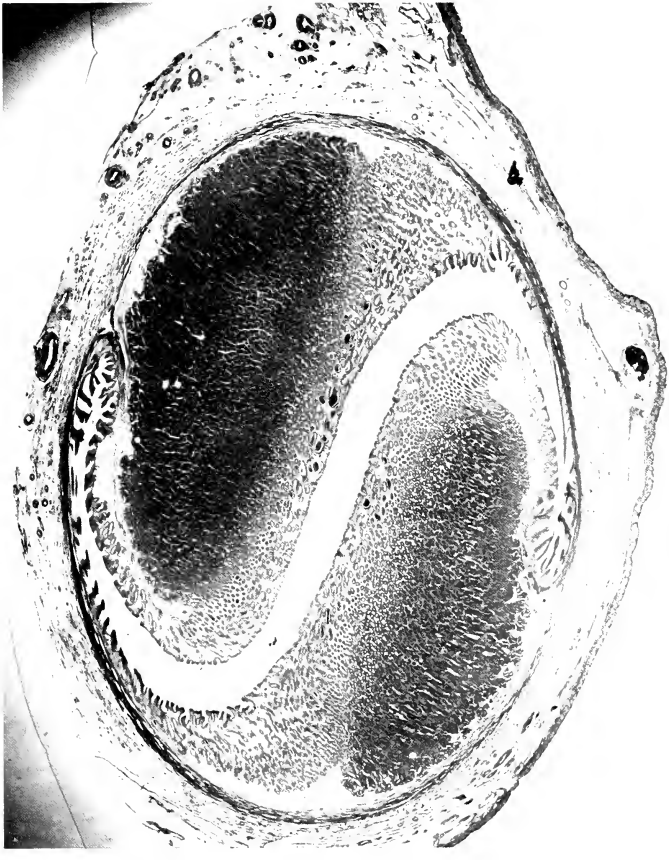


FIGURE 14.—Oviducal gland of female blue shark. Dark contents of central tubes are spermatozoan masses. Cross section (×8).

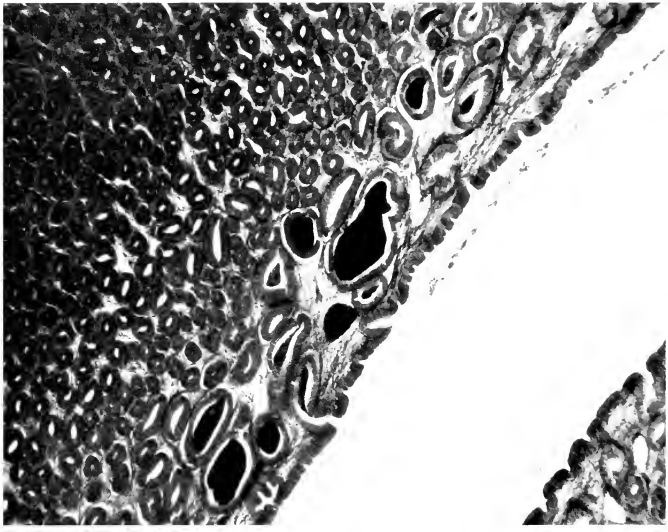


FIGURE 15.—Oviducal gland of female blue shark with spermatozoa clumped in tubules. Enlargement of Figure 14 Cross section (× 80)

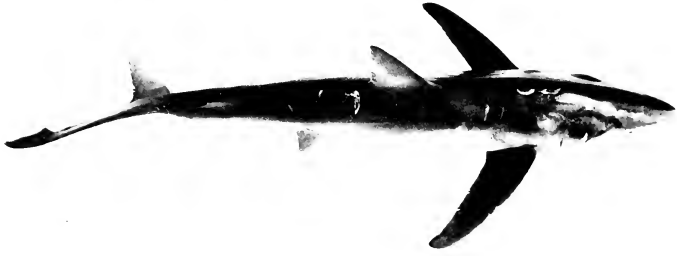


FIGURE 16.—Subadult female blue shark 185 cm FL with tooth cuts (mating scars).

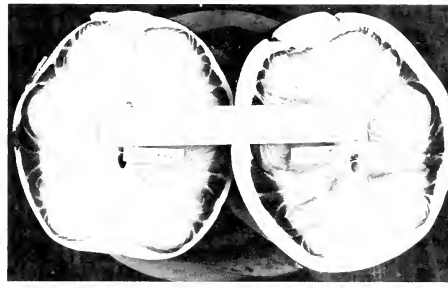


FIGURE 17.—Skin thickness comparison, cross sections of pelvic region of similar-sized male (left) and female (right) blue shark.

that insemination is not always accompanied by internal lesions.

Hermaphroditic Blue Sharks

Hermaphroditic blue sharks have not been mentioned in the literature and are apparently as rare as in other species of elasmobranchs. The only hermaphroditic blue shark I have examined was caught off central Long Island, 14 July 1973. It was 192 cm long and weighed 94 lb. There were many severe dermal lacerations (mating scars), some so recent as to be freshly clotted. There were two similar-sized claspers on the inner margin of the pelvic fins. They were much too short for the body length (17 mm from the margin of the fin to the free tip) and were not calcified. Internally, a small patch of ovary bearing four large (11 mm) ovarian follicles was found in the normal position on the epigonal organ. All of the reproductive organs were reduced; the upper oviduct diameter was 4 mm. Paired oviducal glands were present as 10 mm swellings in the oviducts. Caudally the 4 mm oviduct expanded to a 10 mm uterus. Two small testes were suspended in the usual position forward in the abdominal cavity. Histological sections revealed spermatozoa in the seminiferous ampullae of the testes. The epididymis and vas deferens were identifiable as undeveloped white tubes 1 mm in diameter. Judging from mating scars on the dorsal surface, this fish was treated by at least some of its conspecifics as a female. Although the ovary and testes were developed, the oviduct, ductus deferens, and claspers were too underdeveloped to permit this specimen to be functionally mature as either a male or female.

Indicators of Sexual Maturity in Females

Nearly every structure of the female reproductive tract has been used in the past to determine sexual maturity. Most authors rely on a combination of indicators that account for several stages in the reproductive cycle. Bonham et al. (1949) noted that the length of the ovary increased only slightly faster than did the body length of *Squalus acanthias*. Springer (1960) and Kauffman (1950) used the appearance of the elasmobranch ovary as an indicator of maturity. The development of the oviduct has been considered an index by Springer (1960) and Olsen (1954); the oviducal gland by Olsen (1954) and Nalini (1940); and the uterus by Olsen (1954), Templeman (1944), and Aasen (see footnote 5). In the carcharhinids studied by Clark and von Schmidt (1965), the development of the vaginal opening proved to be the most useful external indicator of maturity. In young carcharhinids the vaginal opening begins as a slit in the urinary papilla.

Defining sexual maturity in female blue sharks is difficult because they pass through a distinct subadult phase in which the organs necessary for copulation are developed and those required for generation are dormant or developing. The subadult stage lasts for two summer seasons and most female blue sharks on the continental shelf in the western North Atlantic are in this stage.

Examination of sex organs in female blue sharks of various sizes reveal that like the male claspers, growth is quite regular in the ovary and oviduct. The oviducal gland exhibits some differential growth after 100 cm body length is attained

(Figure 18), but growth is nearly constant through the subadult sizes. The vaginal opening is occluded by a partial membrane only in the juveniles, disappearing by 135 cm. The membrane may be lost with growth. The first attempt at copulation would remove it.

Sex Products

Another method for determining size at sexual maturity is to examine the sex products (follicles, ova, embryos) in relation to body length.

The presence of mature ova in the ovary is one of the most widely used indicators of elasmobranch sexual maturity. Metten (1941), Bonham et al. (1949), Kauffman (1950), Olsen (1954), and Springer (1960) have all partially utilized the condition of ovarian eggs for this purpose.

In the mature blue shark a generation of 100-130 large ova of fairly equal diameter (15-20 mm) visually dominate the hundreds of smaller follicles in the ovary.

In a 243 cm mature gravid female, the most distinctive ovarian features were 123 yolked ova from 6 to 20 mm in diameter. The larger ova were found at the anterior end of the ovary. A second group of nearly 1,000 follicles, from 0.1 to 1.0 mm in diameter, were found between and attached to the covering of the larger ova.

The diameter of the largest generation of ovarian eggs is a valid index of first maturity when compared with body length (Figure 19). First

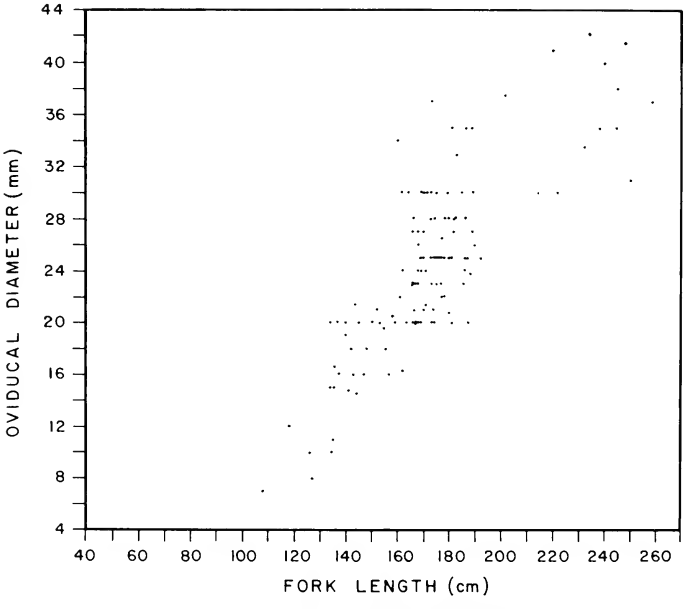


FIGURE 18.—Oviducal outside diameter-body fork length relationship in the blue shark

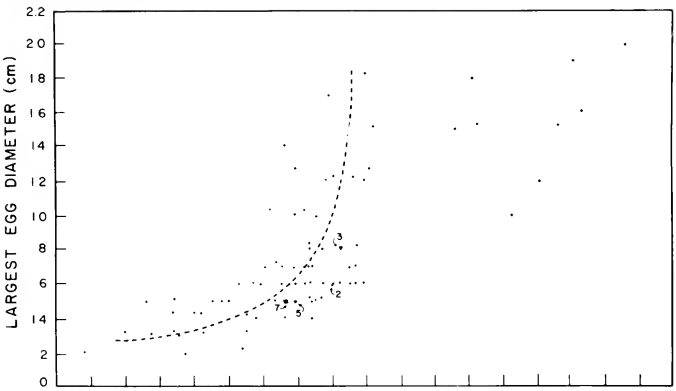


FIGURE 19.—Largest egg diameter-fork length relationship in the blue shark. Hand fit curve follows the first generation of eggs in the subadult population. Egg diameters accompanying lengths ≥200 cm are from mature or gravid females that have released or absorbed one or more generations of eggs and are producing subsequent generations.

maturity is reached at 180-190 cm body length by this criterion. Egg diameters accompanying body lengths ≥200 cm are from mature or gravid females that have released or absorbed one or more generations of eggs and are producing subsequent generations.

Gravid Females

The smallest recorded gravid females should be slightly longer, due to elapsed gestation time, than females carrying their first generation of ripe ovarian eggs (Figure 19). Gravid blue sharks with the smallest fork lengths reported in the literature from the Atlantic are as follows: 166 cm (Tucker and Newnham 1957), 193.3 cm (Aasen 1966), and 177-203 cm (Bigelow and Schroeder 1948); from the Pacific: 168 cm (Suda 1953) and 173.3 cm (Strasburg 1958).

Blue sharks carrying embryos are encountered infrequently in the world ocean. Suda (1953) examined 115 Pacific blue shark females bearing embryos and concluded that gestation lasts 9 mo and birth occurs between December and April. At this time the embryos have attained a maximum length of 39 cm. Strasburg (1958) examined 18 large females from the Pacific of which at least 10 were pregnant. The largest embryos were also 39 cm and occurred in March and May.

Francis Williams[6] caught eight pregnant female blue sharks while longlining in the eastern Pacific. His sample was unique because the size range of gravid females was small (153.3-171.6 cm). The embryos also were in a narrow size range (21.9-34.7 cm).

Gubanov and Grigor'yev (1975) reported small embryos (3.2-28 cm) from February to July in the equatorial Indian Ocean. They speculated that birth of young blue sharks occurs outside of this area.

[6]Williams, F. 1977. Notes on the biology and ecology of the blue shark (*Prionace glauca* L.) in the eastern Pacific Ocean and a review of data from the World Ocean (unpubl. manuscr.). Pers. commun. via John Casey, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, 1977.

There are few published accounts of gravid female blue sharks in the North Atlantic. Aasen (1966) examined 48 caught by longline primarily around the Canary Islands. He reported lengths of 11 individuals and embryo lengths from only 2 specimens with means of 28.1 and 40.0 cm. The largest embryo length he measured was 43.0 cm. From these lengths he concluded that birth occurred between February and April.

Beebe (1932) reported a gravid female taken off Nonsuch Island, Bermuda, in September of 1931. She carried 50 embryos averaging 8.3 cm long. Tucker and Newnham (1957) reported a small (166 cm) gravid female caught in the sport fishery off Looe, England. They summarized the eastern Atlantic and Mediterranean observations of gravid females with embryos.

From 1967 to 1975, I examined 19 gravid female blue sharks from the western Atlantic. These specimens include a blue shark taken in January approximately 300 mi northeast of the Windward Islands (lat. 21°20′ N, long. 58°52′ W); 2 caught in the Gulf Stream south of Sable Island in May; and 16 obtained from off the coast of Long Island, N.Y. These fish were caught within 50 mi of shore during June and July. The embryos from 13 fish were examined, the remainder having been lost or aborted during capture. In addition, Richard Backus[7] has supplied information on 19 gravid females.

Embryos

Growth of the placentally viviparous embryos appears to be linear, gestation taking 9-12 mo. Figure 20 combines all available North Atlantic and Mediterranean data for a summary of embryo length and season. The trend line seems to indicate a gestation of 12 mo, 3 mo longer than reported by Suda (1953). A 12-mo gestation also agrees with my proposed sexual cycle. However, since the left-hand data points are from offshore observations and the right-hand points are from inshore fish, it is quite possible that the offshore embryos may be born in March while embryos from inshore females could have been conceived in September and born in June, 9 mo later. These data cannot therefore resolve gestation time.

On 23 July 1978, a female blue shark in the first stages of pregnancy was examined at Montauk. It contained two embryos 11 and 13 mm long attached to 22 mm yolks with 38 less-developed eggs arranged in a dorsoventral series in both uteri.

[7]Original data from Richard H. Backus of Woods Hole Oceanographic Institute. Pers. commun. via John Casey

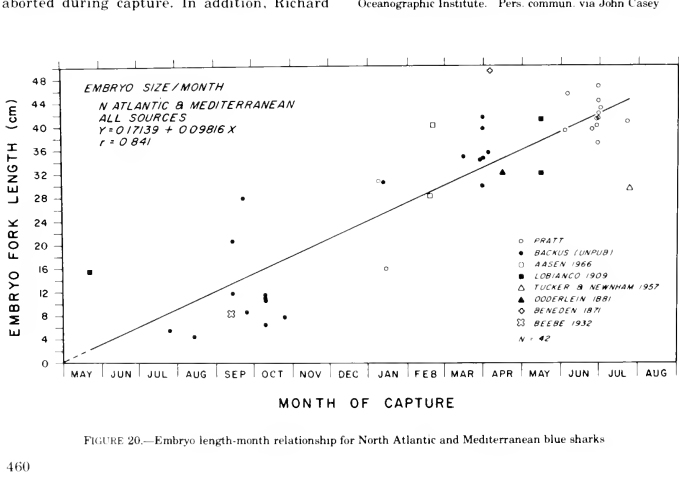


FIGURE 20.—Embryo length-month relationship for North Atlantic and Mediterranean blue sharks

The embryos taken during June and July were full term (mean lengths 37.1-46.6 cm). Some were larger than any reported in the literature (42-46.6 cm) except for one 49 cm embryo reported by Beneden (1871) and cited by Tucker and Newnham (1957).

The range of smaller embryo sizes reported by other authors as "full term" may result from examination of young "in utero" or aborted on deck. Judging from my January sample, after only 4-5 mo gestation embryo blue sharks have lost branchial gills and yolk sacs, and appear to be full-term replicas of the adults. When returned to the ocean they are active and quickly swim away. Premature embryos (up to 30 cm) have a proportionally thin body for the size of the head giving them a tadpolelike appearance. Full-term embryos (Figure 21) have a girth that equals or exceeds the head circumference. The pregnant female sampled in January carried 82 embryos averaging 13 cm long. Suda (1953) indicates this 264 cm female could be between 4 and 5 mo pregnant. Only the report of Gubanov and Grigor'yev (1975) of 135 young exceeds this observation. Minimum number of young could not be determined due to reports of premature parturition while the fish were being boated.

Gubanov and Grigor'yev (1975) agreed with a proposition of Lübbert and Ehrenbaum (1936) that embryo blue sharks develop and are born in stages. No evidence was found in the Atlantic to support this hypothesis. Embryos occurred in the same relative stage of development in each female. This is apparent in Figure 22. The 37 cm ($\bar{x}$) embryos ventral to the 232 cm pregnant female appear slightly smaller due to camera parallax. Nearly every litter contains one stunted or decomposing embryo. The explanation may be failure to attain placentation, dislodgement, or tangling of the umbilical cords. A stunted embryo is 10th from the left in the ventral row of embryos (Figure 22).

The smallest free-swimming young have been observed in the Pacific by Francis Williams (see footnote 6) at 35 cm and Strasburg (1958) at about 38 cm. The smallest Atlantic specimen is Bigleow and Schroeder's (1948) report of 44 cm. These lengths resemble lengths of the largest embryo sizes, and available evidence suggests that size at birth for the blue shark is between 35 and 44 cm. The pupping season can be interpolated from Figure 20 to occur from March to July. The apparent lack of "young-of-the-year" blue sharks suggests an offshore pupping. The blue shark is the most prolific of the large oceanic sharks (Bigelow and Schroeder 1948), yet I have seen only one free-swimming fish that was <1 m FL. Blue sharks in the first and second year of life must, therefore, inhabit an unknown niche.

Structure and Function of the Oviducal Gland

The oviducal gland (Figure 23) as defined by Metten (1941) has also been referred to as the

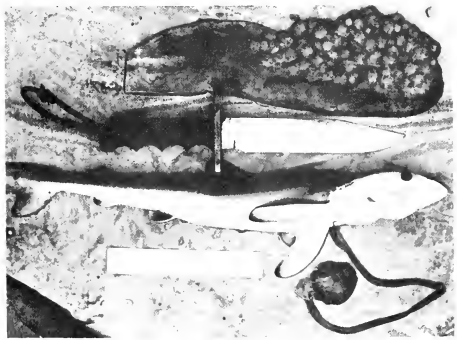


FIGURE 21.—Ovary and 43 cm FL full-term embryo from 220 cm FL gravid blue shark.

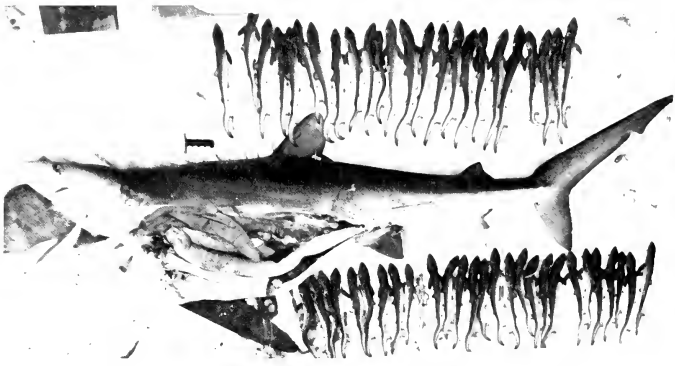


FIGURE 22.—Gravid female blue shark.

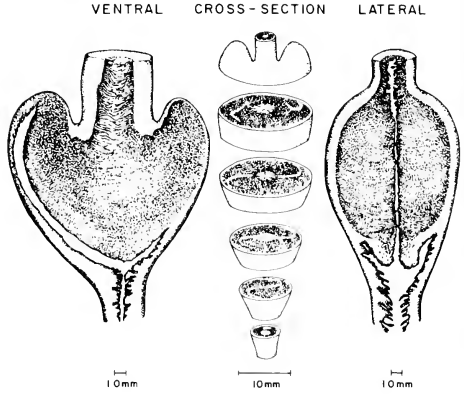


FIGURE 23.—Schematic views of the oviducal gland in the blue shark

nidamental or nidamentary gland and as the shell gland. The term "nidamental" is inappropriate since it is derived from the Latin "to nest" which is not a trait of elasmobranchs. Since a functional shell is produced in only a few species of shark, oviducal is a more accurate term for this specialization of the oviduct.

A sagittal section of the oviducal gland reveals the two major tissues (Figure 24), an anterior albumen-secreting zone and a posterior shell-

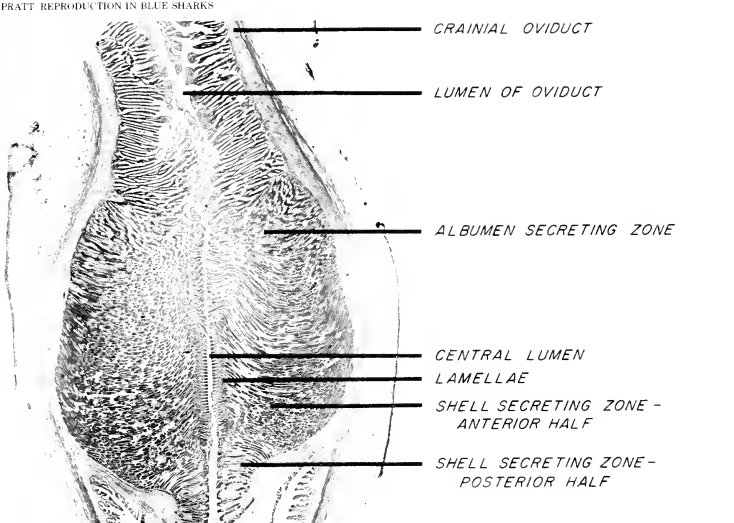


FIGURE 24.—Sagittal section of the oviducal gland in the blue shark (×5 cross section)

secreting zone. The mucus-secreting zone found in some elasmobranchs is reduced or absent in the blue shark, perhaps because of the limited shell that is produced. Secretory tubules originate blindly around the circumference of the gland and extend inward, parallel to one another. In the course of their travel they bow posteriorly for several millimeters, then return to the latitude of their origin where they communicate with the central lumen.

The albumen-conducting tubules enter the lumen as a series of 13-15 evenly spaced lamellae with irregularly flattened ends. The shell-secreting tubules terminate in tufted pockets bordering the central lumen.

The posterior half of the shell-secreting section communicates with the lumen through paired caudal protuberances of secretory tissue (Figure 24). They are embedded in a stroma of connective tissue and run a shorter, more irregular course to the lower central lumen where they end in larger and less uniform lamellae.

As the gland matures the lumen branches into two diverticula, which extend around its circumference and into each lateral horn in a medial cross section. These two diverticula give the lumen a symmetrical S-shaped appearance (Figure 13).

Of those sharks studied by Prasad (1944, 1945, 1948), the oviducal gland of the blue shark most closely resembles that of *Carcharhinus dus-*

sumieri. This is to be expected because both *C. dussumieri* and *P. glauca* are viviparous forms in which a yolk-sac placenta has been developed. (See Prasad 1944, for a discussion of phylogenetic significance.)

Metten (1941) observed that the oviducal gland of *Scyliorhinus canicula* has a function beyond that of albumen and shell production. He found active male spermatozoa in every mature female oviducal gland that he dissected. In *S. canicula* this gland is a seminal receptacle. Eggs are fertilized, not in the anterior oviduct as had been previously suggested, but in the oviducal gland itself. It is not known how many species of elasmobranchs share this trait. Matthews (1950) could not find sperm in the oviducal gland of the basking shark. Prasad (1944) observed the presence of spermatozoa in the oviducal glands of four viviparous species from the Indian Ocean: *Carcharhinus dussumieri*, *Hemigaleus balfouri*, *Scoliodon palasorrah*, and *S. sorrakowah*. He also gives an excellent account of the search for a "receptaculum seminis" and its existence in other animals. Prasad (1945) observed spermatozoa in the oviducal gland of the tiger shark, *Galeocerdo cuvieri*.

Stevens (1974) found that 16% of female British blue sharks had tooth cuts. Of these, three were dissected and oviducal glands examined for spermatozoa. His failure to find spermatozoa could result from technique, sample size, or the dynamics of the British blue shark population which contains very few males (Stevens 1974). Only 4% of the males in his sample reached sexual maturity as defined by my criteria based on the spermatophore development of western Atlantic blue sharks.

I have found spermatozoa in the oviducal glands of 79 of 160 female blue sharks collected over a 3-yr period (Figure 25). In all cases sperm was detected in a cross section of the posterior third of the oviducal gland using light microscopy. Fifteen micrometer sections were examined at 120-500 diameters magnification and the presence of brightly stained sperm confirmed at 1,250 diameters (Figure 26).

In the last year of field collections, comparative tests were conducted to determine if the presence

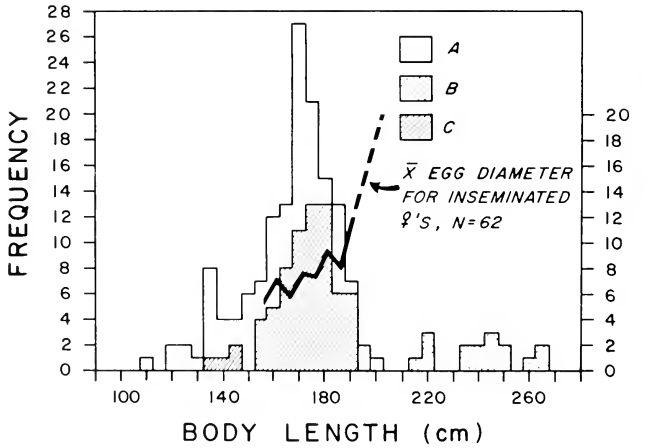


FIGURE 25.—Frequency of occurrence of female blue sharks off Bay Shore, N.Y., with data on insemination, egg diameter, and body length relationship: A) uninseminated females, B) adult females, C) inseminated females.

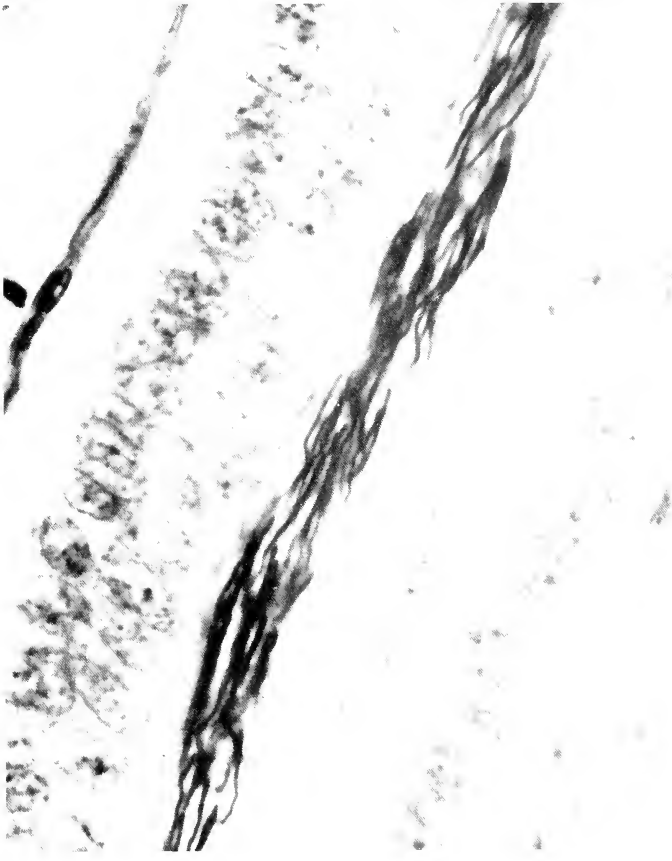


FIGURE 26.—Spermatozoa in tubules of oviducal gland in the blue shark (×2,500).

of spermatozoa in the oviducal gland could be detected using a smear technique as an alternative to the time-consuming process of embedding and sectioning. The oviducal gland was excised with a few centimeters of oviduct attached. The posterior one-third of the gland was removed by cross-sectioning with a clean scalpel. The anterior two-thirds of the gland was then squeezed and the expressed fluid was smeared on a microscope slide. Slides were dried and later fixed and stained with the Harleco Diff-Quik stain system.

Oviducal glands from 21 sharks were prepared. One from each fish was sectioned; the other gland cut and smeared. Both techniques revealed spermatozoa in 15 and both methods proved negative for the other 6. The presence of spermatozoa can therefore be determined from fresh smears of the oviducal gland.

Like Metten (1941), I found varying amounts of spermatozoa in the inseminated glands. Females <200 cm contained relatively few spermatozoa in the tubules. Some fish in the 160-180 cm group had obviously just copulated, because the tubules of the posterior oviducal gland were distended with sperm (Figure 14) and additional sperm was present in the central lumen. The spermatozoa are stored in the lower lobes of tubules which probably once were shell-secreting in function but now are actively evolving into a seminal receptacle. Since sperm may be stored for over 1 yr and possibly two (see Sexual Cycle below) these tubules must have a mechanism for sperm preservation and nourishment. Ducts from the lower lobes also run anteriorly into the upper ends of the lumen's diverticula.

I suspect that the ova are fertilized at this upper level of the oviducal gland. The exact sequence of events is difficult to understand because of the complex nature of the lumen.

Sperm Retention in the Female Blue Shark

Many diverse animals can store spermatozoa for varying lengths of time (Prasad 1944). The presence of spermatozoa in the oviducal glands of pregnant blue shark females would suggest extended storage. Histological examination revealed spermatozoa in the oviducal gland of the Sargasso Sea specimen. The other gravid females examined histologically are from northern waters caught in May, June, and July. A total of nine gravid females contained spermatozoa. Two females did not contain spermatozoa and it is possible that the glands lacking spermatozoa were poorly fixed, or the spermatozoa was destroyed because these sport-caught fish often hang in the sun for hours before dissection. Alternatively, it is possible that the reservoir of sperm has been naturally depleted and another copulation is necessary. If the female could physiologically sense this depletion, the presence in coastal waters of 225-240 cm nongravid females would be explained. In any case, it may be concluded from the above that spermatozoa can persist in the oviducal gland for at least the length of gestation (9-12 mo). If delayed fertilization is a part of the sexual cycle, then storage for 18-22 mo would be necessary for sperm to be found in a gravid female. Since the oviducal gland is at the anterior end of the uterus it is doubtful that spermatozoa could reach the gland if copulation took place while the female was carrying young. In addition to these physical obstacles to the transfer of spermatozoa, the presence of 110-120 ripe ovarian eggs also suggests that the gravid female is ready for fertilization and development of a second litter immediately after pupping. The offshore distribution of most pregnant females (Aasen 1966; Backus see footnote 7) in areas not frequented by adult males and perhaps unreceptive behavior in the female very likely act to prevent males from copulating with pregnant females. Therefore, it is possible that the quantities of spermatozoa found in the nine gravid female oviducal glands are sufficient for fertilization of the ripe ovarian eggs.

Sexual Cycle

The high incidence of mating scars and presence of sperm in the oviducal gland indicate a summer

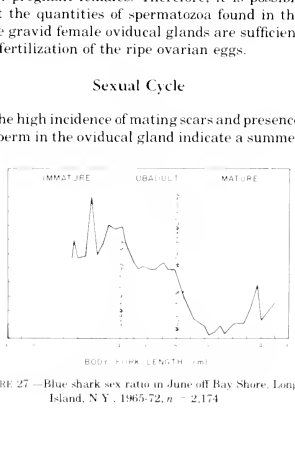


FIGURE 27.—Blue shark sex ratio in June off Bay Shore, Long Island, N.Y., 1965-72, $n = 2,174$.

breeding season for the blue shark on the continental shelf off southern New England. The length-frequency histogram of these inseminated females approximates a curve of normal distribution with a peak at 175 cm (Figure 25). The phenomenon of carrying spermatozoa seems to separate an age-class from the combined length frequency of the female population. If this is an age-class, then Stevens' (1975) age curve for the blue shark indicates that the inseminated females are 5 yr olds and the uninseminated fish are primarily fours and fives. Since most of my samples were taken in June and July, it is possible that the unfertilized 5 yr olds would be inseminated later in the season. Since all nongravid females on the continental shelf bear tooth cuts and many have vaginal scars, it would appear that only females ≥4 yr have organ systems developed enough to retain spermatozoa. The growth curve of ovarian eggs in inseminated females (Figure 25) shows the eggs as half-mature in 5 yr olds. Five-yr-old inseminated females that I sampled as late as October in continental shelf waters off southern New England do not contain mature ova or embryos. Due to immature egg size and the lack of developing embryos, I conclude that this age class is not ready to bear young during the summer of insemination. If fertilization occurred during the winter, the 9-mo gestation proposed by Suda (1953) and Aasen (1966) would produce full-term embryos in gravid females through the following summer and into the fall. This is not the case. Full-term females occur most frequently during the spring and early summer (Figure 20).

The age-6 female length-frequency mode (190 cm; Stevens 1975) is conspicuously absent from the shelf waters in the summer months (Figure 27), while males of this size are numerous. Backus (see footnote 7) caught two females offshore that could be 6 or 7 yr old by Stevens' (1975) criteria (197.4 and 209.5 cm); each carried 11.0 cm embryos in September and October, respectively. I examined one gravid female in July with two embryos 11 and 13 mm. The uterine eggs were otherwise undeveloped. Typically, gravid females in this population are of lengths indicating 7 yr of age and older.

Based on these findings, the sexual cycle of the female blue shark in the western North Atlantic would start as 4- and 5-yr-old fish arrive on the feeding mating grounds of the continental shelf in late May and early June. Here they interact with males receiving dermal punctures and lacerations (tooth cuts). The 5-yr-old females and some 4 yr olds, copulate with the males of 180 cm and larger judging from the size of the tooth interspace reflected in bite marks and male sexual maturity. This process is known to continue as late as November and may continue year round in Bahamian waters (Stephen Connett[8]). The following spring, the 6-yr-old females remain offshore and fertilize their eggs (May, June). Embryos reach full term in 9-12 mo. Pupping is from April to July. At this time the female is 7 yr old. This is the probable trend for most female blue sharks. There are many exceptional bits of data such as reliable reports of small (165 cm) gravid females (Suda 1953; Tucker and Newnham 1957) and embryo sizes that depart from the trend, especially in the eastern North Atlantic (Figure 20). These are to be expected in a wide ranging, abundant species with a long breeding season. A small number of females in the inshore population have very advanced organs and egg development for their length. It is possible that these precocious individuals bear young a year earlier than their siblings or shift completely out of phase by bearing young at random seasons.

Stray gravid females occur regularly in southern New England shelf waters. Their diminuitive numbers are an insignificant part of the spawning population. Too little is known of the early life history and feeding habits of the blue shark to determine whether the young would fare better in the rich waters of the continental shelf or offshore along the margins of the Gulf Stream.

Sex Ratio

Suda (1953) reported the blue shark sex ratio at birth to be 1:1. Data from a population of 2,174 males and females sampled at Bay Shore, Long Island, from 1965 to 1972 is presented in Figure 27. In this sample immature females consistantly outnumber the males until a fork length of 150 cm is reached because unlike females, the males only move inshore when the sex organs start to mature. The sex ratio then becomes equal in the subadult sizes when a large number of mating wounds and inseminated oviducal glands are prevalent. In the adult size group (180-250 cm) the sex ratio shifts rapidly to a preponderance of males. The inflexion point at 180 cm coincides with the size at which

[8]Stephen Connett, instructor, summer oceanography program St. George's School, Newport, R.I., pers. commun. April 1977.

ovarian eggs are reaching maturity (Figure 18) and the greatest number of females are becoming inseminated (Figure 27). Larger females are caught in decreasing numbers on the mating grounds on the shelf. Their absence probably indicates a successful insemination and offshore migration. Since courtship and copulation are not without peril to the female, it is reasonable that they should move offshore at this time. The sex ratio remains between 5 and 10% female, from 200 to 230 cm where a second peak occurs. These are mostly postpartum and gravid females in their first pregnancy. They have probably followed the main population inshore for its summer feeding migration. It is possible that since their eggs are ripe they may also need to supplement the amount of spermatozoa in the oviducal gland.

CONCLUSION

The blue shark's success as a species is partly dependent on a highly evolved system for reproduction. The blue shark differs from other carcharhinids in having a steady growth rate for the sexual organs, a lack of seasonality in the generation of sex products, and a distinct female subadult stage. A different approach has been necessary to discern the size at sexual maturity for both sexes: an analysis of spermatophore development for the male, and an examination of the seminal receptacle present in the female oviducal gland.

There are many stages between the generation of sexual products (sperm, eggs, embryos) and the time of their delivery. Elaborate capabilities have been developed by both sexes for lengthy storage and nourishment of spermatozoa, first in the epididymis, then as spermatophores in the ductus deferens, and finally in the oviducal gland of the female where they are retained for months and possibly years.

Sexual maturity occurs for both sexes at a similar body length when they are together on the continental shelf for the summer season.

While the details of mating and copulation are obscure, it is highly successful since not a single female of age was observed without evidence of mating activity and 49% were inseminated.

With the exception of the strays examined opportunistically during this study gravid females occupy a niche that is different from the continental shelf population. The release of young and their early development apparently occur in oceanic areas. Little is known of this important period in their life history.

SUMMARY

Males

The internal anatomy of the male blue shark is similar to other carcharhinids. The vas deferens is enlarged and convoluted for the storage of sperm and spermatophores. The clasper lacks a spur and resembles that of the basking shark and tope. Juvenile and small mature males 4 and 5 yr old (153-180 cm) are the most commonly encountered size group on the continental shelf off southern New England from June to October. Male blue sharks reach maturity at 180 cm and probably copulate frequently through the summer. Only about 2% of all males caught have claspers swollen and discolored by mating.

Females

The internal anatomy of the female blue shark is similar to other species of placentally viviparous carcharhinids. The single right ovary delivers ova up to 20 mm in diameter to paired oviducts. They are fertilized as they pass through the oviducal gland by stored spermatozoa and develop in paired uteri.

Female blue sharks can be grouped into immature, subadult, and adult categories based on size, behavior, and development.

1. Immature females range from 46 cm (birth) to a maximum of 145 cm long. The ovary is small with many undeveloped follicles. The oviducal gland and uterus are undifferentiated from the oviduct. The vagina is sealed by a membrane which may persist to a fork length of 135 cm.

2. Subadult females range from 145 to 185 cm long and possess differentiated though not completely functional reproductive organs. The ovary contains follicles between 2 and 6 mm. Externally, the oviducal gland is heart shaped and roughly twice the diameter of the oviduct. The uterus is differentiated from the oviduct but not 2 cm in diameter and never contains embryos. The skin begins to thicken to receive the courtship wounds of the males. There are several reasons for considering these females as a separate group. Fish in this condition are the most common group of females on the continental shelf from Hudson

Canyon to Georges Bank. They are sexually active with obvious external mating wounds on every individual in shelf waters. The presence of male spermatozoa in the oviducal gland indicates that a large proportion have successfully copulated. Subadults were found inseminated at a minimum size of 135 cm. They bear abrasive scarring on the lateral walls of the vagina in fish as small as 158 cm.

3. Mature females range from 185 to >300 cm long. They possess fully differentiated organ systems that are actively developing eggs, embryos, or both. The ovary is robust with over 100 ova from 16 to 21 mm in diameter and hundreds of smaller follicles. The oviducal gland is large and heart-shaped with the anterior horns slightly coiled. The uterus when empty is long and flaccid. Skin thickness is increased to over twice that of similar-sized males. Recent internal and external mating wounds are usually not present on mature females. Old healed scars are often present on fins and body.

Spermatozoa Storage

Both sexes store spermatozoa. It is first stored in the epididymis of the male in a matrix of supportive tissue, then as spermatophores in the lower ductus deferens. After copulation, spermatozoa is stored as clusters of individuals in tubes of the oviducal gland of the female. Histological sections of oviducal glands from a full size range of 160 females revealed spermatozoa stored in 79.

Sexual Cycle

Four- and five-year-old female blue sharks arrive on the continental shelf off southern New England in late May and early June. Here they sexually interact with males, receiving tooth cuts. The 5 yr olds and some 4 yr olds copulate with males of 180 cm (6 yr olds) and larger. The 4-yr-old females are too undeveloped to store spermatozoa. Five-year-old females actively mate and retain copious amounts of spermatozoa. The following spring, this age-group, now 6 yr old, remain offshore and fertilize their eggs in May or June. Embryos reach full term in 9-12 mo. Pupping is from April to July with up to 82 young being born. It is probable that the 7-yr-old female again copulates as the oviducal glands of gravid females contain a relatively small amount of spermatozoa. The full complement of ripe ovarian eggs present in every gravid female that I have examined suggests that another fertilization is imminent.

ACKNOWLEDGMENTS

My thanks to the staff of the Oceanic Gamefish Task of the Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, for help in data collection and analysis; to John Casey for guidance and suggestions; to Charles Entenmann and the Bay Shore Tuna Club for providing the opportunity to sample at their annual shark tournament; and also to Carol Kroupa and Carl Darenburg, of the Montauk Marine Basin, who made sampling possible during their tournament. Thanks also to Bob Benway and Steve Szlatenyi for photography, to Jennie Dunnington for manuscript typing, and to Lianne Armstrong for illustrations and artwork. I am grateful to John Colton who reviewed the manuscript, and to Richard Backus and Francis Williams for permission to use unpublished data.

LITERATURE CITED

AASEN, O.
1966. Blåhaien, *Prionace glauca* (Linnaeus) 1758. Fisken Havet 1:1-16.

BEEBE, W.
1932. Nonsuch: Land of Water. Brewer, Warren & Putnam, N.Y., 259 p.

BENEDEN, P. J. VAN.
1871. Les poissons des cotes de Belgique, leurs parasites et leurs commensaux. Mem. Acad. R. Med. Belg. 38, 100 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic, Part One, p. 59-546. Sears Found. Mar. Res., Yale Univ. Mem. 1.

BONHAM, K., F. B. SANFORD, W. CLEGG, AND G. BUCHER.
1949. Biological and vitamin A studies of dogfish landed in the state of Washington (*Squalus suckleyi*). Wash. Dep. Fish., Biol. Rep. 49A: 83-114.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf Coast of Florida. Bull. Mar. Sci. 15:13-83.

DODERLEIN, P.
1881. Manuale Ittiologico del Mediterraneo. Vol. 2, 119 p. Soc. Sci. Nat. Econ., Palermo.

GUBANOV, YE. P., AND V. N. GRIGOR'YEV.
1975. Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. J. Ichthyol. 15:37-43.

KAUFFMAN, D. E.
1950. Notes on the biology of the tiger shark (*Galeocerdo arcticus*) from Philippine waters. U.S. Fish Wildl. Serv., Res. Rep. 16, 10 p.

LEIGH-SHARPE, W. H.
1920. The comparative morphology of the secondary sex-

ual characters of Elasmobranch fishes. I J Morphol 34 245-265
1921 The comparative morphology of the secondary sexual characters of Elasmobranch fishes II J Morphol 35 359-380

LO BIANCO, S
1909 Notizie biologiche riguardanti specialimente il periodo di maturita sessuale degh animale del golfo di Napoli Mitt Zool Stn Neapel 19 513-761

LUBBERT, H , AND E EHRENBAUM
1936 Handbuch der Seefischerei Nordeuropas B II E Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 357 p

MATTHEWS, L H
1950 Reproduction in the basking shark, *Cetorhinus maximus* (Gunner) Philos Trans R Soc Lond , Ser B, Biol Sci 234 247-316

METTEN, H
1941 Studies on the reproduction of the dogfish Philos Trans R Soc Lond , Ser B, Biol Sci 230 217-238

NALINI, K P
1940 Structure and function of the nidamental gland of *Chiloscyllium griseum* (Mull and Henle). Proc Indian Acad Sci , Sect B 12 189-214

NICHOLS, J T , AND R C MURPHY
1916 Long Island fauna IV The sharks Brooklyn Inst Arts Sci , Brooklyn Mus Sci Bull 3 1-34

OLSEN, A M
1954 The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhinidae) in south-eastern Australian waters Aust J Mar Freshwater Res 5 353-410

PRASAD, R R
1944 The structure, phylogenetic significance, and function of the nidamental glands of some elasmobranchs of the Madras coast Proc Natl Inst Sci India, Part B, Biol Sci 11 282-302
1945 Further observations on the structure and function of the nidamental glands of a few elasmobranchs of the Madras coast. Proc Indian Acad Sci., Sect B 22 368-373
1948 Observations on the nidamental glands of *Hydrolagus colliei*, *Raja rhina* and *Platyrhinoidis triseriatus* Copeia 1948 54-57

ROMER, A S
1962 The vertebrate body 3d ed W B Saunders Co., Phila , 627 p.

SKINGER, S
1960 Natural history of the sandbar shark, *Eulamia milberti* U S Fish Wildl Serv , Fish Bull 61 1-38

STEVENS, J D
1974 The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L) from British waters. J Mar Biol Assoc U K 54 373-378
1975 Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L) J Mar Biol Assoc U K 55 657-665

STRASBURG, D W
1958 Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U S Fish Wildl Serv , Fish Bull 58 335-361

SUDA, A
1953 Ecological study on the Blue shark (*Prionace glauca* Linne) South Sea Area Fish Res Lab Rep 26 1-11

TEMPLEMAN, W
1944 The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil Newfoundland Dep Nat Resour , Fish Res Bull 15, 102 p

TUCKER, D W , AND C T NEWNHAM
1957 The blue shark *Prionace glauca* (L) breeds in British seas. Ann Mag Nat Hist , Ser 12, 10(117) 673-688

MORTALITY ESTIMATES FOR THE NEW ZEALAND ROCK LOBSTER, *JASUS EDWARDSII*

JOHN H. ANNALA[1]

ABSTRACT

The instantaneous total mortality rate and instantaneous fishing mortality rate were estimated for an exploited population of male New Zealand rock lobster, *Jasus edwardsii*. Instantaneous total mortality rate estimates were made from the seasonal size-frequency distribution of landed rock lobsters using three different methods and ranged from 0.64 to 1.07. Estimates of both mortality rates were also made from the rate of return of tagged rock lobsters over an entire year and by adjusting the rate for an 8- or 9-month fishing season. These estimates of the instantaneous total mortality rate ranged from 1.92 to 3.13 and were considered too high to be representative of the entire exploited population. Instantaneous fishing mortality rate estimates from the tag returns ranged from 1.17 to 1.85, with the lower rates based on an 8- or 9-month fishing season. Using the results from both types of analyses, and the observed lifespan of rock lobsters in the fishery, the best estimates of the instantaneous total mortality rate are between 1.00 and 1.50 and of the instantaneous fishing mortality rate between 0.90 and 1.40, assuming the instantaneous natural mortality rate equals 0.10.

Knowledge of the total mortality rate, and its components of fishing and natural mortality, is essential for an adequate understanding of the population dynamics of an exploited population. Mortality rates are generally estimated from 1) the age composition of the population, with the age composition of the catch serving as the population sample; 2) the results of mark and release experiments; or 3) some relationship between catch and effort.

The purpose of this investigation is to derive and compare estimates of mortality rates for an exploited population of the New Zealand rock lobster, *Jasus edwardsii*. Rock lobsters do not contain any structural parts retaining annual marks, so estimates of mortality rates cannot be made from the age composition of the catch. However, the total mortality rate can be estimated by analysis of the size-frequency distribution of the catch, and three different methods are employed. The results of these analyses are compared with estimates of the total mortality rate derived from a tag-recapture study conducted over the same fishing season and in the same area from which the size-frequency distributions were drawn. The results of the marking experiment are also used to estimate the fishing mortality rate, which is then compared with the estimates of the total mortality rate using a previously derived estimate of the natural mortality rate.

METHODS AND RESULTS

Analyses of Size-Frequency Distributions

The three methods used to estimate the total mortality rate from the size-frequency distribution were: 1) the approximate method of separating a polymodal size-frequency distribution into its component distributions described by Bhattacharya (1967); 2) Method 2 of Van Sickle (1977), where growth and size-frequency data were used to estimate mortality on a size specific basis; and 3) the partitioning of a size-frequency distribution by the average annual growth increment into components approximating age classes (average annual growth increment method) described by Hancock (1965).

Mortality rates were estimated from the size-frequency distribution of male rock lobsters landed from the Gisborne local area during the 1976-77 fishing season. Females constitute only a small proportion of the landings from this area, so their mortality rates were not estimated. Gisborne is a major fishing port located on the east coast of the North Island (Figure 1). The Gisborne local area is defined as encompassing the rock lobster fishing grounds extending from Young Nicks Head in the south to Gable End Foreland in the

[1]Fisheries Research Division, P.O. Box 19062, Wellington, New Zealand.

Manuscript accepted December 1978.
FISHERY BULLETIN: VOL. 77, NO. 2, 1979.

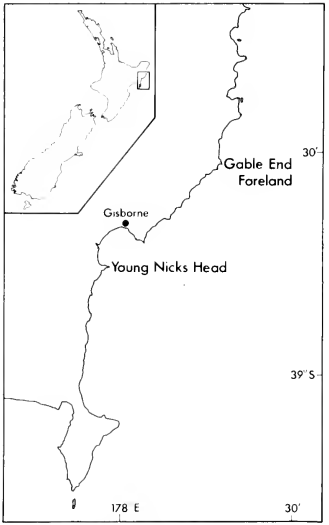


FIGURE 1.—Location of the study area between Young Nicks Head and Gable End Foreland on the east coast of the North Island, New Zealand

north (Figure 1). The landings from this area were chosen for analysis because it has been the site for a series of tag-recapture studies, which were also used to estimate mortality rates. The results reported here are part of an extensive study of the biology of *J. edwardsii* in the Gisborne area.

Size-frequency distributions in the landings were determined on a monthly basis from July 1976 to February 1977, with the exceptions of August and January, during the 1976-77 season. The fishing season is defined as extending from 1 June to 31 May of the following year. There is a natural break between seasons due to a period of low catchability and resulting low effort expenditure during April and May. During each month the landings were chosen on a nonrandom basis for sampling, and the entire landing on a given day for an individual boat was measured. The measurement used was the carapace length taken from the base of the antennal platform to the dorsal, posterior margin of the carapace along the midline. These individual samples were given equal weights and combined directly to yield a monthly sample. The monthly samples were then weighted by the proportion of the total seasonal landings landed during that month and combined to give a weighted seasonal size-frequency distribution (Table 1, Figure 2). This weighting procedure was applied to average out changes in the size-frequency distributions due to fluctuations in catchability, recruitment, and mortality to permit estimation of the average annual total mortality rate.

The approximate method of separating the component distributions of a polymodal size-frequency distribution described by Bhattacharya (1967) involves a cubic approximation of density within a size class and a quadratic approximation to the logarithm of the frequency of each class. It was assumed that the frequency distribution is composed of Gaussian component distributions that are adequately separated so that each component has a sufficiently broad region where the effects of

TABLE 1.—Weighted seasonal size-frequency distribution of male New Zealand rock lobsters from the Gisborne local area during the 1976-77 season. Observed frequency values are weighted frequencies × 10^3.

Class midpoint (mm)	Observed frequency (y)	$\log_e y$	$\Delta\log_e y$
94.5	17	2.8332	0.4990
95.5	28	3.3322	0.3814
96.5	41	3.7136	0.5059
97.5	68	4.2195	0.1872
98.5	82	4.4067	0.1300
99.5	72	4.2767	0.5108
100.5	120	4.7875	0.1335
101.5	105	4.6540	0.1107
102.5	94	4.5433	−0.2126
103.5	76	4.3307	−0.3989
104.5	51	3.9318	−0.0198
105.5	50	3.9120	−0.2484
106.5	39	3.6636	−0.1979
107.5	32	3.4657	0.3302
108.5	23	3.1355	0.8329
109.5	10	2.3026	0.4700
110.5	16	2.7726	0.2877
111.5	12	2.4849	0.2877
112.5	9	2.1972	0.2007
113.5	11	2.3979	1.0116
114.5	4	1.3863	0.2231
115.5	5	1.6094	0.2231
116.5	4	1.3863	0.0000
117.5	4	1.3863	0.2231
118.5	5	1.6094	0.9163
119.5	2	0.6931	0.0000
120.5	2	0.6931	0.0000
121.5	2	0.6931	0.0000
122.5	2	0.6931	0.0000
123.5	2	0.6931	0.6931
124.5	1	0.0000	0.0000
125.5	1	0.0000	0.0000
126.5	1	0.0000	

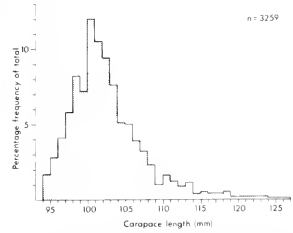


FIGURE 2.—Weighted seasonal size-frequency distribution of male New Zealand rock lobsters from the Gisborne local area landed during the 1976-77 season.

all other components are negligible. Moreover, the class range should be small, and the sample should be of a sufficient size so that the class frequencies are not small in the area of the distribution where the components are being separated.

If the class intervals are assumed to be constant, direct graphical procedures can be used, as simple differencing reduces the quadratic to a straight line. The midpoints of the size classes were plotted on the abscissa and the logarithmic difference in the frequency between successive classes on the ordinate. Each of the regions on the graph containing straight lines with negative slope corresponds to the separate components of the distribution.

The natural logarithms of the abundance of each of the 1 mm size classes and the logarithmic differences between successive size classes are also shown in Table 1. The logarithmic differences plotted against the midpoints of the size classes are shown in Figure 3, as well as the lines fitted by eye through adjacent points. This procedure involved fitting a straight line with a negative slope through successive points and required a certain amount of subjectivity when choosing the positions of the lines. However, the line-fitting was aided by using the average annual growth increment as a guide in determining the positions of the lines and by fitting the lines more closely to the points with the larger than the smaller frequencies.

Using Bhattacharya's (1967) terminology, the revelant parameters from Table 1 and Figure 3 are:

h = the class interval = 1 mm

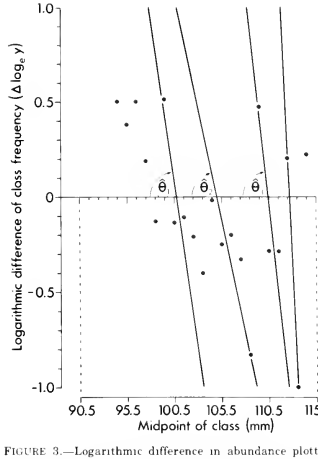


FIGURE 3.—Logarithmic difference in abundance plotted against the midpoints of successive millimeter size classes from the weighted seasonal size-frequency distribution of male New Zealand rock lobsters landed from the Gisborne local area during the 1976-77 season

b = the scale of x = 1

d = the scale of y = 20

$\hat{\lambda}_r$ = the x-intercept of the rth line

$\hat{\lambda}_1$ = 100.7 $\hat{\lambda}_2$ = 105.0 $\hat{\lambda}_3$ = 110.5

θ_r = the angle the rth line makes with the negative direction of the x-axis

θ_1 = 82.0° θ_2 = 78.5° θ_3 = 79.5°

$\hat{\mu}_r$ (the mean of the rth component)
$= \hat{\lambda}_r + h/2$

$\hat{\mu}_1$ = 101.2 $\hat{\mu}_2$ = 105.5 $\hat{\mu}_3$ = 111.0

$\hat{\sigma}_r$ (the SD of the rth component)
$= \sqrt{(dh \cot \theta_r/b) - (h^2/12)}$

$\hat{\sigma}_1$ = 1.6513 $\hat{\sigma}_2$ = 1.9967 $\hat{\sigma}_3$ = 1.9033.

Using Method iv, and following the steps outlined in table 8, of Bhattacharya (1967), the number of individuals (N_r) in each of the first three fully recruited components of the seasonal size-frequency distribution from the Gisborne local area was estimated as shown in Table 2. Male rock lobsters less than the carapace length size class from 100.0 to 100.9 mm were not fully recruited

TABLE 2.—Estimation of the number in each component (N_j) and the annual instantaneous total mortality rate (T) from the 1976-77 weighted seasonal size-frequency distribution of male New Zealand rock lobsters from the Gisborne local area using Method IV of Bhattacharya (1967).

Component	n	α_j	$\lambda = 2\pi(\alpha_j^2 + h^2/12)$	$\Sigma \log_e y$	Σx	μ	b	$\log_e \frac{N_1}{\alpha_1}$	N_1	N_2	N	T
1	5	1.6513	28.1000	4.5184	0.3719	0.0153	5.3047	201.28	332			0.36
2	5	1.9967	20.8000	3.6217	0.7217	0.0105	4.7530	115.93	231			1.75
3	5	1.9033	22.2360	2.5200	0.1237	0.0115	3.0543	21.20	40			
											Average	1.06

into the fishery, so these smaller size classes were not included in the analysis. Moreover, only the first three components were used because the small number of individuals of larger sizes in the sample made it difficult to accurately distinguish any further components. Assuming that each component approximates an individual year class, the annual instantaneous total mortality rate between components 1 and 3 is 1.06.

Estimates of the annual instantaneous total mortality rate were also derived from the six monthly samples (see Table 5). These estimates ranged from 0.00 to 1.15, with a weighted mean (weighted by the proportion of the seasonal landings taken during the month) of 0.49 and 95% confidence limits of 0.06 and 0.92.

The model used by Van Sickle (1977) describes the exact shape of the size distribution of a stationary or steady state population, with the shape expressed as a function of size-specific mortality and growth rates. His Method 2 requires comprehensive growth and size-frequency data to estimate mortality on a size-specific basis. However, it does not require the explicit determination of the age distribution nor a fitted growth curve, which is advantageous for this species.

The size distribution was divided into size classes (indexed by j), and it was assumed that the mortality rate (μ_j) was the same for all individuals in size class j. The size classes can be of any width, but the growth rate and number density must be known at the boundaries of each class.

Using the terminology of Van Sickle (1977), let j stand for the size interval (z_j, z_{j+1}). If the growth rates $g(z_j), g(z_{j+1})$ and the number densities $N_j(z_j)$, $N_j(z_{j+1})$ at the boundaries plus N_j, the total number or proportion of organisms in class j are known, then μ_j is calculated from his equation 8

$$\mu_j = \frac{1}{N_j} \left[\frac{g(z_j)N_j(z_j) - g(z_{j+1})N_j(z_{j+1})}{} \right] .$$

Estimates of the annual instantaneous total mortality rate applying Method 2 of Van Sickle (1977) to the seasonal size distribution of Table 1 are shown in Table 3. The growth rate of 4.8 mm used at the boundaries is an initial estimate of the average annual growth increment of males in the Gisborne local area, and was based on the molt increment of 204 tagged rock lobsters recaptured during 1976-77. The tagged individuals were all in the size range 80-106 mm, due to difficulties experienced in obtaining larger animals for tagging, so growth estimates were not available for the upper part of the size distribution. However, initial growth information from other areas indicates it is not unreasonable to assume a constant molt increment for males between 80 and 115 mm carapace length.

Some difficulty was experienced in determining the 100% retention length for rock lobsters using a carapace measure because the minimum legal size is based on a tail length measure (Annala 1977). The carapace length class from 100.0 to 100.9 mm had the highest proportion of any single millimeter class in the size-frequency distribution (Table 1, Figure 2) and was therefore chosen as the smallest size class fully represented in the landings. The size-frequency distribution was then partitioned into 4 mm and 5 mm size groups, beginning with the 100 mm size class, to bracket the average annual growth increment of 4.8 mm. The

TABLE 3.—Estimation of the annual instantaneous total mortality rate (μ_j) from the 1976-77 weighted seasonal size-frequency distribution of male New Zealand rock lobsters from the Gisborne local area using Method 2 of Van Sickle (1977).

Size grouping	(z_j, z_{j+1})	N_j	$(g(z_j), g(z_{j+1}))$	$\mu_j(T_j)$
4 mm	(100, 103)	395	(4.8, 4.8)	0.53
	(104, 107)	172	(4.8, 4.8)	0.53
	(108, 111)	61	(4.8, 4.8)	0.86
			Average	0.64
5 mm	(100, 104)	446	(4.8, 4.8)	0.74
	(105, 109)	154	(4.8, 4.8)	1.24
	(110, 114)	52	(4.8, 4.8)	1.11
			Average	1.03

estimates of the annual instantaneous total mortality rate were 0.64 and 1.03 for the smaller and larger groupings, respectively.

Estimates of the annual instantaneous total mortality rate from the monthly samples (see Table 5) using the 4 mm grouping ranged from 0.46 to 1.00, with a weighted mean of 0.69 and 95% confidence limits of 0.50 and 0.88. The monthly estimates using the 5 mm grouping ranged from 0.90 to 1.18, with a weighted mean of 0.99 and 95% confidence limits of 0.89 and 1.09.

Hancock (1965) estimated the total mortality rate of *Cancer pagurus* in the Norfolk (England) fishery by partitioning the size distribution into approximate year classes based on the average annual growth increment. If the natural logarithms of numbers are plotted against size, a line whose slope is proportional to the total mortality rate is obtained over the size range where growth is constant. Annala (1977) also used this method for estimating the total mortality rate of *J. edwardsii* in the Otago fishery of New Zealand.

The average annual growth increment of 4.8 mm was rounded to the nearest millimeter, and the seasonal size-frequency distribution of Table 1 and Figure 2 partitioned into 5 mm size classes. The results are shown in Table 4, with the annual instantaneous total mortality rate estimated to be 1.07. The estimates from the monthly samples (Table 5) ranged from 0.78 to 1.25, with a weighted mean of 1.11 and 95% confidence limits of 0.97 and 1.25.

TABLE 4.—Estimation of the annual instantaneous total mortality rate (Z) from the 1976-77 weighted seasonal size-frequency distribution of male New Zealand rock lobsters from the Gisborne local area using the average annual growth increment method of Hancock (1965)

Size class (mm)	N	Z
100.0-104.9	446	
		1.06
105.0-109.9	154	
		1.09
110.0-114.9	52	
	Average	1.07

TABLE 5.—Estimates of the annual instantaneous total mortality rate from the monthly size-frequency distributions of male New Zealand rock lobsters landed from the Gisborne local area during the 1976-77 season. The methods used were Method IV of Bhattacharya (1967), Method 2 of Van Sickle (1977), and the average annual growth increment method of Hancock (1965). N = sample size

Month (N)	Bhattacharya	Van Sickle (4 mm grouping)	Van Sickle (5 mm grouping)	Hancock
July (325)	0.00	0.63	1.14	1.25
Sept (399)	0.45	1.00	1.18	0.78
Oct (1,155)	0.54	0.95	0.90	1.09
Nov (506)	1.03	0.45	0.96	0.92
Dec (247)	0.32	0.82	0.94	1.18
Feb (627)	1.15	0.46	0.91	1.04
Weighted mean mortality rate	0.49	0.69	0.99	1.11
95% confidence limits of the weighted mean	0.06 0.92	0.50, 0.88	0.89 1.09	0.97 1.25

Analyses of Tag Return Data

Mortality rates were also estimated from the rate of return of tagged male rock lobsters released in the Gisborne local area in July 1976 and recaptured during the following 12 mo. The instantaneous total mortality rate was estimated using the method derived by Robson and Chapman (1961) for analyzing a segment of the catch curve. The instantaneous fishing mortality rate was estimated by 1) a method developed by Paulik (1963) for use with recaptures grouped into time intervals, and 2) a method described by Ricker (1975) where estimates are available for the instantaneous total mortality rate and rate of exploitation.

A total of 444 male rock lobsters were caught by pots, tagged using the western rock lobster tag (Chittleborough 1974), and released on the fishing grounds. All of the returned rock lobsters were taken in pots by commercial fishermen. Fishing effort was not constant throughout the 1976-77 season, so the rate of return of tags was adjusted by the effort expended in each month. The best measure of effort available was the average number of days fished per month per boat for 12 selected boats in the Gisborne local area.

The average number of days fished in June 1976 (9.9 days/boat) was used as the basis for determining relative effort. The number of recaptures for July 1976 was not included in the analysis because tags were not returned over the entire month. The number of males recaptured, the relative effort, and the number of recaptures per unit of relative effort for each month are shown in Table 6.

The method of Robson and Chapman (1961) used for estimating the total mortality rate depends on determining a mean coded age, $\bar{x}$ according to the terminology of Jones (1976), where $\bar{x} = X/\Sigma y_i$. The total coded age (X) was calculated from $X = \Sigma(t-1)y_t$ for $t = 1,2,\ldots J$, where J = the number of samples, and y_t = the number of recaptures per sample.

Using the number of monthly recaptures per unit relative effort from August 1976 through April 1977 is shown in Table 6 as an example,

TABLE 6.—Recaptures of male New Zealand rock lobsters tagged and released in the Gisborne local area in July 1976, effort expenditure during 1976-77, and the number of recaptures per unit relative effort (v_i).

Year and month	No. of recaptures	Average no. of days fished/boat	Relative effort	v
1976				
Aug	64	15.4	1.56	41.03
Sept	31	5.5	0.56	55.36
Oct	26	12.5	1.26	20.63
Nov	40	13.5	1.36	29.41
Dec	23	12.8	1.29	17.83
1977				
Jan	13	15.8	1.60	8.13
Feb	23	13.3	1.34	17.16
Mar	12	8.9	0.90	13.33
Apr	1	4.0	0.40	2.50
May	0	1.0	0.11	0.00
June	2	10.8	1.09	1.83
July	8	17.0	1.72	4.65

$$\Sigma(i-1)y_i = 41.03(1-1) + 55.36(2-1) + 20.63(3-1) + 29.41(4-1) + 17.83(5-1) + 8.13(6-1) + 17.16(7-1) + 13.33(8-1) + 2.50(9-1) = 513.09$$

$$\Sigma y_i = (41.03 + 55.36 + 20.63 + 29.41 + 17.83 + 8.13 + 17.16 + 13.33 + 2.50) = 205.38.$$

Thus, the mean coded age ($\bar{x}$) = 513.09/205.38 = 2.4982.

The proportion of tagged individuals remaining free after the last monthly sampling period was too large to be neglected, so the estimate of mean coded age was equivalent to

$$\bar{x} = \sum_{i=1}^{J-1} is^i \Big/ \sum_{i=0}^{J-1} s^i .$$

Estimates of the survival rate (S) that will satisfy a given value of $\bar{x}$ for any given J were determined from table 3 of Robson and Chapman (1961). In this example $\bar{x}$ = 2.4982 and J = 9, so the value of S which satisfied was 0.786. This was a monthly value for S, so an estimate of S for the entire year, assuming total mortality acts uniformly over the 12-mo period, was $S_{annual} = (S_{monthly})^{12} = (0.786)^{12} = 0.0556$. Thus, the annual instantaneous total mortality rate (Z) measured over the 12-mo period = 2.89. However, with fishing effort concentrated in the 9-mo period from mid-June to mid-March and with a low initial estimate of instantaneous natural mortality rate (M) of approximately 0.10 (Annala 1977), it was assumed that mortality acted primarily during the 9-mo fishing season. An estimate of annual total mortality based on this 9-mo period was $S_{annual} = (S_{monthly})^9 = (0.786)^9 = 0.1145$, with Z = 2.17.

The results of this analysis, as well as the results of grouping the tag returns bimonthly and quarterly are shown in Table 7.

Estimates of the instantaneous fishing mortality rate (F) were made using equation 26 of Paulik (1963) for grouped observations, where $\hat{F} = -\mu \ln \hat{S}/(1 - \hat{S}^J)$, and $\hat{\mu} = n/N$, where n = the total number recaptured over the period of observation, and N = the total number of tags released.

In the example cited above, where tag returns were grouped on a monthly basis from August 1976 to April 1977, $\hat{\mu}$ = 223/433 = 0.5381, where the number recaptured in July (11) was subtracted from the number released (444) to estimate the number still at large at the beginning of August (433). Using the monthly value of $\hat{S}$ = 0.786, the monthly value of $\hat{F} = -0.5381 \times -0.2408/[1 - (0.786)^9] = 0.1464$. On a 12-mo basis, the annual estimate of $\hat{F}$ = 1.76. However, based on a 9-mo fishing season, the annual estimate of $\hat{F}$ = 1.32 (Table 7).

The value of F was also estimated from the equation $F = uZ/A$, which was derived from equation (1.13) of Ricker (1975), where u = rate of exploitation, Z = instantaneous total mortality rate, and A = actual total mortality rate.

The value of u was estimated on an annual basis from the equation $u = R/M$, where R = number of recaptures during first year after release and M = number of tags released.

For the July 1976 tagging, u = 251/444 = 0.5653. Thus, for the tag returns grouped on a monthly basis, the annual estimate of $F = uZ/A = 0.5653 \times 2.89/0.9444 = 1.73$ over a 12-mo period.

TABLE 7.—Estimates of the annual instantaneous total (Z) and fishing (F) mortality rates of male New Zealand rock lobsters from the Gisborne local area derived from tag returns of those tagged and released in July 1976.

Method	(Z) Robson and Chapman (1961)	(F) Paulik (1963)	(F) Ricker (1975)
Returned tags grouped			
Monthly, Aug 1976-Apr 1977	2.89(2.17)	1.76(1.32)	1.73(1.30)
Bimonthly, Aug 1976-July 1977	3.13(2.09)	1.84(1.22)	1.85(1.35)
Quarterly, Aug 1976-July 1977	2.56(1.92)	1.56(1.17)	1.57(1.27)

The figures in parentheses are estimates of Z and F taken over 9 mo for the monthly and quarterly groupings and 8 mo for the bimonthly grouping.

On the basis of a 9-mo fishing season, the annual estimate of $F = 1.30$ (Table 7).

DISCUSSION

The weighting procedure used to derive the seasonal size-frequency distribution was designed to average out changes in the monthly distributions due to fluctuations in catchability, recruitment, and mortality, which affect the estimates of total mortality rate. The estimates derived from the seasonal size-frequency distribution using the methods of Hancock (1965) and Van Sickle (1977) were similar to the means of the respective monthly estimates (Table 5). The estimates from the monthly samples using the method of Bhattacharya (1967) were highly variable, probably due to the small sample sizes, and the mean of the monthly estimates was considerably less than the estimate from the seasonal distribution.

The factor having the greatest potential effect on the estimates of mortality derived from the size-frequency distributions is probably the influx of new recruits into the fishery by growth over the minimum legal size. Male rock lobsters in the Gisborne local area exhibit marked periodicity in the molt cycle, with most molting between October and December. However, the monthly estimates using the methods of Hancock (1965) and Van Sickle (1977) do not indicate any changes in mortality rate associated with this molting period. Therefore, estimation of the total mortality rate from the weighted seasonal size-frequency distribution is considered valid in this example.

The estimates of total mortality rate from the weighted seasonal size-frequency distribution using the three methods gave similar results. The method of Bhattacharya (1967) is considered adequate when the sample size is large and an estimate of growth rate is available to aid in fitting the lines. However, when used in analyzing size-frequency distributions whose sample sizes were small, such as those from other areas (my unpubl. data) and the monthly samples in this example (Table 5), the results varied widely. Moreover, when used with data without definite modes, the abundance of the first component often appears to be underestimated, perhaps due to the difficulty of determining the 100% retention length, and greater consistency is obtained if the first three components are included for analysis.

Method 2 of Van Sickle (1977) also requires comprehensive size-frequency and growth data. One of Van Sickle's key assumptions is that the method be applied to a stationary or steady state population, which he defines (after Seber 1973) as one having age and size structures that are cyclic, with a period usually of 1 yr. Thus, size distributions observed at yearly intervals will appear identical. However, he argues that the method can be applied to annual "average" size distributions rather than a distribution at one point in time (Van Sickle 1977, quoting Van Sickle 1975). Growth and mortality rates should not vary with time, and seasonal and year-to-year changes in recruitment and growth should be "averaged out" of the data used.

Estimates derived using the smaller of the millimeter size groupings bracketing the annual growth increment for this example (Tables 3, 5) and for samples from other areas (my unpubl. data) were usually lower than those derived using the larger millimeter size grouping. These lower estimates may be due to the violation of one or more of the above assumptions. Van Sickle's method is very dependent on accurate estimates of growth rates and densities at the boundaries of each size class, and even minor fluctuations in recruitment and for samples from other areas (my unpubl. data) were usually lower than those derived using the larger millimeter size grouping. These lower estimates may be due to the violation of one or more of the above assumptions. Van Sickle's method is very dependent on accurate estimates of growth rates and densities at the boundaries of each size class, and even minor fluctuations in recruitment could affect the estimates of the numbers in the boundary size groups.

The success of the average annual growth increment method of Hancock (1965) is also dependent on the assumptions of constant recruitment and growth rate over the size range considered. However, this method is probably not as susceptible to fluctuations in recruitment as that of Van Sickle (1977), because the use of broad size classes based on average annual growth increments should smooth out any small fluctuations. The accuracy of both these methods may be improved by combining size-frequency distributions obtained over a number of years to reduce the effects of changes in recruitment and growth rates. Continuous monitoring of size-frequency distributions in the Gisborne fishery should result in improved estimates in the future.

In summary, the analyses of the size-frequency distributions using the three methods gave gener-

ally consistent results. The method of Van Sickle (1977) requires the most detailed information on the size distribution and growth rates, and the results are susceptible to the size groupings chosen. Hancock's (1965) method requires less detailed information on growth, as average annual growth increments can be used, but still requires an accurate description of the size-frequency distribution. Bhattacharya's (1967) method does not require information on growth, although knowledge of the annual growth increment does aid in analysis of the data, but again requires an accurate description of the size-frequency distribution.

The instantaneous total mortality rate can also be estimated from length composition data using the expression derived in Appendix B of Beverton and Holt (1956) based on the von Bertalanffy (1938) growth parameters. This method is most accurate when there is a rapid increase in length with age over the important size range and a minimum of overlap between the length distributions of adjacent age groups. Saila et al. (in press) found that growth of male rock lobsters from the Gisborne area during the first few years after recruitment to the fishery (the important size range in this study) is slow relative to earlier years as described by an empirical growth curve. This curve was considered to be a more realistic description of growth than the von Bertalanffy curve at this stage of the species' life history. Moreover, the great variability found in the individual growth increments probably results in a high degree of overlap between the lengths of adjacent age classes. Thus, the conditions for the best use of the Beverton and Holt method do not appear to be met, and it was not applied to this species.

Polymodal frequency distributions may also be separated into their component groups using computer techniques such as ENORMSEP (Extended Normal Separator Program) (Yong and Skillman 1975). An important advantage of this technique over the method of Bhattacharya (1967) is that the goodness of fit of the estimated component distributions to the original polymodal distribution can be determined. However, the accuracy of both techniques is reduced when the modes of the size-frequency distribution are not well separated. The size-frequency distributions analyzed in this example do not exhibit any well-defined modes, so ENORMSEP was not used as it is considered that this technique would not improve the accuracy of the estimates.

The estimates of total mortality rate from the rate of tag returns using the method of Robson and Chapman (1961) are much higher (even when adjusted for an 8- or 9-mo fishing season) than the estimates derived from the size-frequency distributions. Morgan (1974a) suggested that the western rock lobster, *Panulirus cygnus*, caught by pots have a higher probability of recapture by pots than rock lobsters initially captured and released by diving. He further suggests that rock lobsters previously caught by pots, marked, and released, have a greater probability of recapture by pots than the probability of capture by pots of the total population. All of the rock lobsters tagged and released in this study were caught by pots, so they may have been more vulnerable to capture by commercial pot fishermen than the untagged individuals in the population. Moreover, due to the nature of the fishing grounds, the tag and release procedure was not conducted in a strictly random manner, and the resulting distribution of tags in the fishery may have led to a greater susceptibility to capture for the tagged rock lobsters.

The estimates of total mortality rate from the tag returns also may be affected by changes in the catchability of the rock lobsters. Laboratory experiments indicate feeding activity is lowest for individual *J. edwardsii* immediately prior to and after molting (my unpubl. results). Morgan (1974b) found a significant negative correlation between premolt stage D1 animals and catchability for the western rock lobster. Fluctuations in the number of recaptures per unit relative effort between August and April (Table 6) indicate that catchability may vary considerably. Any decrease in catchability during the molting period would act to increase the estimate of the total mortality rate.

Other factors affecting estimates of the total mortality rate (Type B errors, Ricker 1975) include: 1) tag loss, 2) extra mortality of tagged rock lobsters, and 3) emigration of tagged rock lobsters from the fishing area, with all three acting at a steady, instantaneous rate throughout the experiment. These factors all result in an overestimate of the total mortality rate.

Preliminary laboratory and field experiments on the rates of initial tag loss and mortality due to tagging indicate these effects are minimal (my unpubl. data). However, rock lobsters are most susceptible to tag loss and mortality due to the presence of the tag while molting. Laboratory experiments are being conducted to determine the long-term rates of tag loss and mortality.

The third factor, emigration out of the area, does not appear to be important. None of the males tagged in July 1976 had been recaptured outside the Gisborne local area. The inshore fishing grounds outside the Gisborne local area are all heavily fished, so the movement of significant numbers of tagged animals would probably be detected, unless they were migrating to deeper, unfished areas.

The methods of Paulik (1963) and Ricker (1975) used to estimate the fishing mortality rate from the tag returns (Table 7) are both dependent on estimates of the total mortality rate. Any bias in the estimates of total mortality rate will affect the estimates of fishing mortality rate. If the tagged rock lobsters were more susceptible to capture then the untagged individuals, then the estimates of fishing mortality rate may be overestimates.

Other factors affecting estimates of fishing mortality rate (Type A errors, Ricker 1975) include: 1) the death of tagged rock lobsters due to the presence of the tag, or the loss of their tags, shortly after marking; and 2) incomplete reporting of tags recaptured by fishermen. As mentioned previously, preliminary experiments indicate the effects of the first factor are minimal. However, predation by fish on the newly released animals may be important and warrants further investigation. It is known that some of the recaptured tags went unreported by fishermen, although the numbers were not large. This would result in an underestimate of the fishing mortality rate.

The estimates of fishing mortality rate adjusted for an 8- or 9-mo fishing season (1.17-1.35) are considerably lower than the unadjusted estimates (1.56-1.85). If the estimate of $M = 0.10$ (Annala 1977) applies to the Gisborne fishery, then $Z = 1.27$ to 1.45 based on the estimates of F for an 8- or 9-mo season. These estimates of Z are more comparable to those derived from the analyses of the size-frequency distributions (0.64-1.07) than to the estimates derived using the method of Robson and Chapman (1961) (1.92-3.13). Moreover, these lower estimates are more consistent with the estimated lifespan in the fishery than are the higher estimates. Based on the average annual growth increment of 4.8 mm and the seasonal size-frequency distribution in Table 1 and Figure 2, rock lobsters appear to survive for about 4 or 5 yr in the fishery. The preliminary empirical growth model developed by Saila et al. (in press) also indicates that male rock lobsters from the Gisborne local area remain in the exploited phase for a minimum of 4 to 5 yr.

In summary, the estimates of total mortality rate for the entire exploited population from the rate of tag returns are considered too high. The estimates of total mortality rate from the size-frequency distribution analyses, and those based on the estimates of F over an 8- or 9-mo fishing season with the addition of $M = 0.10$, are more consistent with the observed lifespan in the fishery. Thus, the best estimates of Z are between 1.00 and 1.50, and of F are 0.90 and 1.40, assuming $M = 0.10$.

ACKNOWLEDGMENTS

I would like to thank the National Research Advisory Council of New Zealand for fellowship aid during part of this study. Saul Saila provided many helpful suggestions on the application of these methods. J. Booth, R. Francis, J. McKoy, S. Saila, G. D. Waugh, and two anonymous reviewers made many constructive comments on the manuscript. B. Bycroft, B. Hvid, and J. McKoy provided valuable assistance in the field. Finally, I would like to thank the commercial fishermen for their excellent cooperation in returning tagged rock lobsters, and the staffs of the fish processing sheds and the Ministry of Agriculture and Fisheries Office in Gisborne for receiving and holding the same.

LITERATURE CITED

ANNALA, J. H.
1977. Effects of increases in the minimum legal size on the Otago rock lobster fishery. N.Z. Fish. Res. Div. Occas. Publ. 13, 16 p.

BEVERTON, R. J. H., AND S. J. HOLT
1956 A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 140:67-83.

BHATTACHARYA, C. G.
1967 A simple method of resolution of a distribution into Gaussian components. Biometrics 23:115-135.

CHITTLEBOROUGH, R. G.
1974 Development of a tag for the western rock lobster. Aust. C.S.I.R.O. Fish. Oceanogr. Div. Rep. 56, 19 p.

HANCOCK, D. A.
1965. Yield assessment in the Norfolk fishery for crabs (*Cancer pagurus*). Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 156:81-94.

JONES, R.
1976 The use of marking data in fish population analysis. FAO Fish. Tech. Pap. 153, 42 p.

MORGAN, G. R.
1974a. Aspects of the population dynamics of the western rock lobster, *Panulirus cygnus* George. I. Estimation of population density. Aust. J. Mar. Freshwater Res. 25:235-248.
1974b. Aspects of the population dynamics of the western rock lobster, *Panulirus cygnus* George. II. Seasonal changes in the catchability coefficient. Aust. J. Mar. Freshwater Res. 25:249-259.

PAULIK, G. J.
1963. Estimates of mortality rates from tag recoveries. Biometrics 19:28-57.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

ROBSON, D. S., AND D. G. CHAPMAN
1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.

SAILA, S. B., J. H. ANNALA, J. L. MCKOY, AND J. D. BOOTH.
In press. Application of yield models to the New Zealand rock lobster fishery. N.Z. J. Mar. Freshwater Res.

SEBER, G. A. F.
1973. The estimation of animal abundance. C. Griffin & Co. Ltd. Lond., Engl., 506 p.

VAN SICKLE, J.
1977. Mortality rates from size distributions. The application of a conservation law. Oecologia 27:311-318.

VON BERTALANFFY, L.
1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 10:181-213.

YONG, M. Y.Y., AND R. A. SKILLMAN
1975. A computer program for analysis of polymodal frequency distributions (ENORMSEP), FORTRAN IV. Fish. Bull., U.S. 73:681.

WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*: PHYSICAL, CHEMICAL, AND SENSORY CHANGES WHEN HELD IN ICE AND IN CARBON DIOXIDE MODIFIED REFRIGERATED SEAWATER

KERMIT D. REPPOND, FERN A. BULLARD, AND JEFF COLLINS[1]

ABSTRACT

Walleye pollock, *Theragra chalcogramma*, were held in the round in ice and in CO_2 modified refrigerated seawater and periodically examined for physical and chemical changes as well as changes in the palatability of baked portions of blocks of fillets. Taste panel evaluation revealed that satisfactory fillets were obtained from fish that would have been judged spoiled if based on examination of the fish in the round. Sensory evaluation of baked fillet portions indicated that fish were acceptable for consumption to 6 days if heavily iced. The fish held in modified refrigerated seawater were judged acceptable only to 4 days because of lower sensory scores for salt content and flavor. Yield of fillets and protein content did not change significantly with time of holding in either medium. The total volatile acid and trimethylamine data indicated that these tests may prove useful as chemical indicators of spoilage for ice-held fish whereas determination of trimethylamine oxide or extractable protein nitrogen may prove useful for fish held in modified refrigerated seawater. Round weight and dimethylamine content increased in fish from both systems with time of holding as did the salt content of fish held in modified refrigerated seawater. Total volatile base, formaldehyde, and free α-amino-nitrogen content remained unchanged but nonprotein nitrogen and total solids content decreased with time of holding.

Walleye pollock, *Theragra chalcogramma*, have been the subject of several studies concerning changes that occur in frozen storage, and how these changes affect the suitability of pollock in traditional Japanese products (Iwata and Okada 1971, Okada and Noguchi 1974). Uchiyama et al. (1972) and Kramer et al. (1977) reported on changes that occur when pollock are held in ice. If pollock are to be held more than a few hours, ice or some type of refrigeration is needed to retard deterioration in quality. The advantages and disadvantages of refrigerated seawater (RSW) for holding fish and shellfish are well established (Roach et al. 1967). In recent years, reports have appeared on holding fish or shrimp in RSW modified by the addition of dissolved CO_2 (MRSW) (Barnett et al. 1971; Bullard and Collins 1978). These authors reported that deterioration occurred at a slower rate in MRSW than in ice. Lemon and Regier (1977) noted similar results with Atlantic mackerel, *Scomber scombrus*, held in either ice, RSW, or MRSW. Experiments with Atlantic ocean perch, *Sebastes marinus*, (Longard and Regier 1974) also confirmed the superiority of MRSW over RSW or ice as a holding medium. The objectives of this study were to generally characterize the changes that occur in walleye pollock with time of holding in ice and in MRSW, to determine which holding medium is superior, and to determine if some of the common chemical indices for spoilage could be useful for pollock.

METHODS

Sampling

A catch of various species of bottom fish including approximately 135 kg each of walleye pollock and Pacific cod, *Gadus macrocephalus*, was made on 2 November 1976 by the RV *Oregon* near Cape Barnabas, Kodiak Island, Alaska, and shall be referred to as Lot 1. Lot 1 was evaluated by physical and chemical methods and by informal subjective observation on whole fish and their raw fillets. No formal sensory evaluation of cooked pollock was possible because of the limited amount of fish. To obtain fish for formal sensory evaluation, a second catch was made 1 yr later on 13 October 1977 at the same location and shall be referred to as Lot 2. Most of the chemical analyses conducted on Lot 1 were repeated on Lot 2 to see if the lots were similar. Analyses for total volatile base (TVB) and free α-amino acids were conducted on

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615

Manuscript accepted December 1978.
FISHERY BULLETIN VOL. 77, NO. 2, 1979

Lot 1 only. Analyses for dimethylamine (DMA), trimethylamine oxide (TMAO), and formaldehyde (FA) were conducted on Lot 2 only. Analyses for total volatile acid (TVA), trimethylamine (TMA), total nitrogen, total solids, chloride, extractable protein nitrogen (EPN), and nonprotein nitrogen (NPN) were conducted on both lots.

Fish in Lot 1 were held on a sorting table until arrival at the laboratory 6 h later. Ambient air temperature was about 4° C. Pollock and cod were separated from the rest of the catch, individually weighed, tagged, and transferred to the previously described ice or MRSW systems (Bullard and Collins 1978). To simulate a commercial operation, the pollock and cod were not segregated by species within the holding systems. This paper deals with pollock; cod will be discussed in a subsequent article. At regular intervals up to 15½ days, pollock were selected in such a manner that the average weight per fish in a particular sample was close to the average for all the pollock (495±175 g SD). Each sample from the ice system consisted of 13 fish and each sample from the MRSW system consisted of 14 fish.

Prior to loading with fish, carbon dioxide was injected into the refrigerated brine until the pH leveled off at 4.3. Subsequent intermittent addition of carbon dioxide kept the pH between 5 and 6 throughout the experiment. Temperature was maintained at −1° C. The brine to fish ratio was 1.5:1. In the ice system, the fish were mixed in a fivefold excess of ice and fresh ice was added as necessary to replace melted ice. Great care was taken to insure the fish did not touch each other. Although commercial icing conditions are not as thorough, this procedure was used so the data obtained would be based on ideal icing conditions. A control sample was taken 6 h after arrival at the dock.

After removal of a sample from a holding system, the fish were washed briefly to remove slime or ice, drained on a rack for 5 min, and the weight of the individual fish recorded. The fish were filleted by hand and the fillets were rinsed briefly, drained on an inclined screen for 5 min, and weighed. Notes were made on the appearance of the round fish and the condition of the gills, fillets, and viscera. The fillets were then ground using the coarse blade on an Oster[2] food grinder. A composite of 800 g was frozen at −34° C. The remaining ground flesh was washed with cold water (1 flesh:2 water) for 15 min on a reciprocating shaker. The flesh was drained for 30 min on an inclined 16-mesh plastic screen, then weighed and frozen at −34° C for later analysis. All analyses were completed within 2 mo and we assumed no changes took place during frozen storage.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Formal Sensory Evaluation

Pollock (Lot 2) were separated from the rest of the catch and stored on the deck of the boat. The fish were frequently sprayed with fresh seawater to keep them cool. About 6 h after capture, the fish were transferred into the ice and MRSW holding systems. A control sample was taken at this time. The icing was less thorough than in Lot 1. Temperature and pH of the MRSW holding system were maintained at the same values as in Lot 1. At regular intervals, fish were removed from each holding system and filleted by hand. About 7 kg of fillets were frozen as blocks in plastic bags at −34° C for formal sensory evaluation. The remaining fillets were ground and stored at −34° C for later chemical analysis. Chemical and sensory analyses were completed within 2 mo. The last sample (12 days) was not large enough for the taste panel test and was evaluated by chemical methods only.

The blocks were sawed into portions measuring 80 × 50 × 12 mm and thawed at room temperature. The control sample and samples from fish held in ice were salted by immersion in a 5% NaCl solution for 1.5 min. The portions were cooked in individual sealed aluminum pans at 232° C for 20 min in a commercial oven. Because of the difficulty in equalizing the salt content, samples from the two holding systems were not directly compared. Judges were asked to note if a sample were too salty. The results of the sensory tests were evaluated by analysis of variance. If analysis of variance indicated a change had occurred with time of holding, the Student-Newman-Keuls test was used to determine which samples were different.

Chemical Analyses

The frozen samples were tempered overnight in a refrigerator at 3° C and ground twice using the fine blade of an Oster food grinder. Analyses were carried out for total nitrogen, total solids, chloride (Horwitz 1975), total volatile acid (TVA,

Friedemann and Brook 1938), total volatile base (TVB, Stansby et al. 1944), and extractable protein nitrogen (EPN, Dyer et al. 1950). Analyses for formaldehyde (FA, Castell and Smith 1973), trimethylamine oxide (TMAO, Bystedt et al. 1959), free α-amino-nitrogen (Pope and Stevens 1939), and nonprotein nitrogen (NPN, Nikkila and Linko 1954) were carried out on a 5% trichloroacetic acid extract. An aliquot of the extract was neutralized and analyzed for dimethylamine (DMA) by Dowden's (1938) method modified by increasing the time of extraction to 15 min and by using a mechanical shaker. Analysis for trimethylamine (TMA) in fish in Lot 1 was carried out using Dyer's original method (Dyer 1945). For fish in Lot 2, Dyer's method and the modification by Tozawa et al. (1971) were used.

RESULTS AND DISCUSSION

Physical Appearance and Yield

Changes in odor, degree of decomposition of viscera, and physical appearance of fish from Lot 1 and Lot 2 occurred at the same time of holding. Ice-held fish were generally free of slime whereas fish held in MRSW were covered with a thin layer of slime throughout the experiment. After a few days, the gills and fins of fish held in ice were firm but those in MRSW were soft and swollen. After 4 days in ice, the pollock had soft livers and after 6 days, decomposition of the viscera could be detected externally. Softening of fillets became noticeable in 2 or 3 days in fish from both holding systems. An unpleasant odor became noticeable after 3 days in ice and predominant after 4 days. Browning of the fillets appeared after 6 days in ice and seemed to be enhanced by grinding. Based on this informal subjective observation on the physical appearance and odor of the fish in the round and the raw fillet, pollock could be held a maximum of 4 days under ideal icing conditions before becoming unacceptable for human consumption.

Pollock held in MRSW showed the same changes as those held in ice but they occurred several days later. The maximum time the fish could be held in MRSW and still be acceptable for consumption was 8 days based on evaluation of the fish in the round and the raw fillets. The amine odor usually associated with deterioration of fish was not present but there was a distinct and unpleasant smell in the fillets of fish held more than 12 days in MRSW. The changes in odor and texture occurred gradually in fish from either system, so the exact time for onset of spoilage based on these informal, subjective evaluations could not be reliably determined.

Pollock held in either medium gained weight steadily throughout the experiment (Table 1). The increase was more than 6% of the initial weight after 5 days in MRSW but only 3% in ice. The yield of fillets averaged 36% in both media and remained fairly constant. Solids content of the flesh decreased from 18% initially to 16% and 17% after 10.5 days in ice and in MRSW, respectively (Table 1). Solids contents of fish in Lot 2 were similar. The higher solids content of fish held in MRSW was probably caused by the uptake of salt (Table 1).

Sensory Assessments

Differences in odor and firmness were highly noticeable in raw fillets from fish held different lengths of time in the same holding system or

TABLE 1.—Change in weight, salt, and total solids content of fillets and washed ground flesh of walleye pollock (Lot 1) with time of holding in ice and in modified refrigerated seawater

	Ice holding system								Modified refrigerated seawater							
	Round weight[1]		Fillets			Washed ground fillets			Round weight[1]		Fillets			Washed ground fillets		
Time (days)	Initial (g)	Final (g)	Weight (g)	NaCl (‰)	Solids (%)	Weight[2] (g)	NaCl (‰)	Solids (%)	Initial (g)	Final (g)	Weight (g)	NaCl (‰)	Solids (%)	Weight[2] (g)	NaCl (‰)	Solids (%)
0	6 383	6,383	2 268	0 13	18 2	2 661	0 07	12 3	6 383	6 383	2,268	0 13	18 2	2 661	0 07	12 3
0 5	6 616	6,615	2,356	0 14	18 0	2,384	0 05	12 5	—	—	—	—	—	—	—	—
1 5	6 299	6 324	2 333	0 13	17 6	2 718	0 05	12 6	7 456	7 656	2 541	0 58	19 1	2 730	0 23	14 5
2 5	6 433	6 520	2 262	0 14	17 5	2 487	0 07	13 0	6 910	7 244	2 618	0 76	18 5	2 695	0 29	14 8
3 5	6 180	6 271	2 331	0 14	17 1	2 637	0 05	12 9	7 038	7 386	2 642	0 94	18 3	2 685	0 38	15 2
4 5	6 428	6 583	2 483	0 14	17 4	2 947	0 05	12 4	6 835	7 270	2 571	1 07	18 4	2 550	0 42	15 7
6 5	6 630	6 816	2 510	0 15	16 8	2 837	0 04	12 6	7 264	7 882	2 828	1 21	18 0	2 773	0 46	15 0
8 5	6 372	6 713	2,376	0 11	16 6	2 685	0 04	12 4	7 352	8 022	2 872	1 34	17 9	2 805	0 58	15 2
10 5	6 674	6 986	2 441	0 10	16 4	2 799	0 05	12 4	7,017	7 777	2,591	1 55	17 5	2 473	0 66	15 7
12 5									6 845	7 755	2 535	1 64	17 6	2 395	0 64	15 2
13 5									7 096	8 003	2 715	1 64	17 4	2 578	0 69	15 3
15 5									6 750	7,727	2 597	1 69	17 1	2 497	0 70	14 8

[1]Total round weight of the fish that composed the sample.
[2]Weight of ground, washed flesh if no portion had been reserved for analysis of fillets.

equal lengths of time in different holding systems, but were almost absent in the cooked samples (Table 2). The flavor scores of iced pollock did not change significantly until after 6 days and texture remained unchanged throughout the experiment. Kramer et al. (1977) reported that pollock can be held 12 days in ice with only a small decrease in flavor scores and none in texture scores. The pollock used in that experiment were larger than those used in our work, and preparation and cooking of the fish were different.

The flavor scores for the MRSW samples remained unchanged to 4 days and were acceptable to 8 days except for the high salt content. The increased salt content, in addition to the development of a disagreeable taste noted by some panel members, was probably the reason sensory scores decreased after 4 days in MRSW. The scores for texture remained unchanged throughout the experiment.

These conclusions on holding characteristics of pollock were based on fish obtained from one location at one time of year but pollock caught at different locations may have different holding properties (Kramer et al. 1977). Not only does the size of walleye pollock vary from one location to the next (Kizevetter 1973) but there is some evidence of distinct breeding groups (Iwata 1975). Variation due to the yearly reproduction cycle may also affect the holding qualities.

Chemical Analyses

While the salt content of pollock held in ice remained relatively unchanged with time of holding, it increased rapidly in MRSW-held fish (Table 1). Salt contents of fish from both lots were similar. The protein contents ($6.25 \times$ % total N) of the fillets varied little with holding time and averaged 16.5% in either system for both lots. The nonprotein nitrogen content was 11% of the total nitrogen content initially and did not change with time of holding in ice but slowly decreased to 7% after 10 days in MRSW. The free α-amino-nitrogen content did not change significantly during the experiment, averaging 7.1 ± 0.7 (SD) and 6.2 ± 0.9 (SD) mg N/100 g sample in the fillets of fish held in ice and in MRSW, respectively.

Several chemical analyses were performed to determine which, if any, could be used as an index of spoilage. TVB changed little and never exceeded 10 mg N/100 g sample making it unsuitable as an index of spoilage. Tokunaga (1964) reported TVB values of 10-13 mg N/100 g sample for freshly caught pollock. Analysis for TVA in fish from Lot 2 gave values essentially the same as in Lot 1. Except for the 2.5-day sample, values for TVA content of ice-held fish remained largely unchanged at < 0.20 meq H^+/100 g flesh to 4.5 days but then began to increase (Figure 1). The increase at 4 days coincided with the change in quality as determined by informal subjective evaluation of the raw fillets but preceded by at least 2 days the decrease in flavor scores of the cooked fillets. Therefore, TVA content could be used as an index of spoilage for pollock held in ice if supplemented by subjective sensory examination of cooked fish. For MRSW-held samples, a rapid increase in TVA content occurred after 12 days while a significant

TABLE 2.—Change in mean sensory analysis scores for baked portions of blocks of fillets of walleye pollock (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW). SD are in parentheses. Panel had 12 judges. Flavor and texture scores were on the following scale: Very good, 5; Good, 4; Fair, 3; Borderline, 2; and Poor, 1.

Time of holding (days)	Flavor		Texture		Percent responding too salty	
	Ice[1]	MRSW	Ice	MRSW	Ice	MRSW
0	4.0 (0.5)	4.0 (0.5)	4.0 (0.3)	4.0 (0.7)	0	0
2	3.9 (0.5)	3.7 (0.5)	3.9 (0.5)	3.9 (0.5)	0	0
4	3.6 (0.5)	4.1 (0.5)	3.8 (0.5)	4.0 (0.7)	0	0
6	3.8 (0.6)	2.9*(0.9)	3.8 (0.6)	3.9 (0.7)	0	33
8	3.2*(0.8)	3.2*(0.7)	3.8 (0.5)	3.8 (0.4)	0	75

[1]Values with asterisk were significantly ($P < 0.05$) different from zero holding time values.

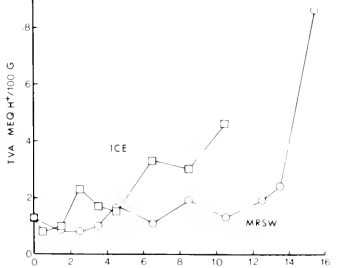


FIGURE 1.—Change in total volatile acid (TVA) content of fillets from walleye pollock (Lot 1) with time of holding in ice and in modified refrigerated seawater (MRSW).

decrease in quality was detected at 8 days in the raw fillets, and at 6 days in the cooked fish. Therefore, TVA could not be used as an index of spoilage for pollock held in MRSW.

In both lots, the TMA values (Dyer 1945) were higher for ice-held fish than for MRSW-held fish (Figure 2). A higher TMA content should have occurred in the fish held in ice if their flesh was at a higher pH because Castell and Snow (1949) showed the rate of formation was higher in a more basic medium. The pH of a 2:1 distilled water-ground flesh mixture was 7.25 and 6.45 for ice-held and MRSW-held fish, respectively, and changed little with time of holding. Another reason for the higher TMA content in iced fish was that the lower pH of the brine should inhibit the proliferation of bacteria. For fish held in MRSW, there was little difference in TMA content between lots but for fish held in ice, values for Lot 2 are about twice the corresponding values in Lot 1. This difference in TMA values between lots was probably due to the fish in Lot 2 being iced in layers while those in Lot 1 were individually iced. Kramer et al. (1977) reported TMA values on iced pollock that were similar to that of Lot 1. Although there was no statistically significant correlation between flavor of iced fish and TMA content, the rapid change in TMA content for iced fish from Lot 2 occurred at the same time as the flavor score decreased. The change in rate of accumulation of TMA in iced fish in Lot 1 was not as discernible but probably occurred between 4 and 6 days. Kramer et al. (1977) reported a large increase in TMA content in pollock after 8 days in ice. Differences in analytical technique, sample preparation, or icing procedure could account for the different times for the sudden increase in TMA. For MRSW-held fish in Lot 2, no rapid change in TMA content was noted even after the flavor scores decreased. Consequently, TMA content may provide a useful index of spoilage for ice-held pollock but may not be usefull for fish held in MRSW.

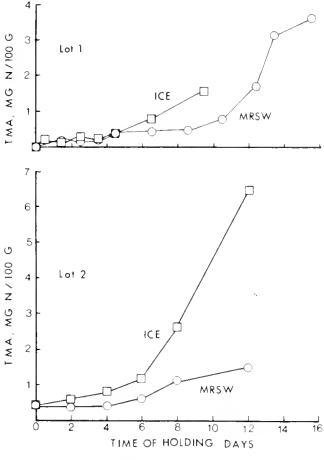


FIGURE 2.—Change in trimethylamine (TMA) content of fillets from walleye pollock with time of holding in ice and in modified refrigerated seawater (MRSW).

Using the modification by Tozawa et al. (1971) of Dyer's (1945) method for determining TMA has reduced the interference from DMA but has not always provided as reasonable or as useful data (Botta and Shaw 1975; Shaw et al. 1977). Fish from Lot 2 were analyzed by both methods and though TMA values were generally lower using the method of Tozawa et al., there was no difference in the way TMA content varied with time of holding. Consequently, the methods of Dyer and Tozawa et al. were equally useful as chemical indices of spoilage for pollock during fresh storage in ice. The TMA values as determined by the method of Tozawa et al. were not included in this report.

The TMAO content (Lot 2) of the zero holding time sample was 69 mg N/100 g flesh. Tokunaga (1964) has reported TMAO values which averaged about 100 mg N/100 g flesh. The TMAO content of the ice-held fish remained essentially unchanged to 8 days but dropped to 36 mg N/100 g flesh on the last day (Figure 3). The TMAO content of fish held in MRSW was about the same as that of fish held in ice to the fourth day then rapidly decreased. Although there was no significant statistical correlation between TMAO values and flavor scores, the decrease in TMAO content coincided with the decrease in flavor scores for MRSW-held fish. The TMAO content of the ice-held fish had not changed significantly at the eighth day of holding even though the flavor score had decreased significantly.

The DMA content was also determined on fish in Lot 2 (Figure 4). The rate of accumulation of DMA

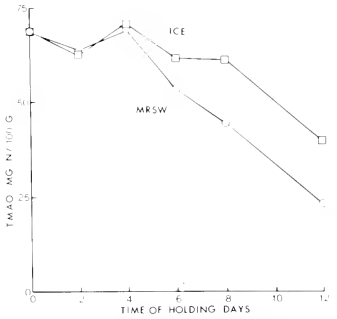


FIGURE 3.—Change in trimethylamine oxide (TMAO) content of fillets from walleye pollock (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW)

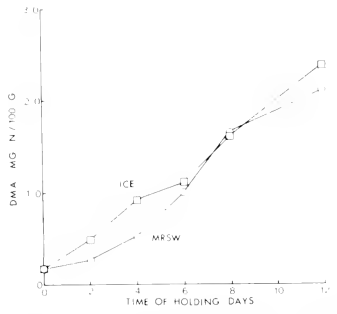


FIGURE 4.—Change in dimethylamine (DMA) content of fillets from walleye pollock (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW)

was linear and equal in both systems and therefore had little usefulness as an index of spoilage. Because of the leaching ability of both the melt water in the ice system and the brine in the MRSW system, the rate of accumulation of DMA in the flesh may be different from the rate of formation of DMA. In the dissociation of TMAO, FA should be formed in equal molar proportion to DMA. The results for analysis for FA in fish from Lot 2 revealed that FA content was 4 ppm in both systems and did not change with time of holding. The lack of an increase in FA content was probably due to its reaction with proteins. Castell et al. (1973) noted that addition of FA lowered the solubility of the protein so the formation of FA can be inferred by a decrease in EPN with time of holding (Figure 5).

Results from an experiment on a control sample to which NaCl was added indicated that the low EPN values of MRSW-held fish were not due to their high salt content. Like the TMAO content, the values for EPN are about the same for either holding system until after 4 days when the values for MRSW-held fish decreased rapidly (Figure 5). Data from fish in Lot 1 also indicated that there was a similar difference in solubility after 4 days of holding. Although there was no significant statistical correlation among EPN values, TMAO content, or the flavor scores, all three of these experimentally determined values decreased at the same time in fish held in MRSW, i.e., after 4 days. With ice-held fish, the decrease in flavor preceded the decrease in TMAO and there was no decrease in EPN values. Evidently, analysis for TMAO and EPN may provide and index of spoilage for MRSW-held fish but not for ice-held fish. Tokunaga (1964) reported data similar to that

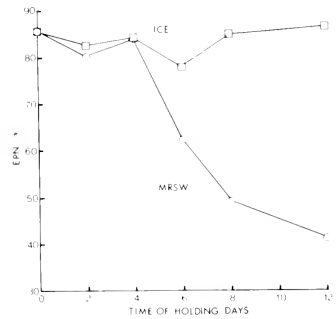


FIGURE 5.—Change in extractable protein nitrogen (EPN) of fillets from walleye pollock (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW)

presented here on the accumulation of DMA and FA in the flesh of walleye pollock stored as fillets at 1°-3° C. Kramer et al. (1977) reported much lower values of DMA but this was probably due to differences in sampling and analytical technique.

Effects of Washing Ground Flesh

Washing improved the appearance of minced pollock (Miyauchi et al. 1977) and is a common procedure in the utilization of pollock in traditional Japanese products (Okada and Noguchi 1974). The water to flesh ratio of 2:1 used in this experiment was much smaller than the 5:1 or larger values used by other investigators. Washing the ground flesh of ice-held pollock increased the apparent yield but no change in yield occurred for samples held in MRSW. If yield data are converted to a salt-free, constant 18% solids basis however, the washing procedure actually decreased the yield to 30% for samples from either system. Yamamoto et al. (1975) reported that 20% of the protein content of ground pollock can be lost under certain washing conditions. Consequently, for commercial purposes, any beneficial results from washing would have to be balanced against a sizable decrease in yield. The advantages of washing are that the product is lighter in color, has less odor, and, in the case of fish held over 4 days in MRSW, has an acceptable salt content (Table 1). TMA, TVA, and NPN content are also reduced by about half on washing.

CONCLUSIONS

Walleye pollock can be held to 6 days if iced thoroughly and still be acceptable for human consumption. Palatable fillets can be obtained from ice-held fish whose physical appearance in the round would probably cause them to be rejected for human consumption. In MRSW, the rapid accumulation of salt in the flesh would prohibit holding pollock more than 4 or 5 days at the 1.5:1 brine to fish ratio utilized in this experiment. The development of a disagreeable taste other than saltiness may be responsible for some of the decrease in flavor scores. The beneficial results of washing the ground or minced flesh of pollock will probably be negated by the decrease in yield and the problems associated with disposing of the wash water. Analysis for TMA or TVA may provide a chemical index of spoilage for pollock held in ice; for pollock held in MRSW, analysis for TMAO or EPN may be useful. Further work is needed before limiting values for TVA, TMA, TMAO, or EPN can be proposed as objective indicators of the acceptability of fresh pollock.

LITERATURE CITED

BARNETT, H. J., R. W. NELSON, P. J. HUNTER, S. BAUER, AND H. GRONINGER
1971. Studies on the use of carbon dioxide dissolved in refrigerated brine for the preservation of whole fish. Fish. Bull., U.S. 69:433-442.

BOTTA, J. R., AND D. H. SHAW
1975. Chemical and sensory analysis of roughhead grenadier (*Macrourus berglax*) stored in ice. J. Food Sci. 40:1249-1252.

BULLARD, F. A., AND J. COLLINS
1978. Physical and chemical changes of pink shrimp, *Pandalus borealis*, held in carbon dioxide modified refrigerated seawater compared with pink shrimp held on ice. Fish. Bull., U.S. 76:73-78.

BYSTEDT, J., L. SWENNE, AND H. W. AAS.
1959. Determination of trimethylamine oxide in fish muscle. J. Sci. Food Agric. 10:301-304.

CASTELL, C. H., AND B. SMITH
1973. Measurement of formaldehyde in fish muscle using TCA extraction and the Nash reagent. J. Fish. Res. Board Can. 30:91-98.

CASTELL, C. H., B. SMITH, AND W. J. DYER
1973. Effects of formaldehyde on salt extractable proteins of gadoid muscle. J. Fish. Res. Board Can. 30:1205-1214.

CASTELL, C. H., AND J. M. SNOW
1949. The effect of pH on the enzymatic reduction of trimethylamine oxide. J. Fish. Res. Board Can. 7:561-562.

DOWDEN, H. C.
1938. LVIII. The determination of small amounts of dimethylamine in biological fluids. Biochem. J. 32:455-459.

DYER, W. J.
1945. Amines in fish muscle. I. Colorimetric determination of trimethylamine as the picrate salt. J. Fish. Res. Board Can. 6:351-358.

DYER, W. J., H. V. FRENCH, AND J. M. SNOW
1950. Proteins in fish muscle. I. Extraction of protein fractions in fresh fish. J. Fish. Res. Board Can. 7:585-593.

FRIEDEMANN, T. E., AND T. BROOK
1938. The identification and quantitative determination of volatile alcohols and acid. J. Biol. Chem. 123:161-184.

HORWITZ, W. (editor)
1975. Official methods of analysis of the Association of Official Analytical Chemists. 12th ed. Assoc. Off. Anal. Chem., Wash., D.C., 1094 p.

IWATA, K., AND M. OKADA
1971. Protein denaturation in stored frozen Alaska pollock muscle—I. Protein extractability and kamaboko forming ability of frozen *surimi*. Bull. Jpn. Soc. Sci. Fish. 37:1191-1198.

IWATA, M.
1975. Population genetics of the breeding groups of walleye pollock (*Theragra chalcogramma*) based on tetrazolium oxidase polymorphism. Sci. Rep. Hokkaido Fish. Exp. Stn. 17:1-9.

KIZEVETTER, I. V.
1973. Chemistry and technology of Pacific fish. Isr. Prog. Sci. Transl., Ltd., Keter Press Binding, Jerusalem, 304 p.

KRAMER, D. E., D. M. A. NORDIN, AND L. J. GARDNER.
1977. A comparison of the quality changes of Alaska pollock and Pacific cod during frozen storage at −28° C. Can. Fish. Mar. Serv. Tech. Rep. 753, 63 p.

LEMON, D. W., AND L. W. REGIER.
1977. Holding of Atlantic mackerel (*Scomber scombrus*) in refrigerated sea water. J. Fish. Res. Board Can. 34:439-443.

LONGARD, A. A., AND L. W. REGIER.
1974. Color and some composition changes in ocean perch (*Sebastes marinus*) held in refrigerated sea water with and without carbon dioxide. J. Fish. Res. Board Can. 31:456-460.

MIYAUCHI, D., G. KUDO, AND M. PATASHNIK.
1977. Effect of processing variables on storage characteristics of frozen minced Alaska pollock. Mar. Fish. Rev. 39(5):11-14.

NIKKILA, O. E., AND R. R. LINKO.
1954. Denaturation of myosin during defrosting of frozen fish. Food Res. 19:200-205.

OKADA, M., AND E. NOGUCHI.
1974. Trends in the utilization of Alaska pollock in Japan. *In* R. Kreuzer (editor), Fishery products, p. 189-193. Fishing News (Books), Ltd., Lond.

POPE, C. G., AND M. E. STEVENS.
1939. CXXX. The determination of amino-nitrogen using a copper method. Biochem. J. 33:1070-1077.

ROACH, S. W., H. L. A. TARR, N. TOMLINSON, AND J. S. M. HARRISON.
1967. Chilling and freezing salmon and tuna in refrigerated sea water. Fish. Res. Board Can., Bull. 160, 40 p.

SHAW, D. H., R. L. GARE, AND M. A. KENNEDY.
1977. Chemical and sensory changes during storage of witch flounder (*Glyptocephalus cynoglossus*) in ice. J. Food Sci. 42:159-162.

STANSBY, M. E., R. W. HARRISON, J. DASSOW, AND M. SATER.
1944. Determining volatile bases in fish. Ind. Eng. Chem., Anal. Educ. 16:593-596.

TOKUNAGA, T.
1964. Studies on the development of dimethylamine and formaldehyde in Alaska pollock muscle during frozen storage. Bull. Hokkaido Reg. Fish. Res. Lab. 29:108-122.

TOZAWA, H., K. ENOKIHARA, AND K. AMANO.
1971. Proposed modification of Dyer's method for trimethylamine determination in cod fish. *In* R. Kreuzer (editor), Fish inspection and quality control, p. 187-190. Fishing News (Books) Ltd., Lond.

UCHIYAMA, H., N. KATO, AND S. EHIRA.
1972. Freshness preservation of Alaska pollock in fishing boats in the North Pacific. Bull. Tokai Reg. Fish. Res. Lab. 72:1-8.

YAMAMOTO, M., A. BARNES, Y. C. LAU, AND J. WONG.
1975. Consequences of washing deboned fish flesh upon appearance and on protein loss. Can. Fish. Mar. Serv. Tech. Rep. 580, 10 p.

NOTES

THICKNESS AND DEPTH DISTRIBUTIONS OF SOME EPIPELAGIC FISH SCHOOLS OFF SOUTHERN CALIFORNIA

Many schooling fish species such as northern anchovy, *Engraulis mordax;* jack mackerel, *Trachurus symmetricus;* and Pacific mackerel, *Scomber japonicus*, are adept at avoidance of surface vessels, even those moving at relatively high speeds. Evasion behavior has complicated measurement of the vertical extent, thickness, and distribution in depth of such fish schools using standard echo sounding techniques. In addition, hull-mounted echo sounders are usually 3 to 4 m below the surface, are blanked for the duration of the transmitted pulses and are relatively ineffective for another 5 to 10 m due to high surface and volume reverberations immediately following the pulse transmission. The combination of evasion behavior and transducer mounting and operation often results in poor sampling of the upper 10 to 20 m of the water column by hull-mounted echo sounders.

Commercial fishermen routinely use air spotters to guide them to school groups (Squire 1972). Fishermen often set their gear visually in water so rich with plankton that visibility is severely restricted. An awareness of these practices and of the implication that many of the fish landed commercially are caught at relatively shallow depths emphasizes the need for a good tool for studying shallow schools. Determination of fish size from swim bladder resonance data requires accurate measurement of the depth and thickness of schools, including those in the upper 20 m (Holliday 1977).

When operating an echo sounder in shallow water, multiple "bottom" echo traces often appear. The second "bottom" in these traces is an image of the sea surface as reflected by the sea floor. With appropriate attention to signal processing it is possible to make measurements on subsurface targets detected via sound which has been reflected from the seabed. Under these conditions, a school of fish near the surface will appear just above the second "bottom." The procedure used to obtain the data presented in this paper is a variation on this observation.

Materials and Methods

Measurements of the mean depth and thickness of schools or aggregations of marine organisms were made at three locations in the California Current near the southern California coast. Each location was occupied during a different season, the first in December 1976, the second in May 1977, and the last during September 1977. The December and May work was done near Santa Catalina Island and the September data were taken about 15 mi southwest of Oceanside, Calif. In December, only 17 schools were studied, because the location of the ship at that time did not coincide with the presence of a large school group. All measurements were made during daylight hours. The schools studied were previously detected on the 30 kHz sonar in its normal side-looking mode. In May, 121 schools were studied and in September measurements were made on 221 targets.

Our bottom bounce system was implemented using the sonar aboard the NOAA ship *David Starr Jordan*. The procedure involved a 30 kHz sonar, steerable in the vertical and horizontal planes, with a capability for depression to 90°, i.e., vertical as in the standard echo sounding mode. Over a flat bottom, the sonar was normally operated at a depression angle of 80° to 85°, depending on water depth. The horizontal steering was to either port or starboard, that is, normal to the ship's track. This allowed sampling of a path whose width varied with water depth on the selected side of the ship and parallel to the ship's track (Figure 1). As an example, for a flat bottom, a depression angle of 80° and a water depth of 500 m, a path was studied with an inner edge which intersected the surface 70 m from the ship's track, and an outer edge which extended to 275 m. These limits were derived from the sonar's 12° beam width, defined as the −6 dB point on the two way (transmit and receive) beam pattern.

The data reported in this note were acquired using 1 ms CW pulse waveforms. It was determined that reliable measurements could be made in water depths up to 500 m with bottom slopes of up to 1.4° using a source level of 216 db//1μPa at 1 m. Bottom characteristics were thought to be

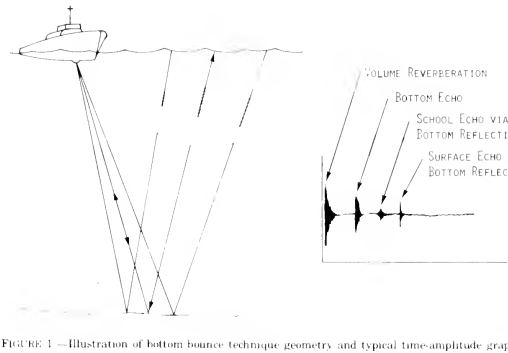


FIGURE 1.—Illustration of bottom bounce technique geometry and typical time-amplitude graph of sonar echo

either mud or mud and sand in the operating areas (Revelle and Shepard 1939:247), but no bottom samples were taken. Relative to that over a flat bottom, performance appeared to be slightly improved in areas with a gentle slope, presumably because of a change in bottom composition or roughness. Schools were easily detected when surface waves were ~3-5 ft, but acoustic measurements became more difficult when the wind increased in strength and whitecaps were formed. This was partly due to uncertainties in the precise location of the surface reflection which is used as a reference in determining target depth. The surface reflection was substantially more diffuse when moderate numbers of whitecaps were visible. This effect may have been due to increased surface scattering and absorption by small air bubbles entrained by wave action near the surface. Although we made no direct measurements of school target strengths, our best estimates range between −5 dB and +10 dB for side aspect target strengths of the schools studied. These estimates are based on earlier measurements made for schools similar in size and suspected composition (Larsen[1]). Ventral aspect target strengths are possibly 3-6 dB less (Love 1977) based on measurements for individuals rather than schools.

[1]Larsen, H. 1974. Distributions of target strengths and horizontal dimensions for aggregations and schools of marine organisms. Tracor Doc. No. T74-SD-1054-U. 66 p.

Results and Discussion

Examination of the bottom bounce data for the depth distribution of schools (Figure 2) revealed an apparent preference of the schools for depths near the seasonal thermocline. The accumulation of the number of observations per depth interval, when normalized to achieve a display with a unit area under the curve, is one means of estimating the probability density function (p.d.f.) for a quantity such as school mean depth (Feller 1971:36). The most probable value (depth, thickness) of a random variable is defined as the value of the quantity at the largest peak in its p.d.f. (Papoulis 1965:140). Though the thermocline was less well defined in May than in December and September, the most probable depth at which a school was found in each survey generally coincided with the maximum thermal gradient (Table 1; Figure 2a, f, k). In order to quantify the apparent relation of fish school distribution and the thermal profile, the mean depth of each school was determined. The data were sorted into 10 m depth intervals. Because of the sonar's beam shape, the volume searched by the bottom bounce procedure varied for a given school depth interval as the bottom depth changed. For a bottom depth of 300 m, about 40% more water was searched for schools at 5 m depth than for schools at 150 m. The number of schools observed during each survey in a particular depth interval (Figure 2a, f, k) was normalized

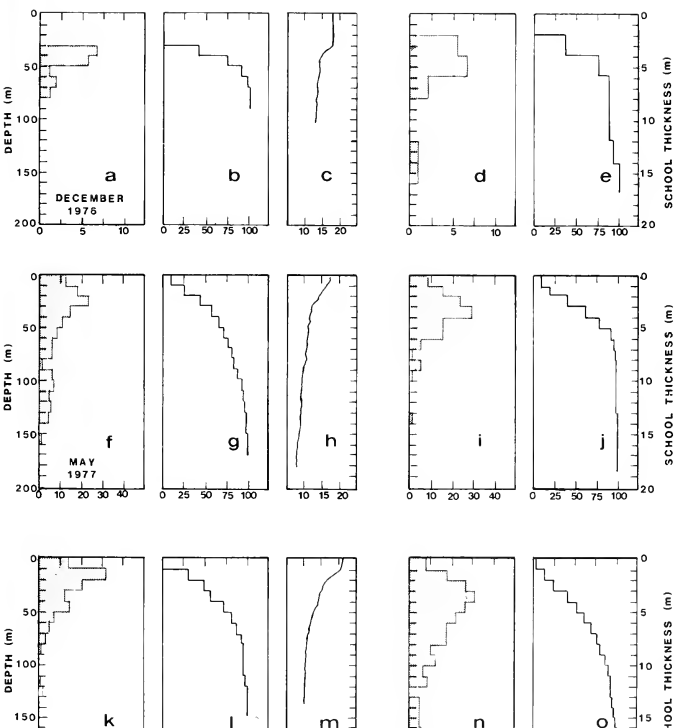


FIGURE 2.—Bottom bounce data and temperature profiles for the December (a-e), May (f-j), and September (k-o) surveys. The distribution of schools mean depth (a, f, k), the cumulative distribution of mean school depths (b, g, l), and the thermal profile (c, h, m) are given versus depth with the scale on the left. The distribution of school thickness (d, i, n) and the cumulative distribution function for thickness (e, j, o) are associated with the scale on the right.

TABLE 1.—Characteristics of depth and thickness of pelagic fish schools studied during three seasons.

Measure	Dec 1976	May 1977	Sept 1977
Total number of schools	17	121	221
Mean depth, m	45	47	22
Most probable depth, m	35	23	12
Median depth, m	37	35	20
Maximum depth, m	70	156	122
Mean thickness, m	4 8	4 1	6 0
Most probable thickness, m	4	4	4
Median thickness, m	3 8	3 4	4 5
Maximum thickness m	15	14	19
Depth of maximum thermal gradient, m	35	22	12

to a common volume before the correlations were calculated. The average temperature gradient was calculated for each depth interval. Correlation coefficients of -0.97 ($N = 9$, 17 schools), -0.95 ($N = 17$, 121 schools), and -0.91 ($N = 13$, 221 schools) were computed between the thermal gradients and the school depth distribution for December, May, and September, respectively. The measurements of temperature gradient, and to some degree the fish distributions, are derived from continuous measures and tend to be serially correlated. Without a measure of the degree of this correlation confidence limits cannot be expressed for the correlation coefficients indicated. Hence, these correlation coefficients are provided as descriptors of this specific data set rather than for predictive purposes. For these locations, times, school groups, and the 10 m vertical resolution, a linear equation based on the thermal gradient described the school vertical distribution with <6% unexplained variation in December, 10% in May, and 17% in September.

We suggest that the observed correlation in all three measurement sets is evidence of a causative factor rather than chance. In December, the most probable school location was at a depth whose temperature was 16°-17° C. Temperatures at the corresponding depths in May and in September were 14°-15° C and 18°-20° C. Within this range of temperatures (16°-20° C) we did not find any seasonal pattern indicating a preference for a particular water temperature. We think the correlation of the thermal gradient with school mean depth and the relatively thin character of the schools is more likely evidence of a thermally associated thin layering of some part of the fishes' food supply rather than a direct result of the temperature profile.

An analysis of the thickness measurements indicates a tendency toward thin schools in each survey (Figure 2d, i, n). To the extent that the data base collected is characteristic of the entire school group, the most probable thickness of a school selected randomly from the three groups studied was consistently near 4 m. In May, one-half of the schools were thinner than 3.4 m. As will be discussed later, the schools in May exhibited sound-scattering characteristics consistent with a dominant population of anchovy larvae. The school horizontal dimensions did not differ substantially from those measured previously for adult fish in other seasons (Hewitt et al. 1976; Larsen see footnote 1; Holliday[2]).

Over one-third of the fish schools observed were at depths <20 m. More than 11% of the schools were above 10 m. An echo sounder operated in the conventional manner would have properly represented the distribution of fish school depths only in December, when the thermocline was relatively deep. A direct comparison of the bottom bounce procedure and conventional sounding was conducted in September when an 18 kHz hull-mounted sounder was used simultaneously with the bottom bounce instrumentation. The bottom bounce data distribution (Figure 2) is seen to differ in both shape and sample size from the comparable conventional sounder data (Figure 3). The differences in shape are principally due to undersampling of the top 20 m of the water column by the conventional system. The large difference in numbers of schools observed simultaneously by the two methods is due to a combination of the factors mentioned in the introduction plus the smaller sampling volume of the conventional system at shallow depths.

Broadband acoustic signatures of the targets within the school group were obtained either during the bottom bounce measurements or within a few hours of the bottom bounce data acquisition. The broadband signatures of the targets varied, but were largely consistent with several sizes of northern anchovy. The acoustic signatures, supporting biological data, and ancillary environmental data are detailed elsewhere (Holliday see footnote 2). The acoustic resonances observed during December were consistent with adult anchovy (0.2 to 0.7 ml swim bladder volume) and a small percentage of unknown targets not containing gas-filled swim bladders. In May, the schools were dominated by acoustic scattering consistent with 25-30 mm anchovy larvae and a few juvenile an-

[2]Holliday, D. V. 1978. MORDAX II III IV. Tracor Doc. No. T-78-SD-002 3 4 -U, San Diego, Calif., 2260 p.

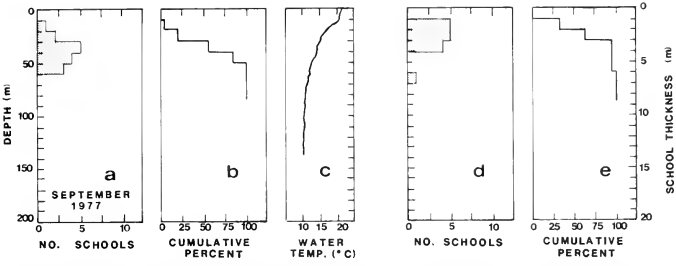


FIGURE 3.—Data measured with a conventional echo sounder operating at 18 kHz. The fish school depth distribution (a), cumulative distribution (b), and thermal profile (c) are associated with the scale on the left. The distribution of school thickness (d) and cumulative distribution (e) are associated with the scale on the right

chovy, 60-90 mm long. The September broadband acoustic work revealed sound-scattering characteristic of a mix of juvenile and adult anchovy with a minor component of jack mackerel. These observations are consistent with known abundances of pelagic fish in the area (Squire 1972). In December and September, the presence of anchovy, jack mackerel, and squid was confirmed by trawl results from depths near the seasonal thermocline. The trawls were conducted during the night following each of the acoustic measurement periods. The trawl results from May were largely negative with respect to adult schooling fish. Qualitatively, increased water clarity in the area off the north end of Santa Catalina Island during May may have permitted greater trawl avoidance than was the case closer to shore at the December and September stations.

Only one of many possible variations of the bottom bounce technique has been discussed. Before attempting an adaptation of the procedure to a particular problem, one should consider, as a minimum, the impact of the following. One of the first parameters at a designer's disposal in acoustics is the frequency to be used. The reflectivity of the target, the bottom, and the surface are all dependent on frequency as is the absorption of the sound in the water column. Ambient noise, ship's self-noise, and reverberation levels are also strongly frequency dependent. Pulse length, pulse type, and a variety of signal processing techniques are also at the designer's disposal and must be determined.

Some important parameters are not available to the designer for selection. These include bottom characteristics (scattering, absorption, and penetration), bottom slope, and surface conditions such as roughness and the presence of entrained bubbles. These characteristics of the intended operating area must be considered as well as maximum and minimum water depths before designing a bottom bounce system for a particular application. While it is readily apparent that there will be a maximum effective operating depth for any given system design in a particular physical environment, it is also important to realize that shallow reflection angles at the bottom and surface may limit shallow water operation. Another important shallow water limitation is the persistence of bottom reverberation for ranges at which one desires to make measurements on schools.

Conclusions

The thickness and vertical distributions of shallow schools of many fish cannot be accurately measured by conventional echo sounding techniques. Consequently, a new approach which makes use of the bottom bounce acoustic propagation path has been developed and used for measurements on northern anchovy schools off southern California. These measurements, at three locations in three different seasons, revealed that the schools occupied a depth zone only a few meters thick. Good agreement was found between occurrences of the mean depths of the schools and the seasonal ther-

mocline, where it is hypothesized that thermal stratification, and associated water density microstructure may lead to an aggregation of some part of the fishes' food supply in thin layers.

Acknowledgments

This work was supported, in part, by the National Marine Fisheries Service, NOAA, under Contract 03-7-208-35037. The authors would like to acknowledge the technical contributions of David Doan and David Horton in the construction of the electronics and the conduct of the measurements. The advice, encouragement, and support of Paul Smith, NMFS, is gratefully acknowledged. Our appreciation is also extended to the reviewers, both formal and informal, and the editor.

Literature Cited

FELLER, W.
1966. An introduction to probabilty theory and its applications, Vol. 2. John Wiley & Sons, Inc., N.Y., 626 p.

HEWITT, R. P., P. E. SMITH, AND J. C. BROWN.
1976. Development and use of sonar mapping for pelagic stock assessment in the California Current area. Fish Bull., U.S. 74:281-300.

HOLLIDAY, D. V
1977. The use of swimbladder resonance in the sizing of schooled pelagic fish. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 170:130-135.

LOVE, R. H
1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. 62:1397-1403.

PAPOULIS, A.
1965. Probability, random variables and stochastic processes. McGraw-Hill, N.Y., 583 p.

REVELLE, R., AND F. P. SHEPARD.
1939. Sediments off the California Coast. *In* P. D. Trask (editor), Recent marine sediments, p. 245-282. Am. Assoc. Pet. Geol., Tulsa.

SQUIRE, J. L., JR.
1972. Apparent abundance of some pelagic marine fishes off the southern and central California coast as surveyed by an airborne monitoring program. Fish. Bull., U.S. 70:1005-1019

D. V. HOLLIDAY
H. L. LARSEN

Tracor, Inc., San Diego Laboratory
3420 Kenyon Street
San Diego, CA 92110

THE EFFECT OF BODY SIZE ON THE STANDARD METABOLIC RATE OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*

The standard metabolic rate (SMR) of fish is the energy requirement of a postabsorptive animal completely at rest (Beamish and Mookherjii 1964; Fry 1971; Brett 1972). It approximates the energy demand of all metabolic processes except swimming and digestion. The SMR (and its relation to fish size) is an important input parameter for energetics, growth, and population models (Kitchell et al. 1974; Kitchell et al. 1977). The SMR may also be used to predict optimal fish cruising speed (Weihs 1973, 1977). I undertook this study to provide SMR measurements for skipjack tuna, *Katsuwonus pelamis*. These measurements may be incorporated into models such as those described in Sharp and Francis (1976), Kitchell et al. (1978), and Sharp and Vlymen (1978).

The SMR is generally determined by extrapolation of a metabolic rate versus swimming activity curve back to a zero activity level (Beamish 1964; Brett 1965; Muir et al. 1965). However, because it is difficult simultaneously to measure metabolic rate and activity level of large, highly active, pelagic species such as skipjack tuna, SMR was measured directly.

Methods and Materials

Skipjack tuna, purchased from local fishermen, were maintained at the Kewalo Research Facility of the National Marine Fisheries Service (described in Nakamura 1972). Fish were kept in outdoor tanks from 2 days to several weeks before use. Food was presented to all fish daily; however, a fish was not fed for at least 20 h prior to its use in an experiment. This allowed sufficient time for an animal to clear its stomach and intestine and for its blood glucose level to return to prefeeding levels (Magnuson 1969).

To reduce struggling and minimize injury during handling, each fish was injected with the neuromuscular blocking agent gallamine triethiodide (approximately 1 mg kg^{-1}). The animal was then placed in a Plexiglas[1] flow-through box respirometer, similar to that described in Stevens (1972). The spinal cord was cut immediately behind the skull to stop all overt muscular activity

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the wound packed with foam rubber to minimize bleeding. Electrocardiogram (ECG) leads were mounted subcutaneously on the ventral body surface and an 18-gage hypodermic needle, with a thermistor bead mounted in its tip, was pushed through the dorsal musculature to the vertebral column. The ECG signal was displayed on an oscilloscope and the red muscle temperature determined by balancing a wheatstone bridge circuit containing the needle mounted thermistor and a 5-decade resistance substitution box.

Oxygen concentration of the water upstream and downstream of the fish was monitored simultaneously with two Yellow Springs Instruments (model 51A) dissolved oxygen meters equipped with Clark-type, polographic electrode, oxygen-temperature probes. Water flow through the respirometer was maintained at approximately 3 l kg^{-1} (body weight) min^{-1}, and was measured by recording the time required to fill a 1 l graduated cylinder. The source of the seawater was the same as that which supplied the holding tanks. No attempt was made to control water temperature which ranged from 23.5° to 25.5° C.

Dissolved oxygen levels, water flow rate, heart rate, red muscle temperature, and water temperature were determined every 10 min and measurements were continued until the fish's metabolic rate remained relatively stable for at least 1 h.

Results and Discussion

The SMR of each fish was determined by finding the minimum predicted metabolic rate based on a second degree polynomial fitted to observed metabolic rate measurements. This method is an acceptable approximation for asymptotic curve fitting (Snedecor and Cochran 1967). To illustrate this technique, the observed and predicted metabolic rate, body temperature, and heart rate are presented in Figure 1.

Heart rate was monitored only as a check on the health of the animal. Experiments were terminated if the heart rate became erratic or slowed

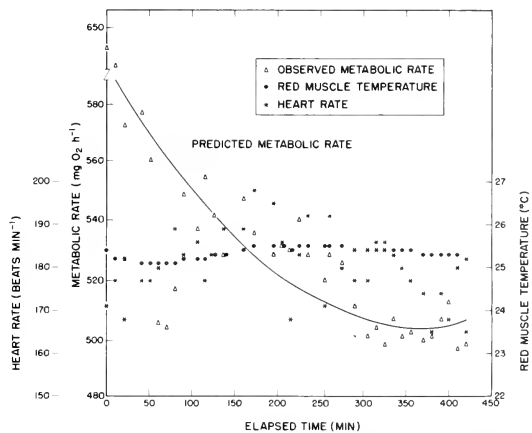


FIGURE 1.—Changes in metabolic rate, heart rate, and red muscle temperature of a 1.456 kg skipjack tuna during an experiment to determine standard metabolic rate (SMR). The predicted metabolic rate is based on a least-squares fitted second degree polynomial. The minimum predicted metabolic rate (i.e., SMR) is 505 mg $O_2 h^{-1}$.

significantly. Red muscle temperature was monitored to test if changes in metabolic rate reflected changes in it. All fish showed red muscle temperatures as stable as those shown in Figure 1. Fish were in the respirometry box approximately 15 to 30 min before data recording began and red muscle temperatures generally approached thermal steady state during this period.

The SMR of 33 fish (0.317-4.737 kg) was successfully determined. A regression line of SMR versus body weight was fitted by Gauss-Newton iteration technique (Biomedical Computer Programs, program number BMDP 3R), rather than by a linear regression technique based on log-log transformation of the data (Figure 2). The advantages of the former method and disadvantages of the latter have been discussed by Zar (1968) and Glass (1969).

The best-fitting allometric equation was found to be:

$$SMR = 412.0\ (\pm 27.1)\ W^{0.563\ (\pm 0.07)} \qquad (1)^2$$

where SMR = standard metabolic rate in milligrams O_2 per hour and
W = body weight in kilograms;

values in parentheses are the standard deviations of the parameters. The coefficient of determination (r^2) is 0.72.

The exponent in the allometric equation describing the effect of body size on the SMR of other teleosts ranges from approximately 0.65 to >1 (Winberg 1956; Fry 1957; Beamish and Mookherjii 1964; Beamish 1964; Glass 1969; Brett 1972). The lower value for the exponent in Equation (1) indicates that the weight specific SMR (i.e., milligrams O_2 per gram per hour) of skipjack tuna decreases more steeply as body size increases than does the weight specific SMR of other species.

The strong influence of body size on the SMR may be a unique characteristic of thermoconserving species such as skipjack tuna. However, the value of the weight exponent could also be influenced by the technique used to measure SMR. For comparative purposes, it would be useful to determine the SMR's (and corresponding allometric equation) of species (e.g., salmonids) where

[2]If the allometric equation to describe the effect of body size on whole body SMR is $SMR = aW^b$ then the corresponding equation to describe weight-specific SMR versus body weight is: $SMR_W = aW^b/W$ or $SMR_W = aW^{b-1}$ where SMR_W = weight-specific SMR, W = body weight, and a and b are fitted parameters.

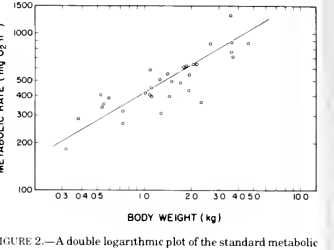


FIGURE 2.—A double logarithmic plot of the standard metabolic rate (SMR) versus body weight (W). The line represents the allometric equation $SMR = 412.0\ W^{0.563}$. The coefficient of determination is 0.72.

these parameters are already known, but employing the methodology outlined in this study.

The SMR has been postulated to be a function of: the diffusing capacity of the respiratory system, whole blood sugar concentration, and the rate at which the circulatory system can deliver substrates and oxygen to the cells (Schmidt-Nielsen 1970; Ultsch 1973; Coulson et al. 1977; Wilkie 1977; Hughes 1977; Umminger 1977). Specifically which of these factors most influence the SMR of skipjack tuna is unknown at this time. Selection pressures apparently favor significant reductions in the weight-specific SMR of skipjack tuna as body size increases (hence the lower exponent in Equation (1)). How the factors that determine SMR could be affected by such selection pressures is also unknown.

The SMR's for skipjack tuna are approximately 5 to 10 times greater than those reported for other teleosts of equal body size (Pritchard et al. 1958; Beamish 1964; Brett 1965, 1972). However, the great difference in the effect of weight on SMR, and the unique methodology employed in this study, makes direct comparisons tenuous.

Application of the Results

Careful application of my results in energetics models is advised for several reasons. First, skipjack tuna attain maximum body size of approximately 22 kg (Kitchell et al. 1978); although the weight range of fish I used in this study covers more than an order of magnitude, there is still a large untested size range. Because skipjack tuna

4 to 5 kg are extremely difficult to capture and transport, it is unlikely that specimens larger than this will be tested in the foreseeable future.

Second, the SMR includes the energetic cost of osmoregulation and cardiac work. The energy requirement of both processes comprises a significant fraction of the SMR (Heath 1964) and more importantly, the energy demand of these processes is dependent on swimming speed (Rao 1968; Farmer and Beamish 1969; Nordlie and Leffler 1975). Therefore prediction of energy demand as a function of swimming speed may not be adequately determined by simple addition of the SMR and the energy cost of swimming based on a theoretical estimate of hydrodynamic drag; an estimate of the increased internal work, due to activity, should also be included.

Third, the scatter in the SMR's presented in Figure 2 is due, in part, to the difficulty of working with animals such as skipjack tuna, which are both highly active and physiologically delicate. There are, however, also at least two distinct subpopulations of skipjack tuna that occur around the Hawaiian Islands (Sharp[3]). It is reasonable to suspect the SMR of individuals from the various subpopulations might be significantly different when measured under identical conditions. Again, reasonable caution in application of the data presented here is urged.

Acknowledgments

I thank the following people for helpful criticisms of the manuscript and useful discussions: Andrew Dizon, Gary Sharp, Don Stevens, Causey Whittow, and Carol Hopper. Randolph Chang, Douglas Davies, and Victor Honda provided technical assistance.

Literature Cited

BEAMISH, F. W. H.
1964 Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Can. J. Zool. 42:177-188.

BEAMISH, F. W. H., AND P. S. MOOKHERJII.
1964 Respiration of fishes with special emphasis on standard oxygen consumption. I. Influence of weight and temperature on respiration of goldfish, *Carassius auratus* L. Can. J. Zool. 42:161-175.

BRETT, J. R.
1965 The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22:1491-1501
1972 The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir. Physiol. 14:151-170

COULSON, R. A., T. HERNANDEZ, AND J. D. HERBERT.
1977. Metabolic rate, enzyme kinetics *in vivo*. Comp. Biochem. Physiol. 56A:251-262

FARMER, G. J., AND F. W. H. BEAMISH.
1969 Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. J. Fish. Res. Board Can. 26:2807-2821

FRY, F. E. J.
1957. The aquatic respiration of fish. *In* M. E. Brown (editor), The physiology of fishes, Vol. 1, p. 1-63. Acad. Press, N.Y.
1971 The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 1-98. Acad. Press, N.Y.

GLASS, N. R.
1969 Discussion of calculation of power function with special reference to respiratory metabolism in fish. J. Fish. Res. Board Can. 26:2643-2650

HEATH, A. J.
1964 Heart rate, ventilation, and oxygen uptake of a marine teleost in various oxygen tensions. Am. Zool. 4:386.

HUGHES, G. M.
1977. Dimensions and the respiration of lower vertebrates. *In* T. J. Pedley (editor), Scale effects in animal locomotion, p. 57-81. Acad. Press, N.Y.

KITCHELL, J. F., J. F. KOONCE, R. V. O'NEILL, H. H. SHUGART, JR., J. J. MAGNUSON, AND R. S. BOOTH
1974 Model of fish biomass dynamics. Trans. Am. Fish. Soc. 103:786-798

KITCHELL, J. F., W. H. NEILL, A. E. DIZON, AND J. J. MAGNUSON.
1978 Bioenergetic spectra of skipjack and yellowfin tunas. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 357-368. Acad. Press, N.Y.

KITCHELL, J. F., D. J. STEWART, AND D. WEININGER.
1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922-1935.

MAGNUSON, J. J.
1969 Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98:379-392.

MUIR, B. S., G. J. NELSON, AND K. W. BRIDGES.
1965. A method for measuring swimming speed in oxygen consumption studies on the aholehole *Kuhlia sandvicensis*. Trans. Am. Fish. Soc. 94:378-382.

NAKAMURA, E. L.
1972 Development and uses of facilities for studying tuna behavior. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Current perspectives in research, Vol. 2, p. 245-277. Plenum Press, N.Y.

NORDLIE, F. G., AND C. W. LEFFLER
1975 Ionic regulation and the energetics of osmoregula-

[3]G. D. Sharp, Inter-American Tropical Tuna Commission, La Jolla, CA 92038, pers. commun., 1978

tion in *Mugil cephalus* Lin. Comp. Biochem. Physiol. 51A:125-131

PRITCHARD, A. W., E. FLOREY, AND A. W. MARTIN
1958. Relationship between metabolic rate and body size in an elasmobranch (*Squalus suckleyi*) and in a teleost (*Ophiodon elongatus*). J. Mar. Res. 17:403-411.

RAO, G. M. M.
1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. Can. J. Zool. 46:781-786.

SCHMIDT-NIELSEN, K.
1970. Energy metabolism, body size, and problems of scaling. Fed. Proc. 29:1524-1532.

SHARP, G. D., AND R. C. FRANCIS.
1976. An energetics model for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean. Fish. Bull., U.S. 74:36-51

SHARP, G. D., AND W. J. VLYMEN III.
1978. The relation between heat generation, conservation and the swimming energetics of tunas. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 212-232. Acad. Press, N.Y.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

STEVENS, E. D.
1972. Some aspects of gas exchange in tuna. J. Exp. Biol. 56:809-823.

ULTSCH, G. R.
1973. A theoretical and experimental investigation of the relationships between metabolic rate, body size, and oxygen exchange capacity. Respir. Physiol. 18:143-160.

UMMINGER, B. L.
1977. Relation of whole blood sugar concentrations in vertebrates to standard metabolic rate. Comp. Biochem. Physiol. 56A:457-460.

WEIHS, D.
1973. Optimal fish cruising speed. Nature (Lond.) 245: 48-50.
1977. Effects of size on sustained swimming speeds of aquatic organisms. *In* T. J. Pedley (editor), Scale effects in animal locomotion, p. 333-338. Acad. Press, N.Y.

WILKIE, D. R.
1977. Metabolism and body size. *In* T. J. Pedley (editor), Scale effects in animal locomotion, p. 23-36. Acad. Press, N.Y.

WINBERG, G. G.
1956 (Rate of metabolism and food requirement of fishes.) [In Russ.] Nauchn. Tr. Belorussk. Gos. Univ. Minsk., 253 p. (Transl. 1960, Fish. Res. Board Can., Transl. Ser. 194, 202 p.)

ZAR, J. H.
1968. Calculation and miscalculation of the allometric equation as a model in biological data. Bioscience 18:1118-1120.

RICHARD W. BRILL

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830, Honolulu, HI 96812
Present address: *Department of Zoology*
The University of British Columbia
2075 Wesbrook Mall, Vancouver, B.C. V6T 1W5, Canada

EFFECTS OF A THERMAL DISCHARGE ON REPRODUCTIVE CYCLES IN *MYTILUS EDULIS* AND *MYTILUS CALIFORNIANUS* (MOLLUSCA, BIVALVIA)

One principal concern about thermal effluents is the effect of altered temperatures on the reproductive biology of organisms near the discharge (e.g., Hedgpeth and Gonor 1969). In marine mussels of the genus *Mytilus*, the role of temperature in regulating the reproductive cycle and the effects of temperature stress on the energy budget for growth and reproduction have been particularly well studied (Bayne 1975; Gabbott 1976; Seed 1976). *Mytilus edulis* has a seasonal cycle of gametogenic activity that is conditioned by temperature and is linked with the storage and utilization of reserve materials in the body (Bayne 1975). Metabolism and filtration rate show complete temperature acclimation from 5° to 20° C, and the scope for growth is relatively independent of temperature over this range (Widdows and Bayne 1971; Widdows 1973, 1978a). However, above 20° C the mechanisms of temperature adaptation break down, producing an increase in the metabolic rate, a decline in filtration rate, and thus a reduced scope for growth (Widdows 1976, 1978a). Above 25° C this scope is so reduced that there is no energy for growth, and energy reserves are depleted in order to survive (Widdows 1978b).

This study examined the effect of a thermal discharge from a coastal steam-electric power plant on reproduction in *M. edulis* and *M. californianus* in central California. The reproductive cycles and gonadal weights of these mussels in the warmwater outfall and in control regions of naturally occurring temperatures were compared using body component index methods. Water temperatures in the outfall exceeded 20° C much of the late summer and early fall, while plant intake temperatures were usually in the 12°-15° C range and rarely exceeded 17° C.

Methods

This study was conducted at the Pacific Gas and Electric Company fossil-fuel power plant at Morro Bay, Calif. (Figure 1). The 1,030-MW plant used ocean water for once-through cooling and discharged warmed water into a canal about 80 m long. The canal released water into the surf, forming a plume with an isotherm 5° C above naturally occurring temperatures of about 0.6-3.0 acres sur-

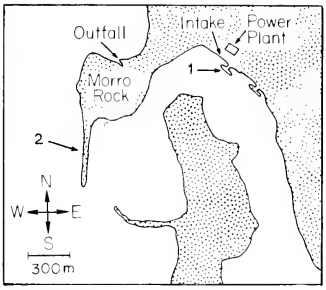


FIGURE 1.—Locations of the intake and outfall of the Morro Bay power plant in California and the collecting sites for mussels in this study. In addition to outfall samples of both species, control samples of *Mytilus edulis* were taken from site 1, and control samples of *M. californianus* were taken from site 2.

face area depending on plant load and weather conditions. The mean temperature differential between the intake and outfall was about 7° C and ranged from about 3° C in spring to about 15° C in late summer and fall (Figure 2). The intake showed a seasonal cycle of low temperatures around 11°-12° C in winter and high temperatures around 14°-15° C in summer and fall. Mean outfall temperatures exceeded 20° C from May through January and varied seasonally from around 18° C in spring to around 26° C from July through October. Daily temperature fluctuations in the outfall were much greater (up to 11° C) than those in the intake (up to 3° C). Also, heat treatment every few weeks to kill organisms fouling the cooling tubes raised outfall temperatures in places to as high as 36° C for about an hour.

Mytilus californianus and *M. edulis* were collected from the warmwater outfall and from nearby control areas of normal temperatures at about monthly intervals from November 1972 to November 1973 (Figure 1). *Mytilus edulis* were collected from shallow (1-2 m) subtidal rocks midway along the discharge canal and from the undersides of floats near the intake. *Mytilus californianus* were collected intertidally at 1-3 ft above mean lower low water at the mouth of the discharge canal and at equivalent tidal heights from the jetty at the Morro Bay harbor entrance. High surf made collecting impossible on the jetty and difficult at the mouth of the discharge canal at

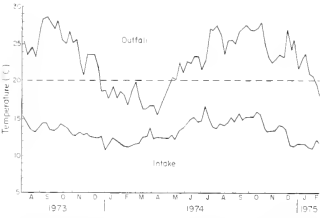


FIGURE 2.—Temperature records from the outfall and intake of the Morro Bay power plant. Weekly mean temperatures were calculated from continuous temperature recorders positioned at mean lower low water near the power plant's intake screens and discharge tubes. The dashed line marks the temperatures above 20° C, which are energetically stressful to *Mytilus edulis*. (Redrawn from Hines 1978.)

times during the winter. Neither outfall nor control *M. edulis* were exposed to significant surf at any time, but the outfall had much stronger currents (up to 0.7 m/s) than the control areas. Salinities in the control and discharge areas did not differ significantly from seawater.

The temperature records closely reflect the thermal environments of the samples of *M. edulis*, because they were collected at nearly the same locations as the recorders. However, the records do not represent as closely the thermal regimes of the samples of *M. californianus*, which were collected from intertidal positions above the recorders and were therefore exposed to air temperatures part of the time, or which were collected at locations distant from the recorders. Seawater temperatures for the control sampling site for *M. californianus* were sometimes 1°-2° C lower than intake temperatures, and temperatures at the mouth of the discharge canal where outfall samples were taken were often 2°-4° C lower than the records show due to dilution of the warmwater discharge by incoming surf.

Monthly samples of 12 mussels 70-110 mm long from outfall and from control populations of each species were processed. For each mussel, the shell length and the internal shell volume determined by the volume (milliliters) of water required to fill the empty valves were recorded. Total wet tissue weight (grams) and wet weight of the gonad tissue dissected from the mantle and body mass were recorded for each mussel. From these data the gonadal index was calculated as: (gonad wt ×

100) total tissue wt. The body weight/shell volume index was calculated as: (total wt − gonad wt)/shell volume. The gonadal index reflects reproductive condition and the body weight/shell volume index reflects nutritional condition (Giese and Pearse 1974). Preliminary work showed that indexes calculated from wet and then dry weights did not have significantly different variances.

Results

Mytilus edulis and *M. californianus* longer than about 50 mm were sexually mature, and the gonadal indexes of both species had large variances. Because gonadal indexes of both species were calculated for a large size range (70-110 mm shell length) in each population, the covariance of gonadal index on shell volume was analyzed for each species. However, regressions of the arcsine transformation of the gonadal index on shell volume calculated for each monthly sample did not have significantly different slopes for either species (ANCOVA, $P > 0.05$): for *M. californianus* the common regression slope = 0.09, $F_{(8,190)} = 0.206$; for *M. edulis* the common regression slope = 0.08, $F_{(21,220)} = 0.217$. Therefore, mussel size was ruled out as a significant source of variability in gonadal index for this study. Rather, the variability was probably a result both of the difficulty in precisely dissecting the diffuse gonad from the body tissues and of a large degree of inherent reproductive asynchrony in the populations.

The gonadal indexes of *M. edulis* from the outfall and from the control populations showed the same distinct cycle of gonads increasing in size during summer and fall and dropping to a low in spring (Figure 3). However, gonadal weights of the outfall population were lower than the controls, as can be seen by the generally lower level of the outfall gonadal index, particularly in the April through November samples. Similarly, the body weight/shell volume index for *M. edulis* showed an annual cycle which peaked in summer and dropped in fall and winter to a low in spring (Figure 3). The phase of this body weight/shell volume index was slightly in advance of the gonad cycle. As with the gonad cycle, the outfall population had the same basic body weight/shell volume cycle as the control, but it showed a generally lower level than the controls and indicated that the outfall mussles were in poorer nutritional condition than the controls.

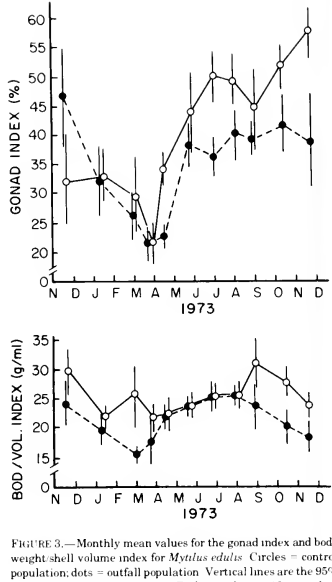


FIGURE 3.—Monthly mean values for the gonad index and body weight/shell volume index for *Mytilus edulis*. Circles = control population; dots = outfall population. Vertical lines are the 95% confidence limits of the means. Each sample was 12 mussels.

In contrast to *M. edulis*, the gonadal index of *M. californianus* did not show a distinct annual cycle (Figure 4). The April and May control samples probably represented a peak of reproductive activity, but the erratic fluctuations of the index made this uncertain without histological information or field observations of spawning. Except for this brief spring peak, the outfall population showed a consistently higher level of ripeness throughout the year than the control mussels. The body weight/shell volume index of *M. californianus* appeared to show a slight annual cycle with a low in March and April and higher levels in late summer (Figure 4). However, this trend was not pronounced and did not appear to correlate with the gonadal index. Contrary to the trend shown by gonadal index levels, outfall body weight/shell volume indexes were consistently lower than the

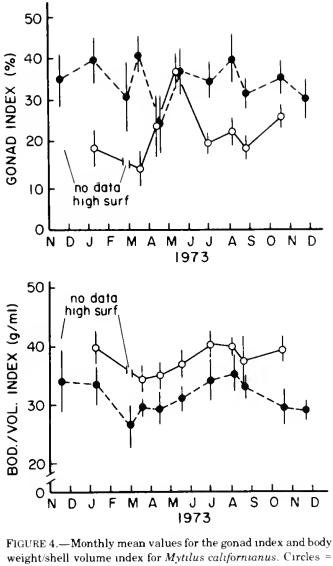


FIGURE 4.—Monthly mean values for the gonad index and body weight/shell volume index for *Mytilus californianus*. Circles = control population; dots = outfall population. Vertical lines are the 95% confidence limits of the means. Each sample was 12 mussels.

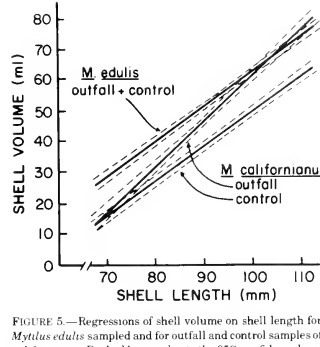


FIGURE 5.—Regressions of shell volume on shell length for all *Mytilus edulis* sampled and for outfall and control samples of *M. californianus*. Dashed lines indicate the 95% confidence limits of the mean predicted shell volumes. For each population of mussels the sample size, correlation coefficient, and regression equation with the 95% confidence limits of the slopes and intercepts in parenthesis was as follows. *Mytilus californianus* outfall: $n = 132$, $r = 0.94$, Vol = 1.48(±0.09)Length − 85.8(±8.5); control: $n = 96$, $r = 0.91$, Vol = 1.13(±0.11)Length − 63.0(±9.0). *Mytilus edulis* outfall: $n = 132$, $r = 0.94$, Vol = 1.07(±0.07)Length − 47.2(±5.2); control: $n = 132$, $r = 0.85$, Vol = 1.12(±0.12)Length − 48.4(±10.8); combined: $n = 264$, $r = 0.88$, Vol = 1.10(±0.07)Length − 47.9(±6.2).

controls, indicating that the control mussels were in better nutritional condition.

For any given body weight, a larger shell volume will result in a lower body weight/shell volume index. Therefore, the relationship of shell volume to shell length was examined for each of the mussel populations. Over the size range of mussels sampled in the study, this relationship was closely approximated by linear regressions, even though it would probably have been curvilinear if much smaller mussels were included in the samples. Shell volumes of outfall *M. californianus* were proportionally larger than the controls over most of the sizes sampled (Figure 5), such that the slope and the intercept of the regression of shell volume on shell length for outfall mussels were significantly different from those of the regression for the control mussels (t-tests, $P<0.05$). However, for *M. edulis* the slopes and the intercepts were not significantly different between regressions of shell volume on shell length for outfall and control populations (t-tests, $P>0.05$). Therefore, a single, combined regression for both populations of *M. edulis* was calculated (Figure 5). The difference in the shells of *M. californianus* may partly account for the apparent differences in the nutritional condition of the outfall and control populations.

Discussion

The reproductive cycle of *M. edulis* varies with geographical location, but reproductive activity is generally correlated with rising water temperatures (Kinne 1970; Seed 1976). Bayne (1975) showed that gametogenesis is regulated by changing temperatures in terms of increasing "day-degrees." In the present study *M. edulis* from both the outfall and control populations also

showed the same cycle of increasing gonad activity in the late spring and early summer when temperatures were increasing, in spite of the temperature differential between the two areas. However, the outfall population did not attain as high gonadal index levels as the control, probably because stressful temperatures above 20° C were reached in June, leaving less energy available for gamete production (Widdows 1976; 1978a, b). Food availability interacts with temperature to influence the energy budget of mussels (Bayne 1973; Widdows 1978a, b), but food availability estimated by dry weight of suspended matter is not significantly different in the outfall and intake water at Morro Bay (Hargreaves 1977). In July through October outfall temperatures exceeded the energetically extremely stressfull level of 25° C (Widdows 1978a, b), and the body weight/shell volume index declined to levels well below the controls. Although the reduced gonadal index of the outfall population at Morro Bay strongly indicated a reduced reproductive output, *M. edulis* under stress apparently conserve the gonad up to a point at the expense of other tissues, so that stressed mussels continue to produce some gametes (Gabbott and Bayne 1973; Bayne 1975). However, gametes from stressed mussels result in embryos and larvae that are less viable than those produced by adults not under stress (Bayne 1972).

In *M. californianus* the relationship of temperature to the energy budget for growth and reproduction is not well studied as it is in *M. edulis*, nor have the critically stressful temperatures been determined for *M. californianus*. *Mytilus californianus* is reported to reproduce year-round with peak periods of more intense spawning at various times, particularly in spring and fall (Seed 1976). In the present study the control population showed a peak of gonadal activity in spring, corresponding with the period of rising ambient temperatures. The outfall population showed higher gonadal index levels than the controls year-round, indicating that in *M. californianus* higher absolute temperatures, rather than a temperature change as in *M. edulis*, stimulate gametogenesis and increased reproductive output. However, the body weight/shell volume index of *M. californianus* in the outfall was consistently lower than the control population. If *M. californianus* conserves its gonad at the expense of other tissues under the increased energetic stress of elevated temperatures in the same manner as *M. edulis*, this would explain the lower body weights of the outfall mussels.

It is not clear why all but the smallest outfall *M. californianus* in my samples had relatively larger shell volumes at the same shell length than the controls. The difference may reflect greater shell erosion of the control mussels, resulting from high surf levels on the jetty, rather than reflecting a temperature effect on the form of shell growth. Seed (1968) showed that shell growth in *M. edulis* is extremely variable, depending upon population density and physical conditions. *Mytilus californianus* also shows great variation in shell form from one locality to another (Coe and Fox 1944), and intertidal height and latitude also affect shell growth (Dehnel 1956).

It is often difficult to apply results from controlled laboratory conditions directly to field situations, where there are multiple and fluctuating variables. I must acknowledge that the ability to interpret the results of the present paper speaks well for the realistic analysis of energetics and stress in marine mussels in recent laboratory work by others. However, very few marine invertebrates have received this level of study critical for the assessment of complex sublethal effects of environmental disturbances such as thermal effluents.

Acknowledgments

I am grateful to Cadet Hand, Virgil Schrock, Ralph Smith, and George Trezek for their advice and support. Bruce Hargreaves, Chris Harrold, and John Pearse gave valuable comments on the manuscript. Linda Hines, Brian Jennison, Marg Race, Jim Rutherford, Jon Standing, Chris Tarp, and John Warrick helped in many ways. The Pacific Gas and Electric Company gave generously of their time and facilities. This study was funded by National Science Foundation Grant GI-34932 to George Trezek and Virgil Schrock of the Department of Engineering, University of California, Berkeley; Sea Grant NOAA 04-5-158-20 to Ralph I. Smith and Cadet Hand of the Department of Zoology; and a grant from the Pacific Gas and Electric Company.

Literature Cited

BAYNE, B. L.

1972. Some effects of stress in the adult on the larval development of *Mytilus edulis*. Nature (Lond.) 237:459.

1973. Physiological changes in *Mytilus edulis* L. induced by temperature and nutritive stress. J. Mar. Biol. Assoc. U.K. 53:39-58.

1975. Reproduction in bivalve molluscs under environmental stress. *In* F. J. Vernberg (editor), Physiological ecology of estuarine organisms, p. 259-277. Univ. S.C. Press, Columbia.

COE, W. R., AND D. L. FOX.
1944 Biology of the California sea-mussel (*Mytilus californianus*). III. Environmental conditions and rate of growth. Biol. Bull. (Woods Hole) 87:59-72.

DEHNEL, P. A.
1956. Growth rates in latitudinally and vertically separated populations of *Mutilus californianus*. Biol. Bull. (Woods Hole) 110:43-53.

GABBOTT, P. A
1976. Energy metabolism. *In* B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 293-355. Camb. Univ. Press, Lond.

GABBOTT, P. A., AND B. L. BAYNE.
1973. Biochemical effects of temperature and nutritive stress in *Mytilus edulis* L. J. Mar. Biol. Assoc. U.K. 53:269-286.

GIESE, A. C., AND J. S. PEARSE.
1974. Introduction: general principles *In* A. C. Giese and J. S. Pearse (editors), Reproduction of marine invertebrates, Vol. 1, p. 1-49. Acad. Press, N.Y.

HARGREAVES, B. R
1977. Growth of two marine mussels, *Mytilus edulis* and *Mytilus californianus*. Ph.D. Thesis, Univ. California, Berkeley, 119 p.

HEDGPETH, J. W., AND J. J. GONOR.
1969. Aspects of the potential effect of thermal alteration on marine and estuarine benthos. *In* P. A. Krenkel and F. L. Parker (editors), Biological aspects of thermal pollution, p. 80-122. Vanderbilt Univ. Press, Nashville.

HINES, A. H.
1978 Reproduction in three species of intertidal barnacles from central California. Biol. Bull. (Woods Hole) 154:262-281.

KINNE, O.
1970. Temperature. *In* O. Kinne (editor), Marine ecology, Vol. 1, p. 321-616. John Wiley and Sons, N.Y.

SEED, R.
1968. Factors influencing shell shape in the mussel *Mytilus edulis*. J. Mar Biol. Assoc. U.K. 48:561-584.
1976. Ecology. *In* B. L. Bayne (editor), Marine mussels: their ecology and physiology, p. 13-65. Camb. Univ. Press, Lond.

WIDDOWS, J.
1973. Effect of temperature and food on the heart beat, ventilation rate and oxygen uptake of *Mytilus edulis*. Mar. Biol. (Berl.) 20:269-276
1976. Physiological adaptation of *Mytilus edulis* L. to cyclic temperatures. J. Comp. Physiol. 105B:115-128.
1978a. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. Mar Biol. Assoc. U.K. 58:109-124
1978b. Physiological indices of stress in *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. 58:125-142.

WIDDOWS, J., AND B. L. BAYNE.
1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. J. Mar. Biol. Assoc. U.K. 51:827-843.

ANSON H. HINES

Department of Zoology, University of California Berkeley, Calif.
Present address: *Center for Coastal Marine Studies University of California Santa Cruz, CA 95064*

INCIDENCE AND DISTRIBUTION OF PISCINE ERYTHROCYTIC NECROSIS AND THE MICROSPORIDIAN, *GLUGEA HERTWIGI*, IN RAINBOW SMELT, *OSMERUS MORDAX*, FROM MASSACHUSETTS TO THE CANADIAN MARITIMES

Since the first discovery by Laird and Bullock (1969) of piscine erythrocytic necrosis (PEN) in the red blood cells of the Atlantic cod, *Gadus morhua*; seasnail, *Liparis atlanticus*; and longhorn sculpin, *Myoxocephalus octodecemspinosus*, 15 genera of fishes, including 17 marine species along the North Atlantic coast of North America have been found to be affected by PEN. Sherburne (1977) reported PEN in the alewife, *Alosa pseudoharengus*, and smelt, *Osmerus mordax*. Walker and Sherburne (1977) reported PEN in the Atlantic herring, *Clupea harengus harengus*; Atlantic tomcod, *Microgadus tomcod*; spot, *Leiostomus xanthurus*; tautog, *Tautoga onitis*; rock gunnel, *Pholis gunnellus*; sea raven, *Hemitripterus americanus*; fourspot flounder, *Paralichthys oblongus*; and winter flounder, *Pseudopleuronectes americanus*. Sherburne and Bean (unpubl. data) have found PEN in pollock, *Pollachius virens*; Atlantic menhaden, *Brevoortia tyrannus*; American shad, *Alosa sapidissima*; and blueback herring, *A. aestivalis*.

PEN has been confirmed by electron microscopy as an erythrocytic icosahedral cytoplasmic deoxyribovirus (EICDV) infection in two of the above species—the Atlantic cod (Walker 1971; Appy et al. 1976; Walker and Sherburne 1977) and the Atlantic herring (Philippon et al. 1977; Reno et al. 1978).

During our investigations of PEN in the Atlantic cod, other marine species were examined for evidence of PEN, especially those forming the diet of the cod. One of these was the rainbow smelt, *Osmerus mordax*. Smelt were examined for both PEN and the pathogenic microsporidian parasite, *Glugea hertwigi*.

This report shows the incidence and geographical distribution of PEN and *Glugea hertwigi* in smelt populations from Massachusetts to the

Canadian Maritimes and indicates that current management practices result in the transfer of PEN and *G. hertwigi* from one area to another via infected smelt.

Materials and Methods

For evidence of PEN, blood samples of 1,412 anadromous *Osmerus mordax* (12.7-27.3 cm total length, TL) were collected at 42 sites from 15 coastal smelt streams from Massachusetts to the Canadian Maritimes (Figure 1) between 3 November 1976 and 17 November 1977: Kittery, Maine (Spruce Creek); Boothbay, Maine (Hodgdon Cove and Boothbay Harbor); Bath, Maine (Whiskeag Creek); Dresden, Maine (Eastern River); Damariscotta, Maine (Damariscotta River); Wiscasset, Maine (Montsweag Creek); Warren, Maine (St. George River); Addison, Maine (Harrington River); Winterport, Maine (Penobscot River); Newington, N.H. (Great Bay); Kingston, Mass. (Jones River); Hingham, Mass. (Weir River); Quarryville, New Brunswick, Canada (Miramichi River); Portapique, Nova Scotia, Canada (Portapique River); and Oxford, Nova Scotia, Canada (Philip River).

In addition, blood samples from 256 landlocked *O. mordax* (7.6-27.0 cm TL) were collected in nine samples from five Maine lakes between 15 January and 5 May 1977: Damariscotta (the lake is approximately 10 mi long, begins at Jefferson, Maine, and empties into the Damariscotta River at Damariscotta); Wyman (Bingham, Maine); South Twin and Millinocket (Millinocket, Maine); and East Musquash (Topsfield, Maine).

For evidence of *G. hertwigi*, 1,692 anadromous *O. mordax* (12.7-27.3 cm TL) were collected in 42 samples from 16 localities (the above 15 plus Casco Bay, Maine) between 3 November 1976 and 17 November 1977. In addition, 254 landlocked *O. mordax* (7.6-27.0 cm TL) were collected in eight samples from the above five lakes between 15 January and 5 May 1977.

Smelt were obtained from our own catches, from those of fishermen and from Massachusetts Division of Marine Fisheries personnel. Depending

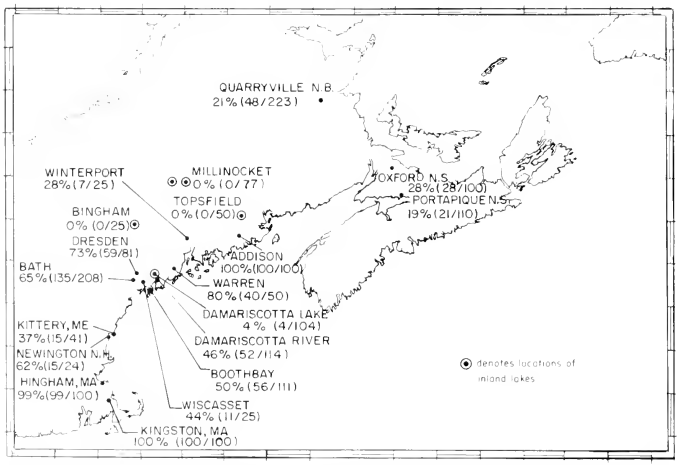


FIGURE 1.—Incidence and distribution of piscine erythrocytic necrosis (PEN) in anadromous rainbow smelt from the Canadian Maritimes to Massachusetts and landlocked rainbow smelt from five Maine lakes (two lakes are located at Millinocket).

upon the location and season, smelt were caught by handline and by dip, cast, bag, and gill nets.

Except for a few instances the same individuals were examined for both PEN and *G. hertwigi*. For evidence of PEN, live smelt were measured for total length, and the caudal peduncle was wiped free of water and mucus with a clean towel and then severed and a smear made from a small drop of blood placed on a clean slide. Smelt were sexed and given a gross external and internal examination for evidence of *G. hertwigi* and other abnormalities. Microscopic examination of unstained and Giemsa-stained spores from cysts was initially made to confirm the presence of *G. hertwigi*. Air-dried blood smears were fixed in absolute methanol for 3 min and stained with diluted Giemsa for 30 min. Smears were examined thoroughly under oil immersion at 1,000 × to determine the presence of PEN.

Results

PEN - Anadromous smelt—Of the anadromous smelt sampled, 55.7% (786/1,412) were infected with PEN (Table 1). By light microscopy, PEN lesions of smelt red cells resemble those of EICDV infected Atlantic cod (Figure 2). Infected smelt occurred in every stream sampled (Figure 1). The highest incidences were in Kingston (100/100), Addison (100/100), and Hingham (99/100). Lower incidences were evident from Nova Scotia and New Brunswick than from Maine, New Hampshire, and Massachusetts.

Individual infections were light; of the 786 infected smelt, the highest infection was 8% in a smelt from Kingston. Overall, 87.7% (689/786) of the infected smelt had <1.0% of their red cells infected; 12.3% (97/786) had from 1 to 8%.

The two areas with the highest incidences, Kingston and Addison, also had the highest individual infections and accounted for 87.6% (85/97) of the smelt in this study with 1% or more infected erythrocytes. Kingston had 64/100 smelt with infections >1%; Addison had 21/100. In contrast, Hingham with an incidence of 99/100 had only four smelt with infections >1%. From a total of 1,387 anadromous smelt sexed, 54.3% of the males and 58.3% of the females had PEN.

PEN - Landlocked smelt—Damariscotta Lake was the only lake with PEN infected smelt, 3.8% (4/104). Individual infections were <1%. Because of the design of the fishway at Damariscotta, anadromous smelt are unable to negotiate the fishway leading into the lake. However, there is a possibility that some of the smelt we sampled could have been from a coastal population. Live coastal smelt are used by ice fishermen as bait for salmon and togue, and there is a possibility that unused bait could have been released into the lake with a resultant intermingling of coastal and landlocked smelt.

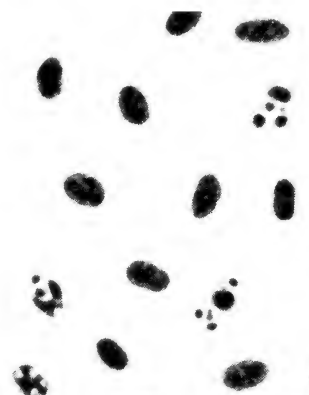


FIGURE 2.—Rainbow smelt erythrocytes with PEN lesions resembling those of PEN (EICDV) infected Atlantic cod. Infected cells show characteristic chromatin condensation and nuclear degeneration. Unlike cod, cytoplasmic virions were not visible by light microscopy in infected smelt erythrocytes.

Glugea hertwigi - *Anadromous smelt*—Overall, 8.0% (135/1,692) of the anadromous smelt were infected with *G. hertwigi* (Table 1). Infected smelt occurred in all 16 coastal areas sampled (Figure 3). Distinctive white, spherical cysts were found primarily along the intestinal tract but often on other internal organs such as liver and gonads. Cysts varied from pinhead size to 5 mm (Figure 4). Degree of infection varied from one cyst to severe infections where the abdominal cavity was nearly filled. Areas with highest incidences were at Kittery 49% (20/41) and Kingston 28% (28/100). The lowest incidence was at Boothbay with 0.9% (1/

TABLE 1.—Incidence of piscine erythrocytic necrosis (PEN) and *Glugea hertwigi* in anadromous and landlocked rainbow smelt from Massachusetts to the Canadian Maritimes, 3 November 1976-17 November 1977

Sample source and category	Date	PEN		*G. hertwigi*		Mean length, SD, and range (cm)	
		Total no examined	% incidence	Total no examined	% incidence		
Anadromous							
[1]Kittery, Maine	3 Nov 1976	41	36.6	41	48.8	16.6 ± 1.8	13.8 22.0
Boothbay, Maine	6 Nov 1976	10	50.0	10	—	18.3 ± 1.3	16.0 21.3
	19 Nov	4	50.0	4	25.0	20.7 ± 1.3	19.7 22.7
	22 Nov	1	100.0	1	—	18.8 ± 0	18.8
	23 Nov	65	44.6	65	—	18.9 ± 2.1	15.2 25.0
	5 July 1977	4	50.0	4	—	16.2 ± 1.4	14.2 17.5
	6 July	12	50.0	12	—	18.0 ± 2.3	15.9 22.9
	7 July	5	60.0	5	—	16.9 ± 0.7	15.9 17.9
	5 Aug	3	67.0	3	—	18.1 ± 1.4	16.5 19.2
	25, 26 Aug	7	86.0	7	—	19.9 ± 1.8	17.8 23.0
[1]Boothbay Total		111	50.4	111	0.9		
Casco Bay, Maine	9 Dec 1976	—	—	50	10.0	16.8 ± 2.6	12.7 21.6
Bath, Maine	14 Dec 1976	52	65.4	52	—	20.8 ± 2.4	15.6 26.7
	15 Dec	46	89.1	46	6.5	21.3 ± 2.8	17.8 27.3
	16 Dec	23	73.9	51	2.0	20.9 ± 2.2	17.8 26.0
	20 Dec	25	76.0	114	5.3	20.6 ± 1.9	15.9 24.8
	6 Jan 1977	—	—	29	3.5	20.5 ± 2.6	15.9 26.7
	6 Jan	4	50.0	4	75.0	17.0 ± 1.9	14.6 18.5
	11 Jan	8	37.0	12	8.3	19.8 ± 1.8	15.9 21.6
	13 Jan	15	60.0	15	6.7	18.3 ± 2.3	13.4 22.1
	17 Jan	7	42.8	7	14.3	20.4 ± 1.6	18.1 22.9
	3 Feb	9	44.4	9	22.2	20.3 ± 2.1	17.8 22.9
	17 Nov	19	15.8	19	15.8	20.3 ± 2.1	16.3 24.3
[1]Bath Total		208	64.9	358	6.1		
Dresden, Maine	27 Dec 1976	25	64.0	25	4.0	18.8 ± 1.6	16.2 22.3
	30 Dec	35	82.8	35	8.6	19.5 ± 2.0	15.6 24.4
	4 Jan 1977	15	60.0	15	6.7	17.8 ± 1.8	15.2 20.7
	11 Jan	6	83.3	6	16.7	18.5 ± 1.5	16.5 20.3
[1]Dresden Total		81	72.8	81	7.4		
Damariscotta, Maine	17 Jan 1977	3	—	3	—	18.1 ± 2.7	15.6 20.9
	21 Jan	70	48.6	70	12.9	19.7 ± 2.8	15.0 26.6
	23 Jan	27	51.8	27	18.5	20.4 ± 2.0	17.1 24.1
	5 Feb	1	—	—	—	16.2 ± 0	16.2
	19 Feb	13	30.8	—	—	19.1 ± 1.3	17.8 22.9
Damariscotta Total		114	45.6	100	14.0		
Wiscasset, Maine	28 Jan 1977	25	44.0	25	8.0	18.7 ± 1.8	16.0 23.4
Warren, Maine	1 Feb 1977	25	80.0	25	—	18.0 ± 2.0	14.9 24.8
	8 Feb	25	80.0	33	3.0	18.6 ± 2.1	14.6 22.2
Warren Total		50	80.0	58	1.7		
[1]Addison, Maine	10 Feb 1977	100	100.0	100	5.0	20.4 ± 2.3	14.0 26.7
Newington, N.H.	27 Feb 1977	24	62.5	24	8.3	18.9 ± 2.0	15.2 21.6
Winterport, Maine	8 Mar 1977	25	28.0	84	2.4	18.5 ± 2.9	14.0 26.7
[1]Kingston, Mass.	15 Apr 1977	100	100.0	100	28.0	18.5 ± 1.3	12.7 21.9
[1]Hingham, Mass.	15 Apr 1977	100	99.0	100	10.0	18.9 ± 2.2	12.7 23.8
Quarryville, N.B.	30 Apr 1977	100	23.0	100	—	19.7 ± 1.8	15.6 25.4
	1 May	70	20.0	97	1.0	19.3 ± 1.5	15.9 23.5
	2 May	53	20.7	53	3.8	19.6 ± 1.6	16.5 24.1
[1]Quarryville Total		223	21.5	250	1.2		
Portapique, N.S.	3 May 1977	110	19.1	110	6.4	20.2 ± 1.9	15.9 26.3
Oxford, N.S.	3 May 1977	100	28.0	100	7.0	16.4 ± 1.5	12.7 20.3
	TOTAL	1,412	55.7	1,692	8.0		
Landlocked							
Jefferson, Maine	15 Jan 1977	7	—	—	—	19.8 ± 2.0	17.8 23.5
(Damariscotta Lake)	9 Feb	10	—	10	10.0	21.0 ± 2.9	18.4 26.7
	18 Feb	12	8.3	12	8.3	18.0 ± 1.4	16.5 20.3
	23 Feb	18	—	18	—	19.5 ± 2.8	16.5 26.3
	24 Feb	32	—	32	—	18.9 ± 1.6	15.9 23.5
	10 Mar	25	12.0	25	8.0	22.1 ± 2.6	17.1 27.0
Jefferson Total		104	3.8	97	4.1		
Bingham, Maine	19 Jan 1977	25	—	25	56.0	13.9 ± 1.1	11.4 15.9
[2]Millinocket, Maine	12 Feb 1977	77	—	82	56.1	8.6 ± 1.7	7.6 12.1
[2]Topsfield, Maine	5 May 1977	50	—	50	—	9.1 ± 0.4	8.2 10.2
	TOTAL	256	1.6	254	25.2		

[1]Areas that include individual PEN infections of 11% or greater.
[2]Smelt from Millinocket and Topsfield, Maine, were within normal size ranges for populations in these lakes and were sexually mature.

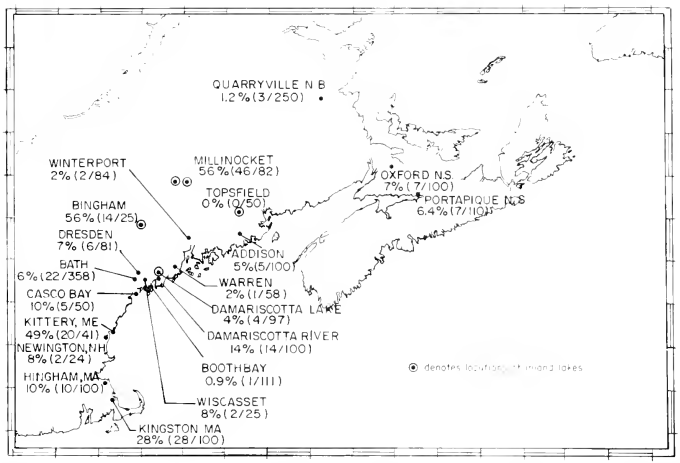


FIGURE 3.—Incidence and distribution of *Glugea hertwigi* in anadromous rainbow smelt from the Canadian Maritimes to Massachusetts and landlocked rainbow smelt from five Maine lakes (two lakes are located at Millinocket).

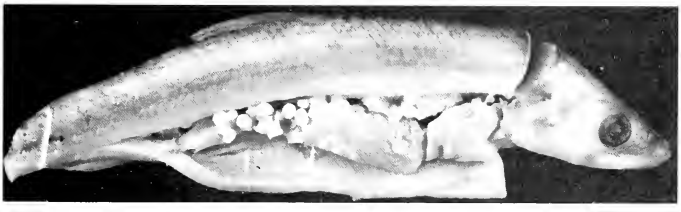


FIGURE 4.—A rainbow smelt infected with *Glugea hertwigi* showing large (up to 5 mm) white spherical cysts associated with this infection.

111). From a total of 1,663 anadromous smelt sexed, 7.8% of the males and 8.4% of the females had *G. hertwigi*.

Glugea hertwigi - *Landlocked smelt*—Infected smelt were found in four of the five lakes sampled. Overall, 25.2% (64/254) were infected. Heavy incidences occurred at Wyman, South Twin, and Millinocket Lakes—each lake had 56% of the sampled smelt infected, (14/25), (5/9), and (41/73), respectively. Infections varied from one cyst to severe infections.

Discussion

PEN and *G. hertwigi* infected smelt will undoubtedly be found in other areas, both within and beyond the geographical range sampled in this study. Management practices involving anadromous alewives have inadvertently contributed to the spread of PEN within the State of Maine (Sherburne 1977). Haley (1954b) reported similar circumstances for *G. hertwigi* infected freshwater smelt in New Hampshire. *Glugea hertwigi* was found in rainbow smelt from Lake Winnisquam, N.H., as well as in other localities where smelt populations were established from the Winnisquam stock. Smelt that were being transported by the Massachusetts Division of Marine Fisheries from Hingham to Cape Cod, Mass., to initiate new runs during the time of this study had incidences of 99% (99/100) PEN and 10% (10/100) *G. hertwigi*.

Because of the known pathogenicity of *G. hertwigi* (Haley 1954a, b; Chen and Power 1972; Nepszy et al. 1978), localities with relatively high incidences may warrant further investigation. At the time of the decline of the smelt population in the Great Bay region of New Hampshire in the 1950's, 23.3% (308/1,323) of the smelt examined had *G. hertwigi* (Haley 1954a). Although our samples were considerably smaller, 33.8% (22/65) of the smelt sampled from Kittery and Great Bay were infected with *G. hertwigi*. The high incidences of *G. hertwigi* (56%) at Wyman, South Twin, and Millinocket Lakes were unexpected. However, Chen and Power (1972) reported that of 1,691 smelt sampled from Lake Erie 62.7% were infected with *G. hertwigi*. They reported that apart from actual mortality the real significance of *G. hertwigi* infection lies in its effect on smelt fecundity. In females, parasitic cysts replaced ovarian tissue, causing a serious reduction in the number of maturing eggs.

There was no apparent relations between *G. hertwigi* and PEN in the populations sampled in this study. Although smelt at Kingston had high incidences of both PEN and *G. hertwigi* (100/100 and 28/100, respectively) other populations with high incidences of PEN did not have high incidences of *G. hertwigi*, i.e., Hingham had 99/100 with PEN, 10/100 with *G. hertwigi*; Addison had 100/100 with PEN, 5/100 with *G. hertwigi*; Warren had 40/50 with PEN, only 1/58 with *G. hertwigi*.

There was no apparent relation between *G. hertwigi* and PEN infections in individuals. Of 135 andaromous smelt with *G. hertwigi*, 71 (52.6%) likewise had PEN.

Chen and Power (1972) reported seasonal fluctuations in *G. hertwigi* infection from Lakes Ontario and Erie, with the highest incidence during the winter, when smelt were undergoing the most active phase of gonadal maturation. Most of our sampling was confined to winter; therefore, we have no evidence of seasonal fluctuations of PEN and *G. hertwigi* infections in this study. However, since different areas were sampled at similar times and all fish sampled were adults, the data obtained should afford a representative comparison between areas.

This study has determined that PEN and *G. hertwigi* are widely distributed in rainbow smelt populations along the North Atlantic coast from Massachusetts to the Canadian Maritimes, that the incidence of PEN in each population is high but the intensity of individual infections is low, and that higher incidences of *G. hertwigi* occur in inland lakes of Maine than in coastal populations. These findings differ from previous studies on the Atlantic cod and Atlantic herring where lower incidences of PEN have been evident but individuals have had nearly every red cell infected (Walker and Sherburne 1977; Sherburne 1973).

Acknowledgments

We thank M. J. Hogan of the Department of Marine Resources and D. C. Harmon of East Boothbay, Maine, for assisting in the field work. Joseph DiCarlo of the Massachusetts Division of Marine Fisheries obtained smelt for us from Hingham and Kingston. We thank Roland Walker of Rensselaer Polytechnic Institute, Jay C. Quast of the Northwest Alaska Fisheries Center Auke Bay Laboratory, NMFS, NOAA, and an anonymous reviewer who critically reviewed the manuscript and made helpful suggestions to improve clarity of presentation. This study was supported by Public Health Service Grant #5R01HL19163 from the National Heart and Lung Institute, National Institutes of Health and Grant #PCM75-22746 from the National Science Foundation.

Literature Cited

Appy, R. G., M. D. B. Burt, and T. J. Morris
1976 Viral nature of piscine erythrocytic necrosis (PEN) in the blood of Atlantic cod (*Gadus morhua*). J. Fish. Res. Board Can. 33:1380-1385

CHEN, M. AND G. POWER.
1972. Infection of American smelt in Lake Ontario and Lake Erie with the microsporidian parasite *Glugea hertwigi* (Weissenberg). Can. J. Zool. 50:1183-1188.
HALEY, A. J.
1954a. Microsporidian parasite, *Glugea hertwigi*, in American smelt from the Great Bay region, New Hampshire. Trans. Am. Fish. Soc. 83:84-90.
1954b. Further observations on *Glugea hertwigi* Weissenberg 1911, 1913 (microsporidia) in fresh water smelt in New Hampshire. J. Parasitol. 40:482-483.
LAIRD, M., AND W. L. BULLOCK.
1969. Marine fish haematozoa from New Brunswick and New England. J. Fish. Res. Board Can. 26:1075-1102.
NEPSZY, S. J., J. BUDD, AND A. O. DECHTIAR.
1978. Mortality of young-of-the-year rainbow smelt (*Osmerus mordax*) in Lake Erie associated with the occurrence of *Glugea hertwigi*. J. Wildl. Dis. 14:233-239.
PHILIPPON, M., B. L. NICHOLSON, AND S. W. SHERBURNE.
1977. Piscine Erythrocytic Necrosis (PEN) in the Atlantic herring (*Clupea harengus harengus*): evidence for a viral infection. Fish Health News 6:6-10.
RENO, P., M. PHILIPPON-FRIED, B. L. NICHOLSON, AND S. W. SHERBURNE.
1978. Ultrastructural studies of piscine erythrocytic necrosis (PEN) in Atlantic herring (*Clupea harengus harengus*). J. Fish. Res. Board Can. 35:148-154.
SHERBURNE, S. W.
1973. Erythrocyte degeneration in the Atlantic herring, *Clupea harengus harengus* L. Fish. Bull., U.S. 71:125-134.
1977. Occurrence of piscine erythrocytic necrosis (PEN) in the blood of the anadromous alewife, *Alosa pseudoharengus*, from Maine coastal streams. J. Fish. Res. Board Can. 34:281-286.
WALKER, R.
1971. PEN, a viral lesion of fish erythrocytes. Am. Zool. 11:707.
WALKER, R., AND S. W. SHERBURNE.
1977. Piscine erythrocytic necrosis virus in Atlantic cod, *Gadus morhua*, and other fish: ultra-structure and distribution. J. Fish. Res. Board Can. 34:1188-1195.

STUART W. SHERBURNE
LAURIE L. BEAN

State of Maine Department of Marine Resources
Fisheries Research Station
West Boothbuy Harbor, ME 04575

A SIMPLE METHOD TO OBTAIN SERUM FROM SMALL FISH

It is desirable to obtain blood serum information from small fish due to their extensive use in pollutant and disease studies (Snieszko et al. 1969; Snieszko 1974; Mulcahy 1975). It is well known that gross observations cannot detect subtle changes in blood chemistry caused by environmental factors such as stress, diet, or inflammation (Mulcahy 1975) and some pesticides (Walker 1963).

Techniques to obtain fish blood for study have been described in reviews by Hesser (1960) and Blaxhall (1972). Cardiac and venous puncture are the most commonly used techniques for fish >150 mm, while severance of the caudal peduncle and insertion of a capillary tube to draw blood is usually employed for smaller fish. Fish <60 mm present problems because the quantity of blood obtainable is small (generally <0.2 ml), coagulation time is quick, and tissue fragments or clots can clog collecting tubes, causing loss of serum in the transfer from one container (or collecting tube) to another for centrifugation. In most cases anticoagulants are used to eliminate some of these problems.

Sodium oxalate, heparin, or dipotassium ethylenediaminetetraacetate (EDTA) are the most commonly used anticoagulants. Unfortunately, oxalate and EDTA anticoagulants can interfere with serum ion determinations, such as calcium, and produce misleading data (Tietz 1976). When many blood serum components are to be measured, especially on instrumentation such as an amino acid auto analyzer, a quantity of serum (at least 0.5 ml and preferably free of anticoagulant) must be obtained for the numerous tests these analyzers can do. Heparinized tubes, excellent for single serum component tests, are limited because the volume of serum they can obtain is generally not enough for use with sophisticated instrumentation. This note describes a simple method to obtain pooled serum samples, without anticoagulants, from fish <60 mm when heparinized tubes are not practical.

Materials and Methods

Small fish < 60 mm fork length should be anesthetized, if desired, and blotted to remove excess water on the fish's body. A dry Kimwipe[1] is wrapped around the fish, covering the vent to prevent contamination of the sample, leaving approximately 2.5 cm of the tail exposed (Figure 1B). A small portion of the Kimwipe is allowed to overlap the fish's head. The caudal peduncle is severed with sharp scissors, leaving a slight point at the caudal region (Figure 1C). The fish is rapidly in-

[1]Reference to trade names does not imply endorsement by the University of Southern Mississippi or by the National Marine Fisheries Service, NOAA.

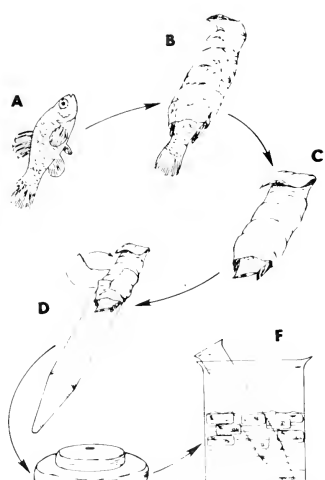


FIGURE 1.—Diagrammatic representation of the centrifuge method for extracting serum from small fishes. A. Blotted fish ready for bleeding. B. Fish is wrapped with Kimwipe, leaving overlap at top. Vent is also covered to prevent contamination of the sample. C. Caudal peduncle is cut at an angle with sharp scissors. D. Fish is fit snugly into a 15 ml centrifuge tube, using more or less Kimwipes to obtain a proper fit, and taped so the fish will not be pulled into the tube. E. Fish, in the tube, is spun at 400 *g* for 3 min. F. Covered tube with blood is kept in an ice water bath until another fish can be processed in the same tube.

serted, tail first, into a 15 ml Pyrex centrifuge tube and secured by taping the overlapping Kimwipe to the side of the tube (Figure 1D). (The fit must be snug but not too tight.) Varying fish sizes can be compensated for by wrapping with more or less Kimwipes; fish will not be pulled into the tube if the wrapping is correct. Fish are spun in a centrifuge at 400 *g* for 3 min. After each fish is centrifuged, the tube of blood obtained (one tube for all fish) is covered and quickly placed in a beaker of ice water to inhibit evaporation of serum obtained and hemolysis of red blood cells. A total pooled sample of approximately 1 ml can be collected from 20 fish. The blood is allowed to clot and the serum drawn off. From 1 ml of pooled whole blood, 0.5 ml of serum can be obtained.

Discussion

Contamination by tissue fluid, lymph, and cell debris is unavoidable but exists in any method which severs the caudal peduncle. Proper wrapping of fish and the use of sharp scissors help to reduce this contamination. The amount of lymph and intracellular fluid gained from the cutting action of the scissors and centrifugation is minimal and does not prejudice one's results significantly. Cellular debris from the actual wound is insignificant because the serum is separated from it before analysis. Careful placement of Kimwipes around the vent eliminates urine or feces contamination of the sample. This method has the advantage of simplicity, speed, and no anticoagulant contamination. Red blood cell hemolysis is minimal, and larger pooled blood samples can be obtained in a single container with little serum loss during unnecessary transfers when heparinized collecting tubes are unfeasible. This technique should be helpful in pathologic studies of small fish used in toxicity tests when it is desirable to monitor many blood serum parameters and where there is no objection to the use of pooled samples.

Acknowledgments

I thank Lee Courtney for help with the figure and John Couch for critical review of the manuscript.

Literature Cited

BLAXHALL, P. C.
1972. The haematological assessment of the health of freshwater fish. A review of selected literature. J. Fish Biol. 4:593-604.

HESSER, E. F.
1960. Methods for routine fish hematology. Prog. Fish-Cult. 22:164-171.

MULCAHY, M. F.
1975. Fish blood changes associated with disease: a hematological study of pike lymphoma and salmon ulcerative dermal necrosis. *In* The pathology of fishes, p. 925-944. Univ. Wis. Press, Madison.

SNIESZKO, S. F.
1974. The effect of environmental stress on outbreaks of infectious diseases of fishes. J. Fish. Biol. 6:197-208.

SNIESZKO, S. F., J. A. MILLER, AND C. R. ATHERTON.
1966. Selected hematological and biochemical tests performed with blood and serum of adult rainbow trout (*Salmo gairdneri*) with a high incidence of hepatoma. Ann. N.Y. Acad. Sci. 136:191-210.
TIETZ, N. W.
1976. Methods for the determination of calcium in body fluids. *In* N. W. Tietz (editor), Fundamentals of clinical chemistry, p. 903-904. W. B. Saunders Co., Phila.
WALKER, C. R.
1963. Toxicological effects of herbicides on the fish environment. Univ. Mo. Bull. 64:17-34.

JAMES T. WINSTEAD

University of Southern Mississippi
Hattiesburg, Miss.
Present address: *U.S. Environmental Protection Agency*
Sabine Island Laboratory
Gulf Breeze, FL 32561

STRANDING OF THE PILOT WHALE, *GLOBICEPHALA MACRORHYNCHUS*, IN FLORIDA AND SOUTH CAROLINA

An opportunity to observe the behavior of stranding pilot whales occurred in February 1977. Before dawn on the 6th, 175-200 pilot whales moved with the rising tide into the Fort George River, 1.5 km north of the mouth of the St. Johns River (lat. 30°25′ N, long. 81°29′ W), near Jacksonville, Fla. The weather was clear, calm, and cold; minimum air temperature was 0° C at Jacksonville Beach (Environmental Data Service 1977:6). Once inside the river mouth, the animals turned south into a small, shallow embayment (Figure 1). A chronology of the events that followed is presented below. Events of 6 February were summarized by Willard Patrick.[1]

6 February 1977.—Sometime prior to dawn the whales began moving onto the southeast shore (Figure 1, Site A), where they were stranded either by their movements or by the falling tide. Throughout the day, many of the whales were refloated repeatedly by Florida Marine Patrol (FMP) officers and local volunteers, but many were immediately stranded again. Some whales thrashed vigorously during attempts to refloat them. By 2100 h, 21 whales were dead on the beach and the remainder were milling around near the middle of the bay in water 1-2 m deep. During the night of 6-7 February, what was thought to be the remainder of the herd approached the surf zone at high tide and an estimated 25 whales moved into the ocean. Those whales not exiting through the surf are believed to have returned to the embayment although some may have stranded and died, then drifted out to sea.

7 February 1977.—At 0845 h, 23 whales, including the 21 from the previous day, were dead on the beach, most near Site A (Figure 1). Two groups of 40 to 60 whales were milling around in the bay, one group approximately in the center and one near Site B (Figure 1). Several smaller groups of up to five animals each were also sighted.

At about 1030 h, the large groups restranded at Sites A and B. Many of the animals near Site A were pushed off by volunteers; approximately 40 whales near Site B died within an hour.

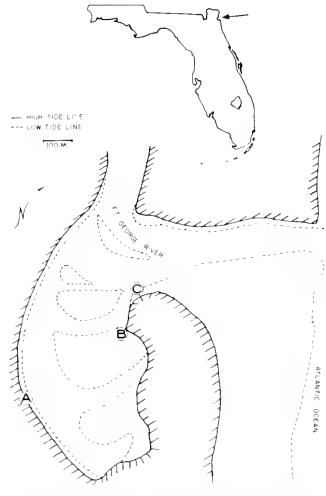


FIGURE 1.—Pilot whale stranding sites (A-C) in the Fort George River, Duval County, Fla., lat. 30°25′ N, long. 81°24′ W.

[1]Willard Patrick, Sergeant, Florida Marine Patrol, District 8, 4124 Boulevard Center Drive, Jacksonville, FL 32207, pers. commun. March 1977.

The whales appeared disoriented and lethargic, but moved steadily ashore. Their behavior and movements appeared similar to the responses of trained dolphins in a strange environment (Irvine 1971). Most animals offered little resistance when pulled by their flukes and turned away from the beach, but they usually turned and again moved slowly toward shore. Some whales grounded on shoals in the bay and either floated off on the rising tide, or died there when the tide ebbed.

The whales pushed off from Site A were prevented from moving toward shore by a FMP motorboat moving around the pod. The whales were herded towards the river mouth and by late afternoon, using the combined action of two FMP boats, the volunteers helped 20-30 whales move past the surf line. Another 10 were counted in the river at dark, and an additional 20-35 whales restranded and died at various locations between Site A and the outer surf zone, including 10-15 at Site C. Other whales apparently moved out to sea without human assistance, or died and drifted out.

Between 0930 and 1440 h, we measured, sexed, and tagged 17 whales (9 males and 8 females) with 16 roto tags (Jumbo Size, Nasco Inc., Ft. Atkinson, Wis.)[2] and three spaghetti tags (Model FH69A, Floy Tag & Manufacturing, Inc., Seattle, Wash.).

We worked opportunistically on animals close enough to deep water to be refloated. Seven tagged whales (4 females, 3 males) eventually stranded and died in the Fort George River area. Total lengths of the tagged whales that restranded and died were males: 308, 450, and 468 cm; females: 277, 350, 380, and 385 cm. Total lengths of unrecovered whales were: males 375, 443, 440, 446, 478, and 547 cm; females: 353 and 374 cm. Two females were tagged but not measured.

8 February 1977—At 0800 h, 1 whale was alive near Site A, as were 10-15 whales near Site C, but all died within a few hours. The whales near Site C apparently drifted inland with the rising tide.

Aftermath—Between 8 and 16 February, about 40 dead whales were recovered from adjacent areas, including river branches and tidal creeks as far as 6-8 km northwest of the principal stranding sites. Several groups of 5-10 whales traveled north up the river on 6 February, but we know neither how many animals stranded and died there, nor how many carcasses were moved to their recovery location by currents. Single whales stranded at Anastasia State Park (lat. 29°53′ N, long. 81°16′ W), 56 km to the south on 9 February, and at Jacksonville Beach (lat. 30°18′ N, long. 80°12′ W), 10 km to the south on 11 February. A total of 135 dead whales were ultimately recovered (Figure 2) and examined by Mead. The size and sex composition of this group is similar to that of other mass strandings of this species (Mead unpubl. data) and probably represents a normal social aggregation. On the same morning (6 February) that the initial stranding took place on Fort George Island, a group of 15 pilot whales stranded on the south end of Cumberland Island, Ga. (lat. 30°45′ N, long. 81°28′ W) 40 km to the north. This group may have separated from the larger school prior to stranding.

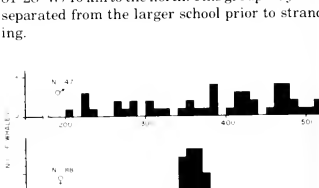


FIGURE 2.—Length-frequency distributions of male and female pilot whales stranded at Fort George River, Duval County, Fla.

Three decomposed carcasses, thought to be *G. macrorhynchus*, were seen, but not recovered, near Mayport (lat. 30°23′ N, long. 81°29′ W) at the mouth of the St. Johns River in June 1977 (D. Gicca[3]).

Two whales stranded on 13 February on Wadamalaw Island (lat. 32°35′ N, long. 80°11′ W) near Charleston, S.C., some 220 km (straight-line distance) to the northeast. Interestingly, the animals entered the mouth of the North Edisito River and moved into Bohicket Creek before stranding at Rockville, 7.5 km from the coast. One was a 478 cm male, tagged near Site C with spaghetti and

[2]Reference to product names does not imply endorsement by the National Marine Fisheries Service, NOAA

[3]D. Gicca, Biological Technician, Gainesville Field Station, National Fish and Wildlife Laboratory, 412 NE 16th Avenue, Room 250, Gainesville, FL 32601, pers. commun. June 1977.

roto tags. The other was an untagged 406 cm female that later died. After both tags were removed from the male, it was refloated by local residents. The whale was followed by P. Laurie[4] for 15-20 min and reported to be respiring without difficulty as it moved seaward.

As with most mass strandings of marine mammals, the cause was not clear. A cold weather frontal system passed through the area on the day prior to the stranding, but was not unusual for that time of year and probably was not related to the stranding. None of the whales were obviously injured and none appeared to follow a lead individual ashore. A combination of the passage through the surf into the river and the shallows in the bay may have confused and disoriented the animals, thus increasing the probability that they would strand. The whales appeared to tire with time, as evidenced by their less vigorous response to being pulled off the beach on 7 February; but why some animals died quickly after stranding on 7 February while others remained alive for hours on the beach or stranded repeatedly is unknown.

On the west coast of Florida, groups of *G. macrorhynchus* (Fehring and Wells 1976) and *Pseudorca crassidens* (Odell et al.[5]) have restranded at different locations, but this is the first report of restrandings at different locations on the Atlantic coast. Until now identification of previously stranded individuals has been based on rope marks and dorsal fin shapes. The use of tags on stranded cetaceans would facilitate the identification of individuals on the shore and the study of herd structure of refloated animals at the stranding site, and would also help identify resighted or restranded individuals.

Motor boats seemed effective for herding the whales and may be a means to keep refloated animals together and prevent immediate beachings at future strandings. Boats have been used effectively to herd *P. crassidens* (Odell et al: see footnote 5), although attempts to drag whales up to 1 km offshore at other strandings have not been totally effective because the animals often immediately restranded.

More data are needed to determine why mass strandings occur and how to deal with the animals once they are on the beach. If efforts to save mass stranding victims prove futile because the animals immediately restrand, euthanasia may be the most humane alternative. As shown by this report, however, some animals may survive a mass stranding and potentially can be a source of valuable data if resighted elsewhere. It would also seem that the spirit of the Marine Mammal Protection Act of 1972 obligates American citizens to save stranded marine mammals if practical. An effort is therefore needed to get experienced people to a mass stranding site quickly so the rescue techniques can be evaluated and data collection can be maximized.

Acknowledgment

We thank R. Jenkins, P. Laurie, and W. Patrick for providing information on the stranding events. D. K. Odell and F. G. Wood offered constructive suggestions on earlier versions of this report.

Literature Cited

ENVIRONMENTAL DATA SERVICE
1977. Climatological data, Florida 81(2), 12 p. NOAA, Environ. Data Serv., Asheville, N.C.

FEHRING, W. K., AND R. S. WELLS.
1976. A series of strandings by a single herd of pilot whales on the west coast of Florida. J. Mammal. 57:191-194.

IRVINE, B.
1971. Behavioral changes in dolphins in a strange environment. Q. J. Fla. Acad. Sci. 34:206-212.

A. BLAIR IRVINE
MICHAEL D. SCOTT

National Fish and Wildlife Laboratory
Gainesville Field Station
412 NE 16th Avenue, Gainesville, FL 32601

RANDALL S. WELLS

Department of Zoology, University of Florida
Gainesville, FL 32611

JAMES G. MEAD

National Museum of Natural History
Smithsonian Institution, Washington, DC 20560

[4]P. Laurie, Information Specialist, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. February 1977.

[5]Odell, D. K., E. D. Asper, J. Baucom, and L. H. Cornell. A summary of information derived from the recurrent mass stranding of a herd of false killer whales, *Pseudorca crassidens* (Cetacea: Delphinidae). Unpubl. manuscr.

FIRST RECORDS OF A GIANT PELAGIC TUNICATE, *BATHOCHORDAEUS CHARON* (UROCHORDATA, LARVACEA), FROM THE EASTERN PACIFIC OCEAN, WITH NOTES ON ITS BIOLOGY

Recent studies (Hamner et al. 1975; Alldredge 1972, 1976a; Silver et al. 1978) have demonstrated the importance of gelatinous macroplankton and their mucous secretions in planktonic communities as sources of particulate organic carbon and surface habitat in an otherwise homogeneous environment. Pelagic tunicates of the Class Larvacea appear to be especially important members of this assemblage because they periodically secrete and release numerous external, mucous, feeding structures or "houses." In midwater trawling off southern California we obtained several specimens of a unique, giant larvacean, *Bathochordaeus charon* Chun 1900. This species may be a major source of suspended organic aggregates, or "marine snow" (Silver et al. 1978), as well as a major consumer of living and detrital particulate organic carbon in mesopelagic regions. Only eight specimens of this unusual tunicate, whose trunk may reach 25 mm long, have been reported. The present material increases the number of known intact specimens to 13 and represents a major extension of the range of the monotypic genus.

History of *Bathochordaeus charon* Collections

Collection data for all known specimens are given in Table 1. *Bathochordaeus charon* was first described as a new genus and species by Chun (1900:519-521) on the basis of two gigantic specimens taken in 1898 in the southeastern Atlantic Ocean by the German Deep Sea Expedition, aboard the *Valdivia*. Lohmann (1914) described these specimens in greater detail and assigned them to the Oikopleuridae. He later (1931) described two additional, smaller animals taken in 1899 in the Indian Ocean during the same expedition. Garstang (1936, 1937) collected two small specimens off Bermuda, which he described as a new species, *B. stygius*, because of minor differences from the original descriptions. Fenaux (1966) synonymized the two species and Garstang (1937) himself believed the differences lay mainly in misinterpretations of morphology by Chun (1900) and Lohmann (1914, 1931). A single specimen was listed, without description, from the German Atlantic Expedition on the *Meteor* (1925-27) (Lohmann and Hentschel 1939). Thompson's (1948) report of a single small specimen from eastern Australia was the first record of the genus from the Pacific Ocean.

These eight specimens were the only reliable records prior to this report. Tokioka (1960) obtained five large (to 20 mm long) isolated larvacean tails from collections of the Shellback (lat. 13° N, long. 99° W) and EQUAPAC (lat. 8° S, long. 164° E) expeditions of the Scripps Institution of Oceanography. Tokioka tenatively assigned these to *Bathochordaeus charon* on the basis of their length; however, all conform in size with *Megalocercus* sp., another large larvacean which also was taken on these expeditions, and only one of the tails had the characteristic shape of *B. charon*. Thus the affinity of Tokioka's (1960) material cannot be established with certainty and only one of his specimens is included in Table 1.

TABLE 1.—Collection and size data for known specimens of the pelagic tunicate *Bathochordaeus charon*. The specimen of Tokioka is only tentatively assigned to this species (see text).

Specimen number	Date of collection	Depth of tow (m)	Location		Trunk (mm)		Tail (mm)		Reference
			Lat	Long	Length	Width	Length	Width	
1	21 Oct 1898	0-2,500	31°00' S	8°00' E	25	19	70	30	Chun 1900, Lohmann 1914, 1931
2	21 Oct 1898	0-2,500	31°00' S	8°00' E	25	19	70	30	Chun 1900, Lohmann 1914, 1931
3	9 Mar 1899	0-2,000	4°34' S	53°43' E	5	—	18	—	Lohmann 1931
4	10 Mar 1899	0-2,000	4°38' S	51°17' E	1	—	4	—	Lohmann 1931
5	25 Mar 1927	50-100	15°04' N	44°39' W	—	—	—	—	Lohmann and Hentschel 1939
6	Mar 1935	0-300	32°50' N	64°50' W	6	5	20	6	Garstang 1936, 1937
7	Mar 1935	0-300	32°50' N	64°50' W	4	3	14	5	Garstang 1936, 1937
8	Feb 1940	8-200	33°55' S	151°10' E	3	—	8	—	Thompson 1948
9	—	—	—	—	12	11	30	11	This report
10	29 June 1976	0-500	33°15' N	118°25' W	12	14	47	15	This report
11	20 Sept 1977	0-300	33°37' N	118°19' W	—	—	34	8	This report (tail only)
12	8 Oct 1977	0-480	33°41' N	118°25' W	16	11	47	9	This report
13	8 Oct 1977	0-200	33°41' N	118°25' W	15	14	34	11	This report
14	8 Oct 1977	0-200	33°41' N	118°25' W	12	11	25	11	This report
15?	18 June 1952	0-300	15°32' N	99°50' W	—	—	20	8	Tokioka 1960 (tail only)

Materials and Methods

Five of the six new specimens (Table 1) were collected in Isaacs-Kidd midwater trawls from about 500 m to the surface, aboard the RV *Nautilus* of the Southern California Ocean Studies Consortium and the RV *Velero IV* of the Allan Hancock Foundation, University of Southern California in 1976-77 off the coast of southern California. Collection data are lacking for specimen number 9.

Bathochordaeus charon reaches a trunk length of at least 25 mm, yet most previously collected specimens were considerably smaller. Even large animals are difficult to sort from samples until one is trained to recognize the unusual body form (Figures 1, 2). I have found it useful to dilute the entire fresh sample into one or more large (20-50 l), glass aquaria and examine it with transmitted light. The mucous house, typical of larvaceans of the family Oikopleuridae (and presumably of gigantic proportions in this species), has never been collected intact in a plankton tow. Turbulence in the net propably causes its disintegration, as is true of many other mucous structures (Hamner et al. 1975; Silver et al. 1978). The animal itself is virtually transparent and is often of delicate consistency. The large trunk is frequently separated from the tail or is otherwise damaged.

Results

Description of *Bathochordaeus charon*

The present specimens (Table 1, Figure 1) conform generally to published accounts of *B. charon*, detailed descriptions of which were given by Chun (1900), Lohmann (1931), Garstang (1937, as *B. stygius*), and Thompson (1948). Final confirmation must await careful morphological study of the new material.

The conspicuous feature of this species is its

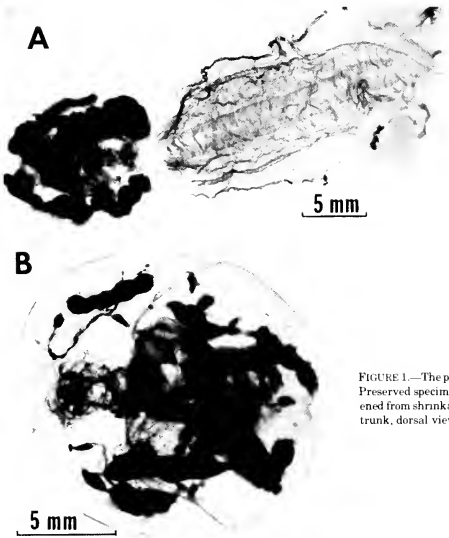


FIGURE 1.—The pelagic tunicate *Bathochordaeus charon*. A. Preserved specimen, trunk and tail, dorsal view. Tail is shortened from shrinkage during fixation. B. Preserved specimen, trunk, dorsal view.

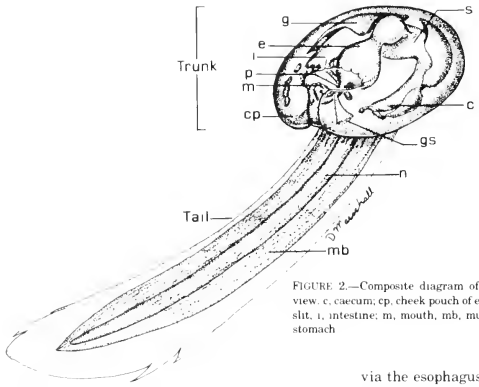


FIGURE 2.—Composite diagram of *Bathochordaeus charon*, anterolateral view. c, caecum; cp, cheek pouch of epidermis; e, esophagus; g, gonad; gs, gill slit; i, intestine; m, mouth; mb, muscle band; n, notochord; p, pharynx; s, stomach

great size relative to other larvaceans, whose adult trunk lengths are usually <5 mm. The present specimens are the largest collected since Chun's (1900) first two giants (Table 1). The ratio of tail length to trunk length ranges from 2.1 to 3.9, but damage to the tail and shrinkage after fixation make these figures unreliable. The mean ratio of 3.0 for all 12 intact specimens indicates that, in contrast to other Oikopleuridae, *B. charon* has a relatively short, broad tail whose width is about one-third its length. The lateral epidermal fin is usually torn or absent, but when present it is widest distally, unique in the Oikopleuridae. The notochord is clearly visible as the central axis of the tail, sandwiched between the two broad muscle bands.

In contrast to other Oikopleuridae, the trunk is strongly compressed dorsoventrally and is nearly as broad as long (Figure 2). The epidermis is thin and often diaphanous, and it protrudes on either side of the oral region as a pair of "cheek" pouches. The mouth, unique in its dorsal and subterminal position, lies atop a low buccal cone and leads into the short, narrow pharynx. The long, spindle-shaped openings of the two stigmata (gill slits) arise from the floor of the pharnyx just behind the level of the dorsal mouth and ventral endostyle. The gut, the only conspicuous internal structure, is light brown in Formalin[1]-preserved material and lies free in the body cavity. The pharynx opens via the esophagus into the large stomach that is expanded laterally as a blind caecum on the left and a right lobe which gives rise to the narrow intestine and rectum. The anus opens ventrally just anterior to the base of the tail. Small masses of gonadal tissue lie in the hemocoel in three of the specimens. In mature individuals the gonad forms a U-shaped mass which protrudes into the cheek pouches.

Distribution of *Bathochordaeus charon*

Only one specimen of *B. charon* was taken with a closing net, thus the depth distribution of the species cannot be determined with certainty. However, all of the remaining 13 specimens were taken well off the bottom in vertical or oblique tows from at least 200 m or in horizontal tows whose time at maximum depth greatly exceeded the time for hauling in the net. This and the lack of specimens in surface tows support the belief of Chun (1900), Lohmann (1931), and Garstang (1937) that *B. charon* is a deep-living, mesopelagic species.

Few specimens have been collected and it is premature to conclusively describe the areal distribution of *B. charon* on the basis of known records (Figure 3). Since the eight previously reported specimens came from the North and South

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

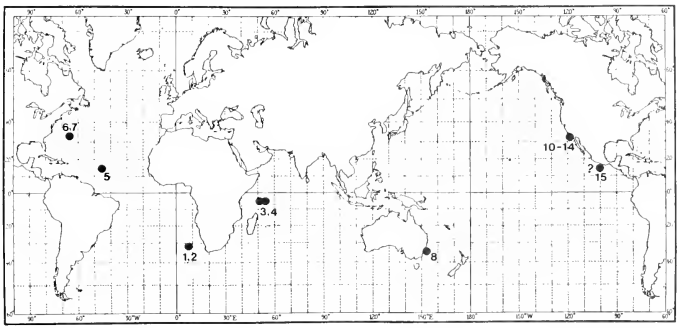


FIGURE 3.—Known collection sites of *Bathochordaeus charon*. Numbers correspond to specimen number listed in Table 1.

Atlantic, Indian, and southwestern Pacific Oceans, this report represents the first clearly established record of the species in the eastern Pacific Ocean. On the basis of the known material, it appears that *B. charon* has a circumglobal distribution in tropical and subtropical oceanic waters between lat. 35° N and 35° S. Forneris (1957) classified it as a "eurythermic thermophile," but such a characterization seems unwarranted, as it was based on only eight specimens obtained from widely separated localities and without associated physical oceanographic data.

Discussion

All known larvacean species secrete a mucous feeding device, the house. The structure of the house varies considerably among the three larvacean families, but in the Oikopleuridae it contains mucous filters which remove particulate matter from the water. Periodically, when the filters become clogged, the animal abandons the old house and within a few minutes produces a new one from a mucous rudiment secreted while in the old house. The type of house produced by *B. charon* is not yet known. Chun (1900) believed it was as large as a pumpkin and that it completely enclosed the animal, as in other Oikopleuridae. Lohmann (1931) believed that the house was probably of the "nose bag" type, as in Fritillariidae, in which a mucous net is cast out from the buccal region and the animal is free in the water.

Barham (1969) observed spherical, mucous structures, at least 25 to 50 cm in diameter, from deep submersibles off San Diego, Calif., at about 200 m. Inside some of these structures, the swimming motions of a large, tadpolelike animal were visible. The structure and size of these "busted balloons" leave little doubt that they were occupied and abandoned larvacean houses, very likely those of *B. charon*. Because the houses have not been collected in nets, Barham's account represents the only observation of them. Studies of photographs from such in situ observations and of the secretory apparatus of the animals themselves may elucidate the structure of the house of *B. charon*.

Bathochordaeus charon is considered to be rare because of sparse records obtained since its discovery in 1900. However, current evidence indicates that the animals and their houses may be relatively common, comparable with other species of similar, large size, at least at certain depths, locations, or times. Barham[2] estimated the densities of presumed giant larvacean houses off Cape Corrientes, Mexico, to be on the order of 1 to 3/m^3 within narrow layers near the thermocline, between about 50 and 300 m. At least six of the known specimens occurred in pairs in the same plankton sample. Thus, despite their large size,

[2]Eric G. Barham, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1978.

they may be difficult to collect because of a vertically stratified distribution or they may remain unrecognized in midwater plankton samples because of their fragility, transparency, and deviation from typical larvacean structure.

Epipelagic larvacean relatives of *B. charon* filter feed on nanoplankton, especially cells <10 μm (Lohmann 1899; Alldredge 1975). The muscular tail pumps water through the house and permits the concentration of suspended particles from larger volumes of water than would be possible using ciliary currents alone. Since food is selected only on the basis of size, detritus may constitute a significant fraction of the food in some locations (Gerber and Marshall 1974).

In waters below the euphotic zone, particulate organic carbon is scarce, generally present at levels from 10 to 10^2 μg C/l, compared with roughly 10^2 to 10^3 μg C/l in the euphotic zone (Holm-Hansen et al. 1966; Hobson 1967; Menzel 1967). Most of the particulate carbon below 200 m contains little or no chlorophyll (Holm-Hansen et al. 1966) and is composed mainly of detritus. However, Fournier (1971) and others have reported the presence of living, pigmented cells ("olive-green cells," or OGC's) averaging 3.5 μm in diameter in virtually all waters sampled deeper than about 50 m in the Atlantic and Pacific Oceans. These cells reach their maximum density of about 10^5/l at 300 to 500 m and may contribute up to about 1 μg C/l, or up to 10% of the total particulate organic carbon in aphotic marine environments. Fournier (1971) suggested that copepods are not likely to be major consumers of OGC's because of their limited abilities to filter such small particles at low concentrations and that pelagic tunicates, which filter water through mucous sheets, may be better suited to utilize such particles. Fournier (1973) demonstrated that the gut contents of colonies of the pelagic tunicate, *Pyrosoma*, from below the euphotic zone consisted mainly of OGC's. If *B. charon* is indeed a resident of midwaters, as suggested above, and if it, like its epipelagic relatives, filters particles <10 to 20 μm in size, then it may be a major consumer of OGC's as well as detritus. The localized occurrence of dense layers of *B. charon* indicated by the in situ observations of Barham (1969) may depend on the presence of peak concentrations of OGC's between 200 and 1,000 m, as observed by Fournier (1971). Alternatively, the filter meshes of the house of *B. charon* may be larger than those of smaller, epipelagic larvaceans and the food may then consist largely of slow zooplankton. Knowledge of house structure and analyses of gut contents of additional specimens may clarify the role of *B. charon* in mesopelagic food webs.

Bathochordaeus charon may contribute large amounts of mucus to the water column in the form of its discarded houses. *Oikopleura dioica* secretes and discards four to six houses per day (Paffenhöfer 1973). Such occupied and empty houses are sources of particulate food and surface habitat for microorganisms in planktonic ecosystems (Alldredge 1972, 1976a) and, along with other organic aggregates, may serve as a barrier to the downward flux of particulate matter and substances adherred or adsorbed to them (Silver et al. 1978). Moreover, such "marine snow" provides a trophic link between large consumers and nanoplankton, protozoa, and microcrustaceans, allowing the former to tap an otherwise unavailable food source (Hamner et al. 1975). Larvaceans and their houses are known prey for fish and planktonic invertebrates (Alldredge 1976a, b; Bailey et al. 1975; Hobson 1974; Hobson and Chess 1976).

Bathochordaeus charon produces large mucous structures, although the size and frequency of production of the houses is not known. The rate of turnover of houses is probably less than in *O. dioica* because of lower temperatures and lower concentrations of particulates which could clog the house filters. Other Oikopleuridae produce houses which are roughly 5 to 15 times the trunk length (Alldredge 1975). If this ratio holds for *B. charon*, then a 25 mm individual would produce a house about 10 to 40 cm in diameter, comparable with in situ estimates (Barham 1969). If *B. charon* is concentrated in layers just above the thermocline, as suggested by in situ observations (Barham see footnote 2), then its houses may form a major component of mesopelagic marine snow.

Note Added in Proof

I am grateful to A. Bückmann and H. Kapp for calling my attention to their paper (Untersuchungen am Zooplankton von der Atlantischen Kuppenfahrt der „Meteor", März bis Juli 1967, published 1973 in „Meteor" Forschungsergebnisse, Reihe D, No. 13:11-36) in which they described and illustrated two additional specimens, referred to as *B. stygius*. The specimens were taken April 1967 in the North Atlantic (lat. 30°18' N, long. 29°20' W) between 100 m and the surface.

One specimen was 6.1 mm trunk length and the other was not measurable. The authors provided a valuable discussion of the taxonomic problems of the genus and suggested that *B. stygius* should be applied at least to all known juvenile specimens.

Acknowledgments

Thanks to Eric Barham for sharing his unpublished observations and for critically reading the manuscript; to Janie Layton, Suzanne Latauska, Robert Frelig, and Michael Schaadt for technical assistance; and to Theodore Pietsch, Laurie Stuart, Jay Quast, and an anonymous reviewer for commenting on the manuscript. This work was supported in part by a grant-in-aid from the Office of Graduate Studies and Research, California State University, Long Beach.

Literature Cited

ALLDREDGE, A. L.
1972. Abandoned larvacean houses: A unique food source in the pelagic environment. Science (Wash., D.C.) 177:885-887.
1975. Quantitative natural history and ecology of appendicularians and discarded appendicularian houses. Ph.D. Thesis, Univ. of California, Davis, 149 p.
1976a. Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments. Limnol. Oceanogr. 21:14-23.
1976b. Field behavior and adaptive strategies of appendicularians (Chordata: Tunicata). Mar. Biol. (Berl.) 38:29-39.

BAILEY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:846-861.

BARHAM, E. G.
1969. A window in the sea. Oceans Mag. 1(1):54-60.

CHUN, C.
1900. Aus den Tiefen des Weltmeeres. Gustav Fischer, Jena, p. 519-521 (2d ed., 1903, p. 554-557).

FENAUX, R.
1966. Synonymie et distribution geographique des Appendiculaires. Bull Inst. Oceanogr. (Monaco) 66(1363), 23 p.

FORNERIS, L.
1957. The geographical distribution of the Copelata. An. Acad. Bras. Cienc. 29:273-284.

FOURNIER, R. O.
1971. Studies on pigmented microorganisms from aphotic marine environments. II. North Atlantic distribution. Limnol. Oceanogr. 16:952-961.
1973. Studies on pigmented microorganisms from aphotic marine environments. III. Evidence of apparent utilization by benthic and pelagic tunicata. Limnol. Oceanogr. 18:38-43.

GARSTANG, W.
1936. On a new Appendicularian, *Bathochordaeus* sp., from Bermuda, with a revision of the genus. (Abstract.) Proc. Linn. Soc. Lond. 148:131-132.
1937. On the anatomy and relations of the Appendicularian *Bathochordaeus*, based on a new species from Bermuda (*B. stygius*, sp. n.). J. Linn. Soc. Lond. Zool. 40:283-303.

GERBER, R. P., AND N. MARSHALL.
1974. Ingestion of detritus by the lagoon pelagic community at Eniwetak Atoll. Limnol. Oceanogr. 19:815-824.

HAMNER, W. M., L. P. MADIN, A. L. ALLDREDGE, R. W. GILMER, AND P. P. HAMNER.
1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol. Oceanogr. 20:907-917.

HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HOBSON, L.
1967. The seasonal and vertical distribution of suspended particulate matter in an area of the Northeast Pacific Ocean. Limnol. Oceanogr. 12:642-649.

HOLM-HANSEN, O., J. D. H. STRICKLAND, AND P. M. WILLIAMS.
1966. A detailed analysis of biologically important substances in a profile off southern California. Limnol. Oceanogr. 11:548-561.

LOHMANN, H.
1899. Das Gehäuse der Appendicularien, sein Bau, seine Funktion und Entstehung. Schr. Naturwiss. Ver. Schleswig-Holstein 11:347-406.
1914. Die Appendicularien der VALDIVIA Expedition. Verh. Dtsch. Zool. Ges. 24:157-192.
1931. Die Appendicularien der Deutschen Teifsee-Expedition. Wiss. Ergeb. Dtsch. Tiefsee-Exped. 21:1-158.

LOHMANN, H., AND E. HENTSCHEL.
1939. Die Appendicularien im Südatlantischen Ozean. Wiss. Ergeb. Dtsch. Atl. Exped. 13:153-243.

MENZEL, D. W.
1967. Particulate organic carbon in the deep sea. Deep-Sea Res. 14:229-238.

SILVER, M. W., A. L. SHANKS, AND J. D. TRENT.
1978. Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations. Science (Wash., D.C.) 201:371-373.

THOMPSON, H.
1948. Pelagic Tunicates of Australia. Commonw. Counc. Sci. Ind. Res., Aust., 196 p.

TOKIOKA, T.
1960. Studies on the distribution of appendicularians and some thaliaceans of the North Pacific, with some morphological notes. Publ. Seto Mar. Biol. Lab. 8(2):129-221.

CHARLES P. GALT

Biology Department
California State University
Long Beach, CA 90840

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including Zip code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¼ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibilty of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations*. (*Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, °C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Jay C. Quast, Scientific Editor
Fishery Bulletin
Northwest and Alaska Fisheries Center
Auke Bay Laboratory,
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

GPO 696-364

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Vol. 77, No. 3

Notes

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

Juanita M. Kreps, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881, it became the Bulletin of the Bureau of Fisheries in 1904, and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46, the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 64 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

[illegible] Fishery Bulletin, [illegible] Northwest and Alaska Fisheries Center, Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821. Controlled circulation postage paid at Seattle, Washington, and at additional mailing offices. POSTMASTER: Send address changes to Fishery Bulletin, Northwest and Alaska Fisheries Center, Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

[illegible] Department of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing this periodical has been approved by the Director of the Office of Management and Budget through [illegible].

Fishery Bulletin

CONTENTS

Vol. 77, No. 3 July 1979

Notes

(Continued on next page)

Seattle, Washington

1980

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington, DC 20402—Subscription price per year $12.00 domestic and $15.00 foreign. Cost per single issue: $3.00 domestic and $3.75 foreign.

Notices

Vol. 77, No. 2 was published on 9 October 1979.

REVISION OF THE SAURIES (PISCES, SCOMBERESOCIDAE) WITH DESCRIPTIONS OF TWO NEW GENERA AND ONE NEW SPECIES

CARL L. HUBBS AND ROBERT L. WISNER[1]

ABSTRACT

The extant members of the Scomberesocidae are: 1) *Scomberesox saurus saurus* of the North Atlantic, ranging into the Arctic north of Europe, and *Scomberesox saurus scombroides*, of disjunct occurrence in the Southern Hemisphere; and 2) *Cololabis saira* of the North Pacific (with one record attributed to release of bait in the Indo-Pacific tropics), two dwarf species, *Nanichthys simulans*, new genus and species, of the central Atlantic and the Indian Oceans, and *Elassichthys* (new genus) *adocetus*, of the eastern central Pacific. Some other names applied to Miocene fossils from southern California have been referred, we believe erroneously, to the Scomberesocidae. *Elassichthys adocetus* is particularly dwarfed but both dwarfs are distinguished by having no gas bladder and by having a single ovary which, at maturity, very largely fills the body cavity with few large ova. All members of the group are epipelagic, and they constitute a major element of that assemblage over a large share of the tropical and temperate world ocean.

Fishes of the family Scomberesocidae form a well-defined unit, due principally to the presence of separated finlets posterior to the dorsal and anal fins (as commonly found in scombroid fishes) and in having a slender, pikelike body with these median fins set far back (Figure 1). We interpret the scomberesocids as more or less akin to the Belonididae, Hemiramphidae, and Exocetidae, largely on the basis of having the lower pharyngeal bones united, and the lateral line low, near the ventral profile, rather than (as in most fishes) high on the lateral aspect of the body.

The ordinal classification of the family has been variously interpreted since the turn of the century. For example, it was placed in a division called the "Scombresocidae microsquamatae" by Schlesinger (1909); in the subfamily Scomberesocinae of the Exocoetidae by Regan (1911); in the family Scomberesocidae of the order Synentognathi by Jordan (1923) and by others of his school; in the Scomberesocidae of the suborder Microsquamati of the order Synentognathi by Nichols and Breder (1928); in the suborder Scomberesocoidei, including also the Belonidae, in the Beloniformes by Berg (1940); and, more recently, in the family Scomberesocidae of the superfamily Scomberesocoidea in the suborder Exocoetoidei and order Atheriniformes by Rosen (1964) and by Greenwood et al. (1966), who deleted the superfamily. Bailey et al. (1970) in general followed Greenwood et al., as did Nelson (1976). Gosline (1971) preferred to recognize the order Beloniformes, suborder Scomberesocoidei, families Scomberesocidae and Belonidae, and suborder Exocoetoidei, families Exocoetidae and Hemiramphidae; Gosline did not refer to Greenwood et al. (1966). Despite varied opinions on the ordinal level, all authors retained the scomberesocid fishes as a familial unit.

The Scomberesocidae appear to comprise a compact group to which we add two new genera and one new species. The genera and their species are characterized in Table 1. *Scomberesox* and *Cololabis* are relatively large fishes (about 350-450 mm), have paired ovaries and a gas bladder, while *Elassichthys* and *Nanichthys* are dwarfed (not known to exceed 126 mm, and one species not exceeding 68 mm standard length (SL)), have a single ovary, and lack a gas bladder. Also, they have fewer pectoral and procurrent caudal fin rays, gill rakers, and vertebrae.

Several of the authorities cited above, and others, have indicated that the Scomberesocidae represent an evolutionary line highly specialized for active life at the surface. The modifications of the posterior dorsal and anal rays into finlets, as in various scombroids, is evidence for this view. As a corollary, it seems obvious that a strong swimmer like *Cololabis saira* or *Scomberesox saurus*, rather than the smaller, probably weaker *Elassichthys*

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093. Carl L. Hubbs died on 30 June 1979.

Manuscript accepted April 1979.
FISHERY BULLETIN: VOL. 77, NO. 3, 1980.

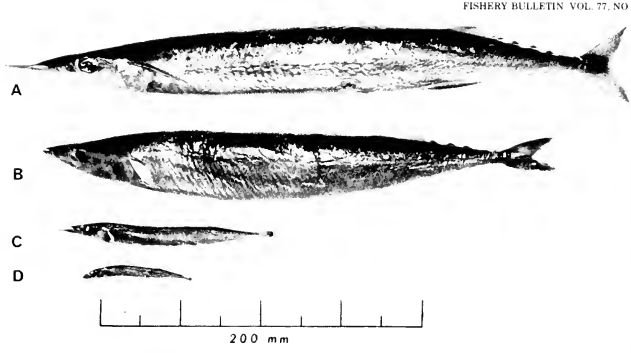


FIGURE 1.—Adults of the four genera and species of scomberesocid fishes: (A) *Scomberesox saurus*; B *Cololabis saira*; (C) *Nanichthys simulans*; (D) *Elassichthys adocetus*.

TABLE 1.—Differential characters of the four genera and species of Scomberesocidae.

Characters	*Cololabis saira*	*Scomberesox saurus*[1]	*Nanichthys simulans*	*Elassichthys adocetus*
Ovaries (Figure 8)	Paired, bilateral	Paired, bilateral	Single, median	Single, median
Testes (Figure 9)	Paired, bilateral, neither overtopping other	Paired, bilateral, neither overtopping other	Paired but forming coherent mass, left overtopping right	Paired but forming coherent mass, left overtopping right
Gas bladder	Large, thin-walled	Large, thin-walled	Completely lacking	Completely lacking
Maximum known length	Ca. 400 mm	Ca. 450 mm	68 mm	126 mm
Developed gonads	Dorsolateral to gut, attached to wall of coelom	Lateral to gut, attached to wall of coelom	Dorsolateral to gut, unattached	Dorsolateral to gut, unattached
Filaments on eggs	Many at pole, single distant one	None	None	None
Upper beak	Pointed, short, stout, overlapped slightly by lower	Greatly produced, very fragile, slightly overlapped by lower	Moderately produced, fragile, ca. half length of lower	No beak, upper jaw broadly curved
Lower jaw (in adult)	Pointed, short, stout	Greatly produced, ca. equal to postorbital head length	Much produced, ca. twice length of upper jaw	Very short, bluntly pointed, tubercular at tip
Teeth on upper jaw	All uniserial	Biserial on beak, uniserial behind	Uniserial behind, biserial forward	Uniserial, few, widely spaced
Teeth on lower jaw	Obsolete except developing forward only in adults uniserial	Well developed throughout life, biserial on beak, uniserial behind	Biserial near gape, uniserial forward	Essentially uniserial, fewer anteriorly
Cartilaginous loops between mandibular rami	Few, but very well developed	Numerous over long area	Few over short area	Wholly lacking
Intermandibular tissue	Covered by upper jaw	Covered by upper jaw	Covered by upper jaw	Tissue largely exposed
Lateral line	Extending to over anal finlets	Extending to over anal finlets	To slightly past pelvic base[2]	Completely lacking
Tubes and pores of head	Numerous and much branched	Numerous and much branched	Intermediate	Few, little branched
Fiber bundles of body muscles (Figure 7)	Fine	Fine	Moderately coarse	Relatively very coarse
Caudal peduncle[3]	Short	Short	Long	Long
Procurrent caudal rays	5-7	5-7	4, rarely 3 or 5	2-3
Gill rakers[4]	37-38 (32-43)	45 (39-51)	22-24 (19-26)	17-18 (15-21)
Pectoral rays[4]	12-14 (12-15)	13-14 (12-15)	10-11 (10-11)	9-10 (8-11)
Vertebrae[4]	165-67 (64-69) 63-67 (62-68)	65-67 (64-70)	59-62 (58-62)	56-57 (54-59)
Scales, lateral midline	128-148, rather firmly attached	107-128, rather firmly attached	77-91, very caducous	70-88, very caducous

[1]Except for gill rakers (5), characters refer to both subspecies.
[2]The lateral lines are incomplete on all our specimens except on the 121.2 mm one from Funchal, Madeira.
[3]Length of caudal peduncle, measured as interval between bases of last finlet and first precaudal ray, is either "short" (about equal to depth of peduncle) or "long" (about twice that depth).
[4]Minimum and maximum values; the most common values first with total ranges in parentheses.
[5]Values in parentheses are those for *S. s. scombroides*.
[6]First values for western Pacific, mean 66.05 (for 248 counts); second values for eastern Pacific, mean 65.11 (for 3,060 counts).

adocetus or *Nanichthys simulans*, is the basic type of the family, and that the dwarf forms are derivative.

DEVELOPMENT OF BEAK

In their early ontogeny, the Scomberesocidae, like other synentognathous fishes, pass through changes in physiognomy (Figure 2), involving especially the upper and lower beaks. The degree of metamorphosis varies greatly among the four species.

The most dwarfed scomberesocid, *E. adocetus*, exhibits the least change, retaining rather heavy, little-produced jaws throughout life. The upper jaw remains relatively short, and rounded in top view, and the lower jaw increases with growth of the fish only very slightly in production and slenderizing.

Next in degree of age changes is *C. saira*, in which the premaxillaries become more pointed forward and the dentaries become slightly produced and slenderized, but not to a degree fully warranting the designation of either jaw as a beak. In contrast with *Scomberesox* and *Nanichthys*, the snout does not further increase in relative length after the fish reaches the standard length of about 50 mm (Figure 2). In contrast, the snout increases in relative length throughout the life span of *Nanichthys* and in *Scomberesox* until a length of about 200 mm has been attained.

Next in the series we may rate the largest, and in many other respects the most extreme form, *S. saurus*. Very small juveniles have a short muzzle, with the lower jaw, as in all the species, the heavier (Figure 2). Very early the jaws both become sharper forward and begin to elongate. The process is initially somewhat more accelerated in the lower jaw, but at no stage do the developing beaks simulate the condition found in halfbeaks, for the developing upper beak is always much more than half as long as the lower. Lütken's (1880) indication to the contrary resulted from his inclusion of *N. simulans* into what he treated as the developmental series of *S. saurus* (see p. 533). In fact, the relative projection of the lower jaw decreases but little with age (Figure 2).

The most extreme ontogenetic changes in physiognomy are displayed by the next-to-most dwarfed form, *N. simulans* (Figure 2). Until it reaches about 30 mm SL the jaws are scarcely produced. Soon, however, the premaxillaries become pointed forward and begin to elongate, but slowly. The dentaries become very slender and, in juxtaposition, elongated forward far beyond the slender conjoined tips of the premaxillaries. When the standard length has reached 60 mm, the lower beak of *Nanichthys*, in contrast with *Scomberesox*, is more than twice the length of the upper. *Nanichthys* thus displays the closest approach to the halfbeak condition, but it can hardly be said to pass through a halfbeak stage, as do the belonids and two genera commonly (*Oxyporhamphus*) and/or regularly (*Fodiator*) placed in the Exocoetidae (Lütken 1880; Nichols and Breder 1928; Breder 1932, 1938; Hubbs 1933; Parin 1961). The projection of the lower jaw as a proportion of length of fish increases sharply with age, at least for the usual standard lengths of about 90 mm in the specimens available to us.

PHYLOGENY

Only two extant genera of the family Scomberesocidae, *Scomberesox* Lacépede 1803, and *Cololabis* Gill 1895, have been recognized. They have been differentiated primarily on the basis of the degree of development of the jaws into beak-like structures; in *Scomberesox* each jaw is definitely prolonged, very slender, fragile, and elongate, whereas in *Cololabis* the jaws remain short, less fragile, and only moderately pointed (Figures 1, 2). In each genus the lower jaw projects slightly beyond the upper. Both genera comprise slender, elongate fishes, bearing, as do the unrelated Scombridae, a file of separated finlets that largely fill the interval between the caudal fin and the main parts of the dorsal and anal fins. *Scomberesox* attains a standard length rarely in excess of 450 mm, although there are undocumented reports of 500 mm. *Cololabis* reaches about 350 mm SL.

Despite the several expressed opinions to the contrary (below), we regard the merely pointed muzzle, with projecting chin, as in *Cololabis* and *Elassichthys* (Figure 2), as a primitive feature, and as also in *Arrhamphus*, *Chriodorus*, and *Melapedalion* of the halfbeaks. We also regard the beaks of *Scomberesox* and *Nanichthys* as derivative therefrom. Jordan and Evermann (1896) surmised that *Cololabis* "represents the immature state of *Scomberesox*"—a view repeated by others of that school. Schlesinger (1909) definitely treated the jaws of *Cololabis* as secondarily foreshortened. Nichols and Breder (1928) went so far as to characterize *Cololabis* as ". . . a recogniz-

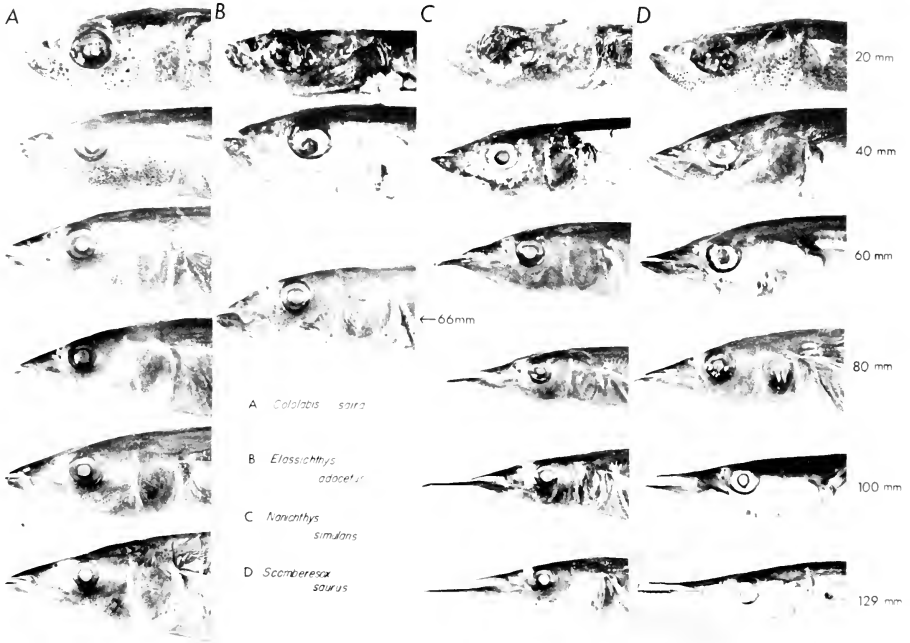


FIGURE 2.—Development of beaks in young of the four genera and species of scomberesocid fishes. Specimens are aligned in rows by size (standard length).

able fixed larva of *Scomberesox*." Knowing *C. saira* well as a moderately large and extremely active surface fish leads us to emphatically disregard its consideration as a larva. There is nothing in the ontogeny of the four species of the family to support the view that beaklessness arose from the beaked condition.

Thus, we arrive at the concept of a relatively large and strong, beakless, surface-swimming fish as the phyletically basic member of the Scomberesocidae: *Cololabis* alone fits this concept. We therefore assume that an immediate ancestor of *C. saira* gave rise to the other members of the family and remains as a relic in the temperate waters around the North Pacific, where it appears to replace *Scomberesox* completely.

The *Cololabis* ancestor presumably gave rise to *Scomberesox* through the development of a long beak, by the loss of filaments on the egg, and through a moderate increase in size and in average number of gill rakers and vertebrae. Perhaps a stock of the ancestor crossed equatorial waters in some past cool period and became isolated when the tropics again became warm; differentiation may then have taken place. From cool South Pacific waters the West Wind Drift may be assumed to have transported the saury to the southern parts of the Atlantic and Indian Oceans. From the Cape region of Africa it could have been carried far northward on the Benguela Current and may somehow, at some time, possibly even in the Pleistocene, have transgressed the tropics to gain the favorable waters of the North Atlantic. Such movements, however, are hypothetical.

The origin of the dwarfs from a type or types more like *Cololabis* and *Scomberesox* seems hardly subject to doubt (as is indicated above). While recognizing the many features, some deep-seated and fundamental, wherein *Elassichthys* and *Nanichthys* closely agree, and jointly contrast with *Cololabis* and *Scomberesox* (Table 1), we strongly favor, albeit somewhat intuitively, the hypothesis that they are the products of convergent evolution: that *Elassichthys* stemmed from *Cololabis* (or an immediate ancestor of that genus), and that *Nanichthys* is an offshoot from *Scomberesox* (or its immediate ancestor).

Circumstances favoring the concept of a dual origin of the two dwarf species follow.

1) Characters held jointly by *Elassichthys* and *Nanichthys*, in contrast with *Cololabis* and *Scomberesox*, are of the sort that might well be related to dwarfing, and hence be susceptible to independent origin. The lack of the gas bladder seems compensated for by the greatly reduced size of the fish (yielding relatively more surface and viscosity per weight), and by the apparently weaker musculature. The single ovary may be related to the minute size of the organ and the proportionately immense size of the few ova containable at any one time. The degeneration of the lateral line is a common feature of dwarfed fishes. The great reduction in number of gill rakers would be expected, as the smaller number should give adequate straining in a space so greatly reduced. Reduced number of vertebrae and rays is a feature of dwarfing, as Te Winkel (1935) showed in her study of a neotenic goby, and as she and the senior writer showed in an unpublished study of the excessively neotenic fish genus *Schindleria* (which was originally misplaced in the Synentognathi, though it is not so related—as Gosline (1959) has shown).

2) The agreement between *Elassichthys* and *Cololabis* in the mere sharpening of the jaws (the upper rounded in *Elassichthys*), without any real beak development, is a compelling reason to regard them as closely related.

3) The circumstance that the gill rakers and vertebrae are fewer in *Cololabis* than in *Scomberesox*, and about proportionately fewer in *Elassichthys* than in *Nanichthys* is at least suggestive evidence.

4) The circumstance that *Cololabis* is somewhat smaller than *Scomberesox*, and that *Elassichthys* is proportionately smaller than *Nanichthys*, seems to provide similar confirmatory evidence.

5) The mutual occurrence of *Elassichthys* and *Cololabis* in the Pacific Ocean, in part sympatrically, and the mutual occurrence of *Nanichthys* and *Scomberesox* in the Atlantic and Indian Oceans, again in part sympatrically, provides strong confirmatory evidence that *Elassichthys* is the dwarf derivative of *Cololabis* and that *Nanichthys* stemmed similarly and independently from *Scomberesox*. This hypothesis is diagrammed in Figure 3A. On this concept, dwarfing and various structural changes (diagrammed as "d g o"), including the loss of the gas bladder and the change to a single ovary, occurred twice, whereas the evolution of a beak (marked as "b") occurred only once.

No such body of evidence seems advanceable for the alternative hypothesis (Figure 3B) that dwarfing and the ancillary changes occurred but

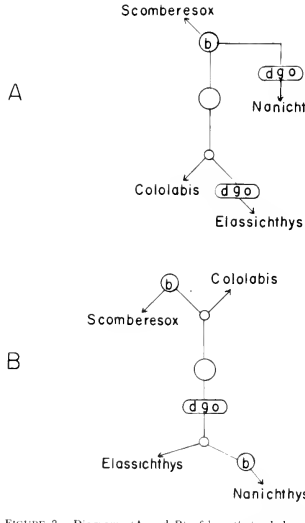


FIGURE 3.—Diagrams (A and B) of hypothetical divergent evolution within the Scomberesocidae: b—well-developed beak, d—dwarfism; g—gas bladder lost; o—ovary single. (A) The larger *Scomberesox* and the dwarfed *Nanichthys*, and the larger *Cololabis* and the dwarfed *Elassichthys*, derived respectively from beaked and beakless ancestors; development of a beak occurred but once, dwarfism and structural changes (d g o) twice. (B) The beaked and beakless larger forms, *Scomberesox* and *Cololabis*, derived from a common ancestor, as did the beaked and beakless dwarfs, *Elassichthys* and *Nanichthys*; development of a beak occurred twice, dwarfism and the structural changes but once.

once, so that *Elassichthys* and *Nanichthys* are of immediate common origin. On this hypothesis, the beak would have developed independently in *Nanichthys* and *Scomberesox*. The differences between the two genera in the lengths of the upper and lower beaks could be cited as confirmatory evidence. As another item of evidence it could be stated that agreement between *Elassichthys* and *Cololabis* breaks down when the structure of the egg is considered.

For some years we have known that there is a distinct dwarf genus (*Nanichthys*) having many characters in common with *Scomberesox*, as well as another dwarf genus (*Elassichthys*) having much in common with *Cololabis*. The species involved we name *Nanichthys simulans*, new species, and *Elassichthys adocetus* (Böhlke 1951).

These conclusions have been rather widely shared with colleagues. Parin (1968a, b) in particular, has discussed these putative relationships, using the names "*Scomberesox* sp." and "*Cololabis adocetus*" for the respective dwarfs; he cited only superficial distinctions, along with reduced numbers of gill rakers and vertebrae, in the dwarf form. Dudnik (1975b), likewise using the name "*Scomberesox* sp.," also discussed *Nanichthys*; he noted one internal morphological feature, that one of the ovaries is rudimentary. We have consistently found, however, no trace of a second ovary in either *Elassichthys* or *Nanichthys*. Our findings have been mentioned also by Collette (1966) as the second case of paedomorphism in the order, during his indication of a third case, that of a "paedomorphic or neotenic" belonid. The first case he indicated as the suggestion by Nichols and Breder (1928) that the scomberesocid genus *Cololabis* is a permanently arrested stage in the ontogenetic development of *Scomberesox*.

TABLE 2.—Numbers of gill rakers for the scomberesocid fishes.

Gill rakers	*Scomberesox saurus*		*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
	scomboides	*saurus*			
15	—	—	—	—	12
16	—	—	—	—	51
17	—	—	—	—	120
18	—	—	—	—	135
19	—	—	—	1	53
20	—	—	—	3	27
21	—	—	—	8	5
22	—	—	—	24	—
23	—	—	—	19	—
24	—	—	—	12	—
25	—	—	—	8	—
26	—	—	—	4	—
32	—	—	2	—	—
33	—	—	5	—	—
34	—	1	23	—	—
35	—	5	34	—	—
36	—	11	47	—	—
37	—	9	84	—	—
38	—	17	63	—	—
39	6	18	50	—	—
40	12	20	43	—	—
41	28	18	16	—	—
42	36	6	8	—	—
43	47	5	3	—	—
44	41	3	—	—	—
45	43	1	—	—	—
46	35	—	—	—	—
47	19	—	—	—	—
48	11	—	—	—	—
49	11	—	—	—	—
50	4	—	—	—	—
51	3	—	—	—	—
N	296	114	378	79	403
$\bar{x}$	44.11	39.19	37.53	22.84	17.66

TABLE 3.—Numbers of pectoral fin rays (both sides counted) and of total anal and dorsal fin rays (including finlets) for the scomberesocid fishes.

Fin rays	*Scomberesox saurus*[1]	*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
Pectoral				
8	—	—	—	6
9	—	—	—	203
10	—	—	99	122
11	—	—	54	1
12	8	124	—	—
13	108	962	—	—
14	37	388	—	—
15	1	8	—	—
N	154	1,482	153	332
x	13.20	13.19	10.35	9.36
Dorsal				
14	—	3	14	31
15	6	97	49	183
16	45	422	16	136
17	26	185	—	19
18	1	15	—	6
N	80	722	79	375
x	16.30	16.16	15.03	15.43
Anal				
16	—	—	—	1
17	1	—	1	13
18	18	24	9	103
19	84	250	48	188
20	30	370	20	49
21	11	67	—	2
N	144	711	78	356
x	19.22	19.68	19.11	18.78

[1]Counts for all fin rays of the northern and southern subspecies of *Scomberesox saurus* are combined.

TABLE 4.—Numbers of vertebrae for the scomberesocid fishes.

Number of vertebrae	*Scomberesox saurus*	*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
54	—	—	—	14
55	—	—	—	74
56	—	—	—	224
57	—	—	—	186
58	—	—	2	52
59	—	—	11	6
60	—	—	30	—
61	—	—	46	—
62	—	12	21	—
63	—	115	—	—
64	9	672	—	—
65	73	1,212	—	—
66	149	840	—	—
67	83	187	—	—
68	20	21	—	—
69	3	1	—	—
70	1	—	—	—
N	338	3,060	110	556
x	66.13	65.14	60.66	56.37

[1]Counts for the southern and northern subspecies are combined.

The much reduced size of *Nanichthys* and the even more extreme dwarfing of *Elassichthys* strongly support the hypothesis that they exhibit neotenic or paedomorphic tendencies, certainly dwarfism; we hold that they are not neotenic, in the strict sense, but merely dwarfed. The reduced numbers of gill rakers, pectoral rays, vertebrae (Tables 2-5), scales, and procurrent caudal rays provide confirmatory evidence (no marked differences were found in the numbers of dorsal and anal rays, either in the main fin or in the finlets). The loss of one ovary (or the complete fusion of the pair), and a tremendous decrease in the production of ova, the more notable in *Elassichthys*, may well be correlated with the dwarfing of the two new genera (the ova, however, have not been notably decreased in size). The less extreme dwarfing of *Nanichthys* could be interpreted as reflecting the larger size of its presumed progenitor, *Scomberesox* (Figure 1, Table 1). The concept of *Nanichthys* and *Elassichthys* being the respective derivatives of *Scomberesox* and *Cololabis* could be interpreted as being supported by their similar beak structures (Figure 2), and by the common occurrence of *Scomberesox* and *Nanichthys* in the Atlantic and Indian Oceans and of *Cololabis* and *Elassichthys* in the Pacific, north of the range in that ocean of *Scomberesox*.

Herein we describe, discuss, and differentiate the two new dwarfed genera, *Nanichthys* and *Elassichthys*, and the new species *N. simulans*, distinguish the Southern Hemisphere population of *Scomberesox* as a subspecies, for which the

TABLE 5.—Correlated counts of precaudal and caudal vertebrae of the four genera of Scomberesocidae. Counts not otherwise marked represent *Elassichthys*; counts in italics refer to *Nanichthys*; counts in parentheses represent *Cololabis*; and counts in bold face type refer to *Scomberesox*.

Genus	Precaudal vertebrae	Caudal vertebrae								
		21	22	23	24	25	26	27	28	29
Elassichthys	32	—	1	1	1	—	—	—	—	—
	33	2	7	23	8	—	—	—	—	—
	34	1	21	52	8	—	—	—	—	—
Nanichthys	35	—	7	5	1 2		1	—	—	—
	36	—	—	1 4	21	14	2	—	—	—
Cololabis	37	—	1	7	41	22	(7)	(8)	(6)	—
	38		1		7	3	(37)	(64)	(21)	(1)
Scomberesox[1]	39	—	—	—	—	(3) **1**	(37)	(63) **1**	(10)	(1)
	40	—	—	—	—	**12**	**13**	(11)	(15)	(4)
	41	—	—	—	**17**	**63**	**31**		**1**	—
	42	—	—	—	**6**	**19**	**6**		**1**	**1**
	43	—	—	—	**2**	**2**	—	—	—	—

[1]Counts for the southern and northern subspecies are combined.

name *S. saurus scombroides* (Richardson 1842) appears to have priority, and we portray the zoogeography of the four genera of the Scomberesocidae that we now recognize. Also, we append a discussion of Miocene fossils from California referred to the Scomberesocidae.

MATERIALS AND METHODS

We have examined material from the following repositories: AMS (Australian Musuem, Sydney); BCFL (Bureau of Commercial Fisheries Laboratories (now NMFS), at Brunswick, Ga.; Honolulu Hawaii (formerly POFI); Seattle, Wash.; and Woods Hole, Mass.); BMNH (British Museum (Natural History)); BU (Boston University); CAS (California Academy of Sciences); CF (Carlsberg Foundation); CFG (California Fish and Game, San Pedro); CNHM, FMNH (Chicago Natural History Museum, Field Museum of Natural History); LACM (Los Angeles County Museum); MCZ (Museum of Comparative Zoology, Harvard University); MMF (Museo Municipal do Funchal, Madeira); SAM (South African Museum, Cape Town); SIO (Scripps Institution of Oceanography); SOSC (Smithsonian Oceanographic Sorting Center); SU (Stanford University; collections now at CAS); TABL (Tropical Atlantic Biological Laboratory, Miami); UMMZ (University of Michigan Museum of Zoology); USNM (United States National Museum); UW (University of Washington, Seattle); WHOI (Woods Hole Oceanographic Institution); ZMUC (Zoological Museum, University of Copenhagen); and ZSZM (Zoologisches Staatsinstitute und Zoologisches Museum, Hamburg).

Counts of dorsal and anal rays include the succeeding finlets because the last rays of the main fin proper are often too much like those of the first finlets for definitive separation, particularly in adults; usually the last rays of the fin proper are thickened at the base and much branched and fanlike distally—in shape much like that of the first finlet. In young and subadults a space greater than that between the last rays of the fin proper usually separates the last ray and the first finlet, but this space is often obscured by a membrane or is not apparent in large specimens, particularly of *Scomberesox* and *Cololabis*. Pectoral rays of small and juvenile fish were counted using an air jet, or when submerged. Vertebrae were counted from radiographs or stained material (the latter method was used primarily for juveniles of *Cololabis*). The urostyle was included in the count.

Numbers of gill rakers for specimens of *Scomberesox* and *Cololabis* >70 mm SL and of *Nanichthys* and *Elassichthys* >30 mm SL are not included in the tabular data because at shorter sizes the anterior rakers fade gradually into diminishing nubs of tissue that require highly subjective interpretation.

Lateral lines scales were removed from the left side within a distance no >10 mm anterior to the origin of the pelvic fin. To enhance visibility of circuli the scales were lightly stained in a weak solution of Alizarin Red S and visually monitored for adequate uptake of stain. The scales of both *Scomberesox* (particularly) and of *Cololabis* were quite tenacious, so much so that they needed to be cut away from the body and the adhering tissue manually removed. Remaining bits of tissue often were so firmly attached that they could not be pulled off with forceps; immersion in 2% KOH eroded the scales without removing the bits of tissue.

As most specimens of *Scomberesox* examined had the tips of the beaks broken off, proportions in all the species are based on body length rather than standard length. Body length is defined as the distance from the posterior margin of the orbit to the end of the hypural plate; this end point was determined by flexing the caudal fin until a crease appeared, approximately at the end of the hypural.

KEY TO SPECIES OF SCOMBERESOCID FISHES

1a. Gill rakers numerous (34-51), very closely spaced. Pectoral rays 12-15. Procurrent caudal rays 5-7. Depth of caudal peduncle equal to or less than its length 2

1b. Gill rakers fewer (15-26), less closely spaced. Pectoral rays 8-11. Procurrent caudal rays 2-5. Depth of caudal peduncle one-half to less than its length 3

2a. Both jaws produced into long, slender beaks in specimens >100 mm SL, the lower slightly longer. Maximum size about 450-500 mm SL. Known from temperate waters of North Atlantic and all southern oceans ..... *Scomberesox saurus*

2b. Jaws only moderately produced into blunt beaks, the lower slightly longer. Maximum size about 400 mm SL. Native only in North Pacific Ocean ..... *Cololabis saira*

3a. Jaws of adults produced as slender beaks, the lower about twice the length of upper. Gill rakers 22-24 (19-26). Procurrent caudal rays 4 (3-5). Maximum size to 126 mm, usually about 100 mm. Known only from warm-temperate waters of Atlantic and Indian Oceans ..... *Nanichthys simulans*

3b. Upper jaw very little produced, bluntly rounded, the lower jaw slightly more produced and more pointed at all sizes. Gill rakers 17-18 (15-21). Procurrent caudal rays 2-3. Maximum size to 68 mm SL. Known only from eastern tropical Pacific and westward to Hawaii ..... *Elassichthys adocetus*

AIDS TO IDENTIFICATION

If the specimen is determined to be one of the larger species, pertinence to *S. saurus* or *C. saira* will be obvious from the oceanic source of the material, and, for all but the very young, from the presence or absence of a beak (Figure 2); even if the long beaks of *Scomberesox* are broken off near the base the stubbed condition will be obvious. However, if the very young of one or both species should be taken in the eastern Pacific Ocean in the upwelling area along the Equator (which now seems unlikely from the distributional evidence discussed below), it would hardly be feasible to arrive at a certain identification on the basis of beak development alone until the beak begins to develop at about 40 mm SL; but the reduced numbers of pectoral and procurrent caudal rays and of gill rakers (rather short and widely spaced) readily distinguish *Elassichthys* from *Scomberesox* and *Cololabis*. The development of the beak is the most trenchant distinction between *Scomberesox* and *Cololabis*; counts (Tables 2-5) and morphometric values (Table 6) overlap widely.

If the specimen is determined to be a dwarf, its pertinence to *E. adocetus* or *N. simulans* will probably always be determineable from the locality of capture, and, for specimens longer than about 50 mm, from the incipient to full development of the beak (Figure 2); in fact, in *Elassichthys* the upper jaw never becomes really beaklike, only broadly rounded, not moderately pointed as in *C. saira* of comparable size (Figure 4). If further check is desired, separations may be attained by counting gill rakers, pectoral rays, or vertebrae (Tables 2-5). Ueyanagi and Doi (1971) showed that in young of *Elassichthys* (≤30 mm) the depth of the caudal peduncle was one-half or less of its length, but was about equal in *S. saurus* and *C. saira*. We find (original data) *N. simulans* to have a ratio of depth to length of caudal peduncle similar to that of *E. adocetus*. These ratios hold for all sizes of the four species.

The scomberesocid fishes inhabiting the Atlantic or Indian Oceans may be either *N. simulans* or *S. saurus*, determinable by the meristic counts (Tables 2-4). At lengths greater than about 60 mm, the relative development of unbroken beaks should ordinarily be decisive (Figure 2).

TABLE 6.—Selected body proportions from 36 specimens each of the four species of scomberesocid fishes (thousandths of body length).

	Scomberesox saurus saurus (26-223 mm)		*Scomberesox s. scombroides* (63-300 mm)		*Nanichthys simulans* (32-77 mm)		*Elassichthys adocetus* (29-60 mm)		*Cololabis saira* (50-239 mm)	
Body proportion	*x*	Range	*x*	Range	*x*	Range	*x*	Range	*x*	Range
Orbit length	49	36-39	45	37-59	52	41-64	50	43-58	43	35-53
Postorbital head length	104	82-124	105	92-120	99	88-111	89	80-102	113	103-126
Body depth at origin of pelvic fin	132	109-160	128	115-139	113	95-135	115	95-131	136	121-153
Distance from origins of dorsal and anal fins	127	105-143	123	111-137	108	98-119	107	93-116	127	111-147
Posterior margin of orbit to origins of										
Pelvic fin	513	474-525	501	475-536	460	444-487	447	417-485	478	457-502
Anal fin	661	611-692	669	642-707	621	604-645	628	606-654	643	620-668
Dorsal fin	684	650-715	685	658-723	648	631-672	652	630-673	679	661-707
End of hypural to origins of										
Pelvic fin	512	487-538	515	483-542	549	529-565	560	529-586	529	518-546
Anal fin	354	317-396	343	314-371	388	363-406	380	351-400	361	326-381
Dorsal fin	330	298-369	322	281-350	359	341-379	357	330-374	329	312-350

FIGURE 4.—Upper—Dorsal view of bluntly rounded tip of upper beak of adult *Elassichthys adocetus*, 59.0 mm SL. Lower—Dorsal view of moderately pointed tip of upper beak of juvenile *Cololabis saira*, 58.0 mm SL.

DESCRIPTION OF NEW TAXA

Nanichthys Hubbs and Wisner, new genus

New genus, Hubbs and Wisner.—Collette 1966:4, 6, 7, 20 (reduced counts; neotenic [this seems to be the only published reference to *Nanichthys* as a genus]).

Genotype, *Nanichthys simulans*, new species.

Diagnosis.—A dwarfed scomberesocid (maximum known standard length 126 mm), agreeing with *Elassichthys* in having a single median ovary, when ripe largely filling the expanded coelom, and the testis folded together into a single median band. Gas bladder completely obsolete. Lateral line developed only anteriorly. Premaxillary and mandibular tooth rows closely approximated at front. Upper jaw produced as an extremely slender beak about half as long as in *S. saurus* and much slenderer (in both lateral and dorsal aspects) than the much stronger but still slender lower beak, which is only about half as long as, and much less attenuate than, that in adult *S. saurus*. The major

counts are much reduced: vertebrae 58-62, transverse scale rows along midlateral line 70-88, procurrent caudal rays 4 (rarely 3 or 5), pectoral rays 8-11, rakers on first gill arch 19-25 (usually 22-24).

Derivation of generic name.—From the Greek *νάνος* (nanos), a dwarf, and *ιχθύς* (ichthys) a fish.

Nanichthys simulans Hubbs and Wisner, new species Figure 5

Derivation of species name.—From the Latin, *simulans* (imitating).

Holotype.—SIO 63-546, an adult male 89.5 mm SL, dipnetted at surface under a light in the south central Atlantic Ocean at 24°02.5′ S, 15°32.0′ W, on 9 June 1963; deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography.

Paratypes.—All dipnetted in the southern Atlantic Ocean at night under a light. Marine Vertebrate Collection of the Scripps Institution of Oceanography: SIO 63-545, 8 (46-69 mm), 12 June 1963, 29°51.5′ S, 11°07′ W; SIO 63-546, 17 (47-90 mm), 19 June 1963, 24°02.5′ S, 15°32.0′ W; SIO 63-548, 16 (20-76 mm), 20 June 1963, 23°42.0′ S, 12°12.5′ W; SIO 63-549, 6 (55-87 mm), 22 June 1963, 21°21.0′ S, 11°34.5′ W; SIO 63-550, 7 (45-80 mm), 24 June 1963, 20°10.5′ S, 11°30.5′ W; SIO 63-553, 4 (67-90 mm), 26 June 1963, 17°39.0′ S, 12°22.0′ W; SIO 63-555, 11 (38-66 mm), 28 June 1963, 15°48.0′ S, 16°50.0′ W; SIO 63-571, 2 (38 and 44 mm), 22 July 1963, 11°35.0′ S, 44°01.0′ W

USNM 204257, 2 (68 and 101 mm), 15°45′ S, 08°45′ E; USNM 204258, 4 (42-66 mm), 32°57′ N, 39°21′ W.

We plan to transfer some of the Scripps paratypes listed above to USNM, MCZ, Philadelphia Academy of Natural Sciences (ANSP), CAS, and BMNH.

We do not assign paratype designation to many additional specimens, mostly very small, from the mid-Atlantic, nor to the few examples seen from the Indian Ocean, nor to two specimens, unusually large for this dwarf species, from Funchal, Madeira (these two are discussed on p. 541).

Synonymy of *Nanichthys simulans*

Scombresox scutellatus (not *Scomberesox scutul-*

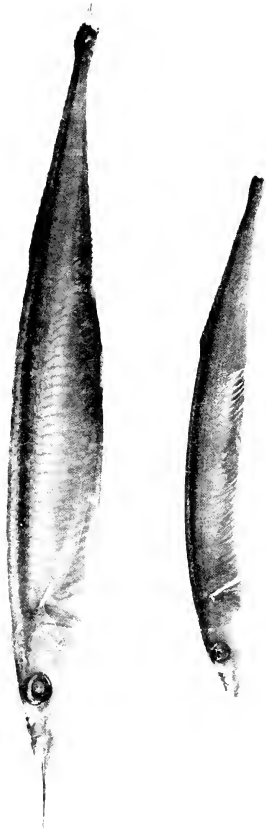


FIGURE 5.—Upper—*Nanichthys simulans*, holotype, adult male, 89.5 mm SL, SIO63-546. Lower—*Elassichthys adocetus*, adult male, 64.7 mm SL, SIOH52-380.

latum LeSueur 1822:132-133[2])—Valenciennes 1846:477-479 (description: "en le retirant de l'estomac d'un coryphène (*Coryphaena equisetis*) . . . venait de pecher à vingt-cinq lieues [ca. 2.76 mi] au nord de Sainte-Hélène [St. Helena Isle, about 16° S in mid-Atlantic Ocean]; nous avons un second exemplaire de la même espèce . . . fit à l'Isle-de-France [Mauritius Island, Indian Ocean] ou pendant sa traversée de retour" [to France].

Scombresox saurus (misidentification).—Günther 1866:257-258 ("Atlantic, 3° N of the line"; St. Helena; probably also 20° N, 22°53′ N and other series); 1889:34 (". . . fry and young . . . belong to most common forms of pelagic life . . . from the Atlantic . . . .").[3] Sauvage 1891:526 (listed from near Madagascar, between 3° and 26° S, 42° and 65° E; presumed from locality). Murray and Hjort 1912:89, 90, 94, 607, 613 (14 stations listed), 633, 635, 644, 670, 741, 747-748, figs. 541-542, all in part or questionable, listed both as "*Scombresox*" and as "*Scombresox saurus*," from open Atlantic in area between Iceland, Morocco, and Newfoundland; size to 50 cm. Barnard 1925:259, fig. 16b (St. Helena record only). Cadenat 1950:298 (presumed from locality off Iles du Cap Vert).

Scomberesox saurus (misidentification).—Lütken 1880:564-569, 1 fig., repeated by Murray and Hjort, see above (in part: in Atlantic Ocean from 11°30′ to 48° N, 9° to 40° W, and from 12° to 40°32′ S, 52° W to 16°30′ E; in Indian Ocean from 27° to 38°20′ S, and from 24°30′ to 101°40′ E; measurements and counts presumably also in part). Regan 1916:142 (postlarvae from south of Azores, at 29°10′ N, 33°36′ W, identification dubious). Bigelow and Welsh 1925:166, fig. 71 (range, 11°-12° to 40° N in Atlantic (presumably in part), figure repeated from Murray and Hjort, see above). Hildebrand and Schroeder 1928:151-152 (range, in part, and description of young, from Bigelow and Welsh 1925). Sivertsen 1945:6 (in part, St. Helena record only). Bigelow and Schroeder 1953:170-171, fig. 83 (in part, doubtful, description; young—100 to 150 mm "hemiramphus stage," most numerous in open Atlantic between 11° or 12° and 40° N). Smith 1955:308 (presumptive, listed from Aldabra Island). Fowler 1956:141-142 (reference to Borodin's 1930 dubious (unverified) Red Sea record; South Africa, description taken from New England and New York material of *S. saurus* and not "Indo-Pacific" entry). Briggs 1958:264 (presumptive, in part, western Atlantic from Newfoundland and Bermuda to Argentina, 35° to 30° S). Rodríguez-Roda 1960:115 (presumed from locality; southern Spain, Strait of Gibralter). Hotta 1964:4-5 (in part, presumptive, distribution). Leim and Scott 1966:168 (in part, presumptive, in western Atlantic south to West Indies; fry abundant between 11° and 40° N; jaws do not reach full length until fish are 4 to 6 in long). Sauskan and Semenov 1969:250-252, fig. 157 (two populations inferred in North Atlantic, 32° to 36° N, 50° to 70° W, and near Azores; feeding migration) (in part, presumed from locality). Zilanov and Bogdanov 1969, fig. 158 (size groups, migrations, northeast Atlantic, 30° to 60° N, 8° to 40° W) (in part, presumed from locality). Hartmann 1970 (2.0 mm eggs in 68 mm scomberesocids from northeastern Atlantic can refer to only *N. simulans*).

Scomberesox sp.—Parin 1968b, fig. 31 (planktonic, records mapped in tropical eastern Atlantic and north of Madagascar, Indian Ocean); 1968a, fig. 1 (undescribed species under study by Hubbs and Wisner). Parin and Andriashev 1972 (dwarf Atlantic species, along 26° W between 24° and 30° S, and in western cruise track off South America in area of 32° S, temperature 20.4 to 22.4 C). Parin 1973 (reference to Parin 1968a; to be described by Hubbs and Wisner; abundant, epipelagic, Atlantic off Madeira, Canaries, Morocco, Portugal, to 40° N). Ueyanagi et al. 1972, fig. 1, 2 (sizes graphed, distribution in Atlantic mapped). Suda 1973, fig. 7 (life history presumably similar to that of *Cololabis adocetus;* not suitable for commercial fishery). Dudnik 1975b, fig. (general discussion; comparison with *S. saurus* in range and characters; one ovary developed, second rudimentary; ova sizes; spawning prolonged). Wisner 1977, fig. (description, key; compared with *S. saurus*, Belonidae, and Hemiramphidae; distribution in northwestern central Atlantic). Hardy 1978, fig. 29-34 (in part, North Atlantic; "*Scomberesox* sp." in reference to Hartmann, 1970, statement of 2.0 mm eggs in females 68 mm and over).

[2]LeSueur's type-specimen was "small," with upper beak about half of other; it was " . . . found in the stomach of a fresh codfish which had been brought to Boston from the Bank of Newfoundland," therefore in the appropriate range of *Scomberesox saurus* and far north of the range of *Nanichthys simulans*.

[3]At least in part, one of three specimens involved, but not mentioned, from Tenerife (one of the Canary Islands) has been identified for us as *N. simulans* by G. Palmer of the British Museum (Natural History), using characters outlined by us.

Discussion of Synonymy.—It has been consistently overlooked that Valenciennes [1846 (XVIII):477-479] recognizably described this dwarf scomberesocid, from 25 leagues north of Saint Helena Island in the tropical Atlantic Ocean and from Mauritius Island in the Indian Ocean or on the return journey [to France]. He misidentified this species as *Scombresox scutellatum* LeSeuer. However, *Scombresox scutellatum* LeSueur (1822) was based on a small specimen, obviously of *Scomberesox saurus*, that was taken from the stomach of a cod brought to Boston from the bank of Newfoundland. The Atlantic specimen described by Valenciennes also was supposed to be a young saury that had been eaten by a dolphin fish, identified as *Coryphaena equisetis*, caught "à vingt-cinq lieues au nord de Sainte-Hélène." Assuming this to be the island on which Napoleon was confined, on the basis of 2.76 mi to a league, from the old French system, the location was approximately 14°48′ S, 05°42′ W (marked as an open circle on Figure 12). This location is obviously within the now known habitat of *Nanichthys simulans* and far from the range of *S. saurus*, whereas the specimen treated by LeSueur was centered within the area where *S. saurus* alone occurs, in abundance.

That Valenciennes had an example of the dwarf Atlantic saury is obvious from his description of the beak in a small specimen. Valenciennes wrote: "La brévité du museau est aussi non moins remarquable; car le longueur du bec n'est quère moitié du reste de la tete; le bec supérieur lui-meme n'est pas beaucoup plus prolongé que celui des plusieurs hémiramphes." He further stated (p. 478), "Ce petit poisson, long de deux pouces neuf lignes . . ." Since the old French "pouce" was 27.07 mm long, and a "ligne" one-twelfth of a pouce, we compute the length of the fish as about 75 mm. A scomberesocid of this size, with beak scarcely half the length of the head behind the beak, and with snout comparable with that of a hemiramphid, could scarcely be other than a *Nanichthys*. Since the specimen collected at "l'Isle-de-France" [Mauritius], or on the return journey, was described as of the same size and of the same species, and since *N. simulans* is now known to occur in the southern Indian Ocean, it has seemed highly probable that it also pertains to that species. This assumption has been verified for us, very kindly, by Marie-Louise Bauchot[4] who has found that the two specimens, respectively 66.9 and 67.1 mm SL, have 11 and 10 pectoral rays, 23 and 22 gill rakers, and 59 and 60 vertebrae (within the range for *N. simulans* but far below the range for *S. saurus*).

It is now clear that Lütken (1880:564-569, fig. a-h) unknowingly included *N. simulans* as well as *Scomberesox s. saurus* in his account of *S. saurus*. This is evident from his statement of latitudinal distribution in the Atlantic Ocean from 11°30′ to 48° N and from 12° to 40°32′ S, and in the Indian Ocean from 27° to 38°20′ S, as well as from his figures; figures c, d, and e represent fish 51, 60, and 100 mm TL from tip of mandible to caudal-fin fork (corresponding to standard lengths of about 47, 55, and 89 mm, from tip of upper jaw to base of caudal fin). Beaks of specimens f-h (170 mm to full adult) pertain to *Scomberesox*. Comparison of these three figures with our illustrations of growth changes in the four species (Figure 2) demonstrates agreement only with *N. simulans*. The divergent approach toward hemiramphine beak structure in this developmental series of *Nanichthys* apparently did not disturb Lütken, for he showed in the same compilation of figures the development of *Belone vulgaris* from the beakless very young through the halfbeaked juveniles to the nearly full-beaked adult stage. In the lack of locality data it is not clear which species are represented by Lütken's figures a and b, which represent prejuveniles, 16 and 30 mm in fork length, with almost no beak development.

The epochal treatise of Atlantic epipelagic fishes by Murray and Hjort (1912), expanding that of Lütken (1880), recognized the preponderance of Scomberesocidae in the mid-Atlantic but failed to distinguish between *S. saurus* and *N. simulans*. Evidence in these classics, however, renders it clear that both accounts dealt with both species. Murray and Hjort's figure 541 of a 6.2 cm saury (on p. 747) almost surely represents *N. simulans* by reason of the better development of the beaks at that size (although the body was drawn too deep). Their figure 542 is a copy of Lütken's figure 567 (discussed above). The well-filamented egg labeled "Egg of Scomberesocid" (fig. 531) was obviously misidentified and very probably represents an exocoetid (Orton 1964). The treatment of sauries by Murray and Hjort pertains almost wholly to young (the maximum size given, 50 cm, was presumably drawn from some other source); they

[4]Marie-Louise Bauchot, Fish Division, Museum National d'Historia Naturelle, Rue Cuvier, 57, Paris, France, pers. commun. 2 May 1968

stated that only "young scomberesocids" were taken on the cruise.

The accounts of *S. saurus* by Bigelow and Welsh (1925) and by Bigelow and Schroeder (1953) definitely also involved *N. simulans*. The figure of the young, after Murray and Hjort, definitely represents the dwarf species, as does the text account of the "young": "The most interesting phase in the development of the skipper is that its jaws do not commence to elongate until the fry have grown to about $1^{5}/_{8}$ inches (40 mm.), and that the lower jaw out-strips the upper at first, so that fry of 4 to 6 (100 to 150 mm.) inches look more like little halfbeaks ('Hemiramphus' stage) than like their own parents" (quoted from Bigelow and Schroeder). These confusions were also expressed by Hildebrand and Schroeder (1928).

Inclusion of *Scomberesox s. saurus* (Günther 1889) in part, in the synonymy of this species, and the inclusion of this species in the British Museum collection, have been verified for us by G. Palmer[5] by examination, with our findings at hand, of the following specimens: six young, 31-61 mm, from St. Helena; three, 64-68 mm, from "Atlantic" (Godfrey); three, 29-93 mm, collected by Jones; one of 96 mm of the two without locality collected by Haslar; one of 69 mm taken by Vallentin at 18°32' N, 29°09' W; one of 52 mm, with two of *S. s. saurus*, taken at Tenerife (Canary Islands) by the *Challenger*; and one of 131 mm (total body length—see p. 541) by G. Maul in Funchal Harbor, Madeira. Günther (1866, vol. 6:257) reported *Scomberesox saurus* "From $1^{1}/_{2}$ to 7 inches long" from "Atlantic, 3 N. of the line," which, on distributional grounds, assuming correct latitude, would be expected to be *Nanichthys*. However, G. Palmer reports an extant specimen 156 mm long, listed with three of 66-98 mm, from "Atlantic (Godfrey)" that is probably the 7-in specimen, but Palmer finds it to be *Scomberesox*.

Zoogeographical considerations might lead to the citation in the synonymy of *Nanichthys simulans* of the material recorded as *Scomberesox saurus* by Arnoult et al. (1966) from off Liberia and Equatorial Guinea [Iles Principe], but Marie-Louise Bauchot (see footnote 4) has informed us that a reexamination of the five specimens involved led her to reidentify them as *Strongylura senegalensis* (Valenciennes) and *Platybelone argalus* (LeSueur).

[5] G. Palmer, Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7, England, pers. commun. 1 May 1968.

Although Valenciennes (1846) applied the name *Scomberesox scutullatus* to what now seems surely to be *Nanichthys simulans* (q.v.), we regard the original *Scomberesox scutullatum* LeSueur as having been based on *S. s. saurus*. The locality "Bank of Newfoundland" is in the range of that form and probably far outside the range of its dwarfed relative. The one pertinent key character given, that of 13 pectoral rays, confirms pertinence to *Scomberesox*.

Elassichthys Hubbs and Wisner, new genus

New genus, Hubbs and Wisner.—Collette 1966:4, 6, 7, 15, 20 (reduced meristics; neotenic [this seems to be the only published reference to *Elassichthys* as a genus]).

Genotype, *Cololabis adocetus* Böhlke 1951.

Diagnosis.—A greatly dwarfed scomberesocid (maximum known standard length ca. 68 mm), agreeing with *Nanichthys* in having a single median ovary largely filling, when ripe, the expanded coelom, and the paired testes folded together into a single median band with the division on the right side. Gas bladder and lateral line scales obsolete. Upper jaw very broadly and evenly rounded in dorsal aspect and only moderately pointed in lateral view; lower jaw only moderately pointed at the tuberculate tip (Figure 4). Premaxillary and mandibular tooth rows very broadly separated at front. Counts minimal for the family: vertebrae 52-59, usually only 56 or 57; transverse scale rows along midlateral line 70-78; procurrent caudal rays reduced to only 2 or 3; rakers on first gill arch 15-21, usually 17 or 18.

Derivation.—From the Greek, ἐλάσσων, smaller, less, and ἰχθύς, a fish.

Elassichthys adocetus Böhlke 1951 Figure 5B

Scomberesox sp.—Kendall and Radcliffe 1912:84, 167 (in part).[6]

[6] Young of *Scomberesox saurus scombroides* may well have been included, only three specimens (in Museum of Comparative Zoology), among those listed, have been examined by us and all were found to be *E. adocetus* from *Albatross* stations 4657 (07°12'30" S, 84°09' W), 4708 (11°40' S, 96°55' W), and 4730 (17°19' S, 100°52'30" W). *Scomberesox s. scombroides* also occurs in these areas.

Cololabis saira (misidentification).—Schaefer and Reintjes 1950:164 (between California and Hawaii at 28° 22′ N, 137° 12′ W; 25° 14′ N, 144° 41′ W; 23° 52′ N, 148° 41′ W; 23° 04′ N, 153° 19′ W; compared with "*Cololabis adocetus*," these records thought [erroneously] to confirm reference of *Cololabis brevirostris* to *C. saira* by Hubbs 1916:157 and by Schultz 1940:270). Ramirez Hernández and González Pagés 1976:74 (reference to Perú only).

Cololabis sp.—Clemens 1955:165 (3°31′ S, 81° 11′ W [presumptive identification due to locality]). King and Iversen 1962:301, tables 19-20, appendix table 8 (one 86 mm specimen taken in Equatorial Counter Current) [identification presumed from locality].[7]

Scomberesocidae.—Mais and Jow 1960:131 (02° 54′ S, 99° 37′ W) [identification presumed from locality].

Cololabis adocetus.—Böhlke 1951:83-87 (original description; comparison, phylogeny; from 160 mi southwest of San Juan, Perú (17° S, 76° 50′ W) (holotype); and off Perú at 10° 01′ S, 80° 05′ W, west of Chincha Isles, Perú, 13° 35′ S, 76° 50′ W, arrested development). Knauss 1957:236 (in oceanic front at about 3° N, 120° W). Gosline 1959:73 (neotenic); Gosline and Brock 1960:128, 318 (Hawaii; compared with *C. saira*). Chyung 1961:277 (reference to Böhlke 1951). Koepcke 1962:197 (references; known only from Perú, 10° to 17° S). Clemens and Nowell 1963:251-255 (records off Ecuador, Perú, Chile). Hotta 1964:4, fig. 22 (distribution off Perú). Orton 1964:144-145, 148-149 (description of pelagic and ovarian eggs from off Perú, 8° 07′ to 10° 51′ W; range overlaps that of *S. saurus*; vertebral numbers). Lindberg and Legeza 1965:209 translation, 1969:201 (Perú). Collette 1966:3, 15 (neoteny; meristic reduction; phylogeny; generic status). Ebeling 1967:599 (distribution mainly in central water mass in eastern Pacific Ocean). Parin 1967b:150 (117 in translation) (larvae may be caught near surface at any time of day); 1967a many pages (distribution in very warm water). Rass 1967:58, 60, 63-66, 129 (distribution). Parin 1968b: many pages (an epipelagic fish said to be limited to tropical waters of eastern Pacific and near Hawaii); 1968a: many pages, fig. 2, 3, 5 (comparisons, relationships; distribution and ecology). Chirichigno F. 1969:40 (vernaculars in Perú, Chile). Parin 1969a:715, 719, fig. (epipelagial; distribution, dwarf fish, false pike; eastern tropical Pacific); 1969b:577 (462 in translation), fig. 2 (northern part of area surveyed off west side of South America; numerical abundance charted; as many as 1,000 trawled in 20 min with pleuston net south of Galápagos Islands). Ueyanagi et al. 1969:6-7, fig. 12 (occurrence off Perú). Ueyanagi and Doi 1971:17-21, fig. 15 (distribution in southeastern Pacific mapped; characters distinguishing juveniles of *C. adocetus* from *C. saira* and *S. saurus*). Ahlstrom 1972:1192, 1196, fig. 14 (occurrence of larvae in eastern tropical Pacific). Suda 1973:2134-2135, fig. 7 (range in eastern Pacific; dwarf species; not suitable for a commercial fishery). Chirichigno F. 1974:318-319, 331, fig. 628 (characters in key; Perú, 10° to 12° S). Nelson 1976:172 (neotenic). Parin 1975:314-316 (records near Equator at about 97° W).

The Southern Subspecies of *Scomberesox saurus*

We have found that the disjunct, widespread, circumglobal Southern Hemisphere population of *Scomberesox saurus* is slightly differentiated from the topotypic Northern Hemisphere Atlantic form, as Parin (1968a) has tentatively suggested. Before presenting the evidence we list, with annotations, the rather complicated synonymic references that apply distinctively to the southern form, and here eliminate references in which the names used are synonyms of the North Atlantic subspecies *Scomberesox saurus saurus*, namely *Scombresox*, *Scomberesox*, or *Scombresose*, *equirostrum* or *aequirostrum*, *Scombresox* or *Scomberesox rondeletii*, or *Scomberesox storeri*. We have, however, retained carded citations to those references.

Scomberesox saurus scombroides (Richardson 1842)[8]

Esox saurus.—Schneider *in* Bloch and Schneider 1801:394 (in part; "J. R. Forster MSS. II. 63"; New Zealand).

[7]The general area of the Equatorial Countercurrent, in which the small specimen was taken, is stated as between about 05° and 10° S (fig. 12). No coordinates were given for the capture but the area sampled within this current extended from about 108° to 160° W (fig. 4).

[8]The synonymy of what we treat as the Southern Hemisphere subspecies of *Scomberesox saurus* lists in sequence of first usage the varied names that have been applied thereto, whether originally based on the Northern Hemisphere form or on Southern Hemisphere material.

Scombresox saurus.—Günther 1866, vol. 6:257 (in part; records from Cape of Good Hope only). McCoy 1888:135, fig. 2 (description; Queensland). Jordan and Evermann 1896:726 (in part; reference for *S. forsteri* only). Gilchrist 1901:152 (occurrence off South Africa). Miranda-Ribeiro 1915:22 (reference to C. Berg's original account of the species in South America); 1918:16 (characters and range, in part; Montevidéo; no Brazil locality included). Barnard 1925:259-260, fig. 16 (in part; references; characters; St. Helena Bay, Table Bay, and Cape Point to Mossel Bay, South Africa; New Zealand; Australia; synonymy; general remarks). Ehrenbaum 1936:75 (Pacific and Indian Oceans only). Barnard 1950:72 (characters; St. Helena Bay to Mossel Bay in South Africa, southern Australia, and New Zealand; large schools near surface; leaping; prey).

Scomberesox saurus.—Berg 1895:25 (in part; Montevidéo). Schreiner and Miranda-Ribeiro 1902:37 (in part; habitat: Atlantic from coast of North America to Montevidéo (Berg), Africa and Europe). Gilchrist 1904:145-147, 152, pl. 10 (eggs and larvae; off Cape Point, South Africa). Devincenzi 1924:190 (reference to Berg; counts; apparently rare in Uruguay). Devincenzi and Baratini 1928:152, pl. 18, fig. 4, 5 (Uruguay). Hildebrand and Schroeder 1928:152 (in part; New Zealand). Pozzi and Bordalé 1935:159 (35°30′ S to Argentina, habitat). Fowler 1936:436-438, fig. 216 (in part; synonymy; description based on North Atlantic material; South Africa record from Barnard 1925); 1942a (Brazil)[9]. Sivertsen 1945:6 (in part; description; from stomach of *Dromedia*; North Atlantic; St. Helena, South Africa, New Zealand, S. Australia). Lozano Rey 1947:597 (in part; New Zealand and South Africa in range). Smith 1949 (and 2d ed., 1953):129, fig. 224 (along most of South Africa; remarks). De Buen 1950:92 (in part; reference to Montevidéo reports). Fowler 1956:141-142 (characters; in part; South Africa; Indo-Pacific). López 1957:145-151, fig. 1-8 (synonymy and records for South American Atlantic; mouth of Rio de la Plata at 36°52′ S, 54°02′ W; development of beak; mucus canal system of head; digestive canal). Briggs 1958:264 (Atlantic, Indian, and western Pacific Oceans; in western Atlantic to Argentina). Wheeler and Mistakidis 1960:334 (in part; Tristan da Cunha, record only). Clemens and Nowell 1963:253-255 (17°30′ S, 71°30′ W; 20°25′ S, 70°43′ W). Hotta 1964:4-7, fig. g, 2-5, table 1 (in part; distribution mapped, southern oceans). Parin and Gorbunova 1964:224 (translation, 1966:237) (Indian Ocean; mentions *S. saurus* having pelagic eggs in open ocean, reference to Haeckel 1855 and Sanzo 1940). Parin 1967a (translation 1971): many pages (in part; epipelagic fish; distribution in Pacific; development); 1967b:150 (117 in translation) (among most plentiful fishes in moderately warm waters of both hemispheres; larvae common at surface day and night). Penrith 1967:524, 544-545 (Tristan da Cunha, at 37°05′ S, 17°40′ W [error for 12°17′ W]; surface-living). Rass 1967:58-66, fig. 10 (in part; distribution in Pacific; general remarks). Parin 1968b (and translation 1970): many pages (in part; world distribution in epipelagic zone); 1968a:275-290, fig. 2-5 (in part; development and numbers of gill rakers; distribution, with records; synonymy); 1969a:719, fig. (in part; place in high-seas fauna; distribution mapped in North Atlantic and in Southern Hemisphere); 1969b:577, 579 (462, 464 in translation), fig. 2 (in part of area surveyed off west coast of South America; numerical abundance charted). Ueyanagi et al. 1969:6-7, fig. 12 (occurrence in all southern oceans). Tortonese 1970:366 (in part; temperate region of whole ocean). Ben-Tuvia 1971:10, 29, 35 (cosmopolitan [in part]). Ueyanagi and Doi 1971:17-21, fig. 15 (distribution in southeastern Pacific mapped; characters distinguishing juveniles of *Cololabis adocetus*, *C. saira*, and *S. saurus*). Parin and Andriashev 1972:963 (866 in translation) (along 26°W between 37° and 39° S, and along west profile off South America between 34° and 45° S; temperature from 14.3° to 20.4° C). Chigirinsky 1972:151-165, fig. 1-13 (size and composition in southeastern Pacific); 1973:198-215, fig. (in part; "winter" range 5°-7° S in southeastern Pacific; spawning intermittent throughout year; stock and catch estimated). Ueyanagi et al. 1972:15-19, fig. 1-2 (size of fish graphed; distribution in Atlantic Ocean mapped). Parin 1973:261-262 [in CLOFNAM] (in part; southern

[9]Fowler entered, under the species name, merely "Brasil (Ribeiro, 1915)," but Miranda-Ribeiro (1915), in his Fauna Brasiliense, Scombresocidae, p. 21, the 16th or 22d page of the book, gave as the basis for including the species in his treatise on Brazilian fishes the range statement "habita o Atlantico desde Cap. Cod na America do Norte, costas da Europa e da Africa e foi constatado em aguas de Montevideo pelo Dr. Carlos Berg." This circumstance was probably the basis for the listing of the Scombresocidae in Brazil by Fowler (1942b:384).

form in synonymy; reference to Parin's (1968a) use of *S. s. scombroides*). Suda 1973:2134-2135, fig. 7-9 (in part; distribution of larvae and pre-adults; potential fishery). Kawamura 1974: many pages (in food of southern sei whale; seems to swarm at surface, probably at patches of crustacea on which it may feed). Kusaka 1974:26, 111, fig. 163 (urohyal of 318 mm specimen from off Cape Town similar to that of *C. saira*). Dudnik 1975a:203-210 (182-188 in translation), fig. 1-2 (limits of distribution of larvae, fingerlings, and juveniles in winter in South Atlantic from South America to Africa); 1975b:738-743 (503-506 in translation, in which names were misspelled *Scombresox* and Scombresocidae), fig. (*S. saurus* compared with *Scomberesox* sp. Parin [= *Nanichthys simulans*]; distribution in Atlantic Ocean). Robertson 1975:7, 18, fig. 4a (planktonic egg; offshore waters around New Zealand). Smith 1975:22 (southern Africa; Afrikaans and English vernaculars). Wheeler 1975:324 (circumpolar in Southern Hemisphere; off South America, South Africa, South Australia, and across Pacific to American continent). Paxton *in* Allen et al. 1976:387 (references; circumglobal in Southern Hemisphere, including eastern Australia and New Zealand as *S. forsteri*; North Atlantic and Mediterranean).

Sairis scombroides.—Richardson 1842:26 (synonymy; valid characters adopted[10] verbatim from manuscript on "*Esox scombroides*, Solander, p. 40; *Esox saurus* G. Forster [MS], ii. t. 233; J. R. Forster, MS II 65, apud Bl. Schneider, p. 394 . . . lat 39½° S, 204¼° W, [sic] between New Zealand and New Holland . . . . The specimen figured by G. Forster was captured . . . in Dusky Bay [New Zealand]. The aborigines named it 'he-eeya.' ").

Scombresox scombroides.—Scott 1962:77, 1 fig. (brief description; western and southern Australia, Victoria, New South Wales, and Tasmania; vernaculars).

Scomberesox saurus scombroides.—Parin 1968a:284 (tentative name for Southern Hemisphere subspecies of *S. saurus*, based on fewer gill rakers). Chirichigno F. 1974:90, 318, 349, fig. 18-19 on p. 91 (characters in key; Punta Aguga, Perú, to Chile; Isla Juan Fernández and [in error] Isla de Pascua).[11]

Scombresox Rondeletti (misidentification on subspecies level).—Valenciennes 1846:475 (in part; Cape of Good Hope record only). Bleeker 1860:56 (Cape of Good Hope only).

Scomberesox rondeletti.—Gilchrist 1901:152 (South Africa).

Scombresox equirostrum (misidentification on subspecies level).—Valenciennes 1846:479-481 (description based on specimen from Chile reported by Guichenot in 1848). Guichinot 1848:318-319 (description; rarely found in Chile). Rendahl 1921:50-51 (Isla de Juan Fernández; also off Perú, New Zealand, southeast Australia, and [in error] Japan).

Scomberesox equirostrum.—Fowler 1940:757, fig. 27 (Valparaíso; 1944a:491 (Valparaíso and Isla de Juan Fernandez, Chile); 1944b:30-31 (synonymy; republished in book form under same title, 1945:78-79). Mann 1950:25 (key; distribution, Arica to Valparaíso, Islas de Juan Fernandez; found in markets of central Chile, May-July; vernaculars). Fowler 1951:282 (in key; Chile). Mann 1954a:47, 79, 169-171 (description; distribution; restricted to pelagic warm water, Arica and Islas de Juan Fernández and [in error] Isla de Pascua; vernaculars); 1954b:77 (listed off Chile in subtropical waters). De Buen 1955:154 (listed off Chile as food of *Germo alalunga*).

Scombresox aequirostrum.—Günther 1866:258 (references; Chile; Chilean fish described by Valenciennes may prove distinct). Reed 1897:18 (listed for Chile). Delfin 1900:4 (listed for Chile; generic name misprinted as *Scombresose*). Quijada 1912:95 (Valparaíso).

Scomberesox aequirostrum.—Delfin 1901:45 (synonymy; in part; Islas de Juan Fernández). Quijada 1913:84 (listed for Chile; edible; commercial importance).

Scomberesox storeri.—Storer 1853:268 and 1867:137-139 (status of LeSueur's "*S. equirostrum*" from Chile).

Scombresox forsteri.—Valenciennes 1846:481-482 (original description [indicated by "nob"]; received from Forster; New Zealand). Günther 1866:258 (synomy; diagnosis; validity doubted; New Zealand). Hector 1872:118 (rare in New Zealand waters; compared with "Half Beak").

[10]Not all "nomina nuda" as stated by Whitley (1968:35); applicable characters were given.

[11]The Isla de Pascua record of a 480 mm "Scomberesox" listed by Wilhelm and Hulot (1957:148) was referred to *Belone* (*Euryeaulus*) *platyura* by de Buen (1963a:16), who, we presume, examined the specimen (43C).

Macleay 1881:244 (description; Melbourne and Sydney). Günther 1889:34[12] (unable to separate young of *saurus* and *forsteri*). Hutton 1872:53 (description; 12-in specimen; New Zealand); 1889:283 (New Zealand). Sherrin 1886:305 (New Zealand). Hutton 1904:50 (New Zealand). Stead 1906:70 (Australia); 1908:39 (characters; immense shoals of half-grown fish inside Port Jackson Heads). Regan 1916:134 (northern New Zealand and Three Kings Islands). Phillipps 1921:120 (food value; highly esteemed edible fish at Bay of Islands; probably spawns in mid-May). Waite 1921:64 (South Australia; often netted with garfish); 1923:88, fig. 96 (length to 15 in; surface skipping and jumping).

Scomberesox forsteri.—Brevoort 1856:281 (New Zealand; seems closest to *S. saira*). Jordan et al. 1930:197 (questioned synonymy with *S. saurus*; New Zealand). Munro 1938:55, fig. 389 (diagnosis; habitat: New South Wales, Victoria, Tasmania, South and West Australia). Berg 1939:207, and 1941 (reprint):654 (closely repeated species; New Zealand and southern Australia). Whitley 1948:15 (off Albany and Perth, Western Australia). Andriashev 1961:345, 348—as "*Scomberesox forsteri*"; 397, 422, 424, 442—as "*Scomberesox*"; 421, 426, 442, 443, 445—as "*Scomberesox* sp" (taken at "Ob" stations in southern Pacific Ocean); 1962:285 (north of 46° S in "Zone of *Scomberesox*"). Whitley 1962:52, fig. (habits; characters; southeast Australia, New Zealand, and Tasmania to West Australia, and elsewhere). Moreland 1963:18, fig. (general remarks). Parin 1963:134, 139 (attracted to light at night). Heath and Moreland 1967:16, fig. 17 ("needlefish" and other vernaculars; general remarks; New Zealand). Parin 1967a:58 (42 in translation) (doubtful status as species). Berman and Ryzhenko 1968:10, 12, fig. (young and adults off Chile and Perú; potential fishery). Whitley 1968:35 (synonymy). Scott et al. 1974:88 (description; distribution; West and South Australia, Victoria, New South Wales, and Tasmania; uncommon off South Australia).

[12]Günther referred the pelagic fry and young saurus "up to 12 inches in length". Taken in the Pacific Ocean, to *S. forsteri* while acknowledging that he could not distinguish them from *S. saurus*. But he stated that these specimens were taken in July 1875, during which month the ship was running east from Japan near 35° N, thence due south to Hawaii (Moseley 1879:495 and track chart, also p. 750 and Sheet 36 of Part 1 of Vol. 1 of Challenger Report). Although the specimens are apparently not extant in the British Museum (see footnote 5), it seems safe to conclude that the record was based on *Cololabis saira*.

Scomberesox saurus forsteri.—Chirichigno F. 1969:40, fig. 85 (vernaculars; Perú, Chile, Islas de Juan Fernández; detailed description).

Scomberesox stolatus.—de Buen 1959:262-264 (original description; synonymic references to *Scomberesox* and *Scomberesox equirostrum* and *aequirostrum*; types from 35°20′ S, 75°23′ W; vernaculars). Chirichigno F. 1962:2, 8-9, fig. 6 (Callao and Isla Chincha, Perú; from Arica to central zone of Chile; Islas de Juan Fernández, and [in error] Isla de Pascua; not previously known from Perú). Koepcke 1962:196-197 (references; high seas; west coast of South America from central Chile to Callao, Perú; Islas de Juan Fernández, and [in error] Isla de Pascua [see footnote 11]). De Buen 1963b:81, 83, 85 (key; brief description; Antofagasta). Medina 1965:260-261 (habitat; central Chile from Callao, Perú, and Juan Fernández Islands, and [in error] Isla de Pascua).

Cololabis saira (misidentification).—Chirichigno F. 1962:9, fig. 7 (description of young; Paita, Perú). Koepcke 1962:197 (in part; reference to Chirichigno's Paita record only). Fourmanoir 1971:492 (87 specimens, 8-30 mm, from 180 mi west of Port Macquarie, New South Wales, Australia).

Scomberesocidae.—Lönnberg 1907:15 (Straits of Magellan, "Smyth Channel, Eden Harbour"). Fowler 1942b:384 (Brazil, Patagonia, West Africa).

Scomberesox.—Böhlke 1951:85-86 (Chile; *Cololabis adocetus* compared).

Needlefish.—McKenzie 1964:14, 1 fig. (in part; vernaculars; color; size; habits; New Zealand).

Discussion of Synonymy.—The synonymy of *Scomberesox* has some complications but in general is relatively clear taxonomically and nomenclaturally. The name was spelled as *Scomberesox* twice by Lacépède (1803), hence can hardly be treated as a misprint, though in naming the species *Scomberesox Camperii* he gave the French vernacular as *Scombresoce camperien*. Many authors, beginning apparently with Rafinesque (1810), adopted the classically more correct but unacceptable (unauthorized) emended spelling *Scombresox* for the genus, and this spelling is still occasionally followed in Europe (viz. Zoological Record (Pisces), 1956-59). The type-species of *Scomberesox*, by monotypy, is *S. camperii* Lacépède, a synonym of *S. saurus saurus* (Walbaum).

The earliest synonym, *Sayris*, was proposed by Rafinesque (1810), with the statement: "Cosrisponde al genere *Scombresox* di Lacepede, il di cui nome essendo formato dall'unione di due altri nomi generici e talmente contra la leggi della nomenclatura zoologica, ..." Since *Sayris* was obviously proposed as a replacement name for *Scomberesox*, it takes, according to Article 67 (i) of the International Code, the same type-species, namely *Scomberesox camperii* Lacépède. The type-species has been designated (Jordan and Evermann 1896) as *Sayris "recurvirostra = camperi,"* obviously on the basis of the original indication of *Sayris recurvirostra* as a replacement name for *S. camperii*. This type of designation was repeated by Jordan (1917). Jordan et al. (1930) gave the type as "*S. recurvirostra* Rafinesque = *Esox saurus* Walbaum," but *Camperii* is not an objective synonym of *saurus*.

Gramminocotus Costa (1862) is clearly a subjective synonym of *Scomberesox*. The type-species, by monotypy, is *G. bicolor*, an obvious synonym of *Scomberesox saurus saurus*. The statement by Jordan et al. (1930) that *Grammiconotus* is "said to lack the air bladder" seems to have no basis other than the erroneously indicated lack of the gas bladder as a character of *Scomberesox* in the Mediterranean, from which the 40 mm type of *G. bicolor* came. Various authors have reported on the presence or absence of a gas bladder in *S. saurus* from the Mediterranean. Valenciennes (1846) based *S. Rondelettii* on the belief that it had no gas bladder; Günther (1866:258) and Moreau (1881) accepted this action. Lütken (1880) and subsequent authors accepted the presence of the bladder, but Supino (1935) failed to find it. Scordia (1936, 1938) found it in specimens from Messina and Naples. Further supporting its presence, Enrico Tortonese[13] stated: "Personally, I believe it is present, as I have found it in all the dissected specimens from Nice and Genoa. Its walls are thin and easily broken; this may perhaps explain why it was sometimes overlooked." One of us (Wisner) has found the gas bladder in a 197 mm SL subadult from the Straits of Messina, as has N. B. Marshall[14].

There was also no basis for the indication (Jordan 1921) that the genus *Grammiconotus* lacks a beak (it had not yet elongated in Costa's type, "Long. corp. millim. 40"). The generic recognition by Jordan and by Golvan (1962, 1965) was an anachronism.

JUSTIFICATION OF SUBSPECIFIC SEPARATION

Parin (1968a) reported differences in the numbers of gill rakers of *Scomberesox saurus* between 7 specimens from the North Atlantic and Mediterranean (average 40.75) and 64 specimens from the Southern Hemisphere (average 44.67). On this rather limited basis he concluded that the two populations may be separable, at least at the subspecific level, and, if so, the southern subspecies should be named "*S. saurus scombroides* (Richardson)." Parin also stated: "There are no significant morphological differences between populations inhabiting southern regions of the Atlantic, Indian and Pacific oceans." We concur in this latter statement and include populations from the Northern Hemisphere (not included by Parin, perhaps due to limited material, seven specimens). Furthermore, we agree with Parin that the populations of the two hemispheres may be separable as subspecies and that the name *Scomberesox saurus scombroides* (Richardson 1842) is applicable to the Southern Hemisphere form.

While we are aware of the highly subjective criteria for subspecific separations, and despite the extensive overlap in counts of gill rakers between populations of the two hemispheres (Table 7), we favor the distinction of the two populations as subspecies. We base this action both on probably highly significant statistical differences (untested) in numbers of rakers and on the presently known distribution of the genus (see below). We cannot conceive of any recent intermingling across the equatorial region of the Atlantic Ocean, at least since the glacial period; the species does not occur in the North Pacific, and, presumably, the northern Indian Ocean is too warm for it.

The statistical reasoning on which we base subspecific distinction involves both a method of graphical analysis of variation (Hubbs and Perlmutter 1942, revised by Hubbs and Hubbs 1953) (Figure 6) and a value, "coefficient of difference (C.D.)," from Mayr et al. (1953); this latter value is derived by dividing the difference between means by the sum of their standard deviations.

[13] Enrico Tortonese, Director, Museo Civico di Storia Naturelle, 16121 Genova, Via Brigata Liguria N. 9, Italy, pers. commun. 8 July 1968.

[14] N. B. Marshall, Curator of Fishes, British Museum (Natural History), Cromwell Road, London SW7, England, pers. commun. 21 June 1968.

TABLE 7.—Numbers of gill rakers, by areas, for the two *Scomberesox saurus* subspecies.

	Scomberesox saurus saurus				*Scomberesox saurus scombroides*					
							South Pacific[2]			
Gill rakers	Northwest Atlantic[1]	Northeast Atlantic	Mediterranean[1]	Total	Southwestern Central Atlantic	Atlantic near South Africa	New data	Parin (1968a)	Indian Ocean[1]	Total
34	—	1	—	1	—	—	—	—	—	—
35	1	2	2	5	—	—	—	—	—	—
36	4	4	3	11	—	—	—	—	—	—
37	6	1	2	9	—	—	—	—	—	—
38	8	5	4	17	—	—	—	—	—	—
39	13	—	5	18	—	—	5	1	—	6
40	13	4	3	20	—	—	10	2	—	12
41	13	2	3	18	—	1	23	4	—	28
42	3	1	2	6	1	6	21	5	3	36
43	5	—	—	5	1	4	34	7	1	47
44	2	1	—	3	2	10	19	2	8	41
45	1	—	—	1	8	8	17	4	6	43
46	—	—	—	—	11	4	10	3	7	35
47	—	—	—	—	4	5	5	2	3	19
48	—	—	—	—	2	3	3	1	2	11
49	—	—	—	—	4	3	—	3	1	11
50	—	—	—	—	1	1	—	1	1	4
51	—	—	—	—	1	1	—	1	—	3
N	69	21	24	114	35	46	147	36	32	296
$\bar{x}$	39.70	38.24	38.58	39.19	46.29	45.13	43.01	44.17	45.28	44.11
SD	2.13	2.61	2.08	2.28	1.93	2.38	2.35	2.95	2.76	2.52

[1]Counts by Parin (1968a: 280, fig. 3) for specimens 75 mm and longer are included in the above counts for Northwest Atlantic (5 specimens) and Mediterranean (5 specimens).
[2]Data from Peru, Chile, Central Pacific, and Australia-New Zealand are combined since counts from each area are very similar, the means ranging from 42.87 to 43.08 gill rakers.

FIGURE 6.—Graphed variation in numbers of gill rakers of *Scomberesox saurus saurus* and of *S. s. scombroides*, by area. *Scomberesox s. saurus*: 1—Northwest Atlantic, $N = 69$; 2—Northeast Atlantic and Mediterranean, $N = 45$; 1 + 2—total for Northern Hemisphere, $N = 114$. *Scomberesox s. scombroides*: 3 + 7—total for Southern Hemisphere, $N = 296$; 3—Southwest-central South Atlantic, $N = 35$; 4—Atlantic near South Africa, $N = 46$; 5—South Pacific (new data), $N = 147$; 6—South Pacific (Parin 1968a), $N = 36$; 7—Indian Ocean, $N = 32$ (26 from Parin (1968a), 6 new data). In each sample the baseline shows the total range in variation, and the short vertical line the mean of the sample; open (white) bars delineate 1 SD on each side of the mean, and the solid (black) bars 2 SE of the mean on each side of the mean.

The difference between means for gill rakers (39.19 vs. 44.11) of the total populations of *S. s. saurus* and *S. s. scombroides* (Table 7; Figure 6, lines 1 + 2 and 3 + 7) appears to be highly significant, the probable odds (untested) being billions to one against the two areas comprising a single, homogeneous population. Despite a large overlap in numbers of rakers, the calculated C.D.

value is 1.025, a value approaching subspecific distinctness (as interpreted by Mayr et al.), in that it indicates a joint nonoverlap of about 85%. Of even greater significance, perhaps, is the difference in means (7.93 rakers) between populations from the southwestern-central Atlantic and the combined northeastern Atlantic-Mediterranean areas (46.29 vs. 38.36 rakers); the graphed data (Figure 6, lines 1 and 3) indicate again probable odds (untested) of billions to one that the two populations are not homogeneous; in addition, the C.D. value of 1.88 indicates about 99% joint nonoverlap in numbers of rakers—virtually that of separation at the species level.

As sampled (Table 7, Figure 6), the total population of *S. s. saurus* appears to be relatively homogeneous, but that of *S. s. scombroides* may be less so. Heterogeneity of populations in the Southern Hemisphere is indicated by a difference of 3.28 rakers between the areas of southwestern-central South Atlantic and the entire South Pacific (new data) (46.29 vs. 43.01); this may indicate that little or no intermingling occurs around the tip of South America. Conversely, the close agreement in means for rakers between specimens from the South Atlantic near South Africa and from the Indian Ocean (45.13 vs. 45.28) may indicate that considerable, if not complete, intermingling occurs around South Africa. The entire South Pacific area (as sampled) appears to contain a homogeneous population; a difference of only 0.21 rakers was found between samples of about 50 specimens each from the Peru-Chile, central, and Australia-New Zealand areas.

DESCRIPTION OF GENERA AND COMPARISONS

Inasmuch as we treat each of the four obviously distinct saury species as constituting a monotypic genus, the comparisons of these genera, as previously discussed, and epitomized in Table 1, provides a comparison of *Nanichthys simulans* with each of the three other scomberesocid species. It certainly ranks as one of the two dwarfed species. The largest specimens of this species examined by us were taken in Funchal Harbor, Madeira (126.2 mm SL, Museo do Funchal No. 2866, shown in Figure 1, and 121.2 mm SL, BMNH 1953 · 3 · 13 · 7). No other specimens >101 mm SL (USNM 204257) have come to our attention and none other among hundreds examined by us have exceeded 90 mm. Parin (1968a) recorded 90 mm SL as the largest of his material. Dudnik (1975b) reported that the longest of about 200 specimens of "*Scomberesox* sp" was 112 mm. The occurrence of the two "giants" in Funchal Harbor leaves us to wonder if the inshore habitat may have led to increased or sustained growth. G. E. Maul[15] has told us that the genus is rare near Funchal.

Nanichthys simulans, unlike *Elassichthys adocetus*, has retained the lateral line; it extends to about midway between the origins of the pelvic and anal fins, but not, as in *Scomberesox* and *Cololabis*, to opposite some one of the anal finlets. The upper and lower jaws, instead of remaining short and pointed as they do in *Cololabis*, or short and rounded (in the upper) as in *Elassichthys* (Figures 5, 6), become definitely elongated as beaks, but remain shorter than in *Scomberesox*; the upper is about half as long and produced as the lower, and much less slender and fragile than they are in *Scomberesox*.

Counts for *N. simulans* are given in Table 2 (gill rakers), Table 3 (fin rays), and Tables 4 and 5 (vertebrae), and are contrasted with similar data for *E. adocetus* and for the larger forms, *C. saira* and *Scomberesox*; numbers of gill rakers are given for both subspecies of *Scomberesox* in Table 7.

The pectoral rays of *N. simulans*, numbering 10 or 11, average more than in *Elassichthys* (8-11, usually 9 or 10), but fewer than in *Cololabis* and *Scomberesox* (12-15 in each). The procurrent caudal rays number 4, rarely 3 or 5, vs. 2 or 3 in *Elassichthys* or 5-7 in *Cololabis* and *Scomberesox*. The vertebral counts are 58-62, mean 60.68, contrasting with 54-59, mean 56.37, in *Elassichthys*, 62-69 in 3,160 specimens of *Cololabis*, with means of 66.05 for 248 counts for the northwestern Pacific and of 65.03 for 2,812 counts for the northeastern Pacific, and 66-70, mean 66.13, for 338 counts for *Scomberesox* (both subspecies).

Scale counts (lateral midline rows) number 77-91 vs. 70-88 in the other dwarf species, *E. adocetus*, as mutually contrasting with counts of 128-148 in *Cololabis* and of 107-128 in *Scomberesox*. Counts of gill rakers in *Nanichthys* (19-26, mean 22.80) average higher than for *Elassichthys* (15-21, mean 17.64), but much lower than in either *Cololabis* (32-43, mean 37.53) or *S. s. saurus* (34-45, mean 39.19) and 39-51 (mean 44.11) for *S. s. scombroides* (Table 7). The ovary, as in *Elassichthys*, is single instead of paired (as

[15] G. E. Maul, Curator of Fishes, Museu Municipal do Funchal, Madeira, pers. commun. 5 May 1978

noted below in the general description of the ovary in the two dwarf species).

In life *Nanichthys* is silvery ventrally and laterally, becoming greenish with brown specks dorsally; this is also the basic coloration of the other three genera. In preserved specimens the anal fin is essentially colorless, but the dorsal, pectoral, and caudal fins bear microscopic spots of dark pigment along the edges of the outer rays. The caudal fin, in addition, is pigmented in the crotches of the first branching of the rays and sometimes in the second branching of both dwarf species (the resulting streaking shows in Figures 5, 8, 9). In preserved specimens of this (and of other) scomberesocid species, a dusky underlying streak parallels the dorsal margin of the body (evident in Figure 5). *Elassichthys adocetus* has basically the same coloration.

JUSTIFICATION OF GENERIC SEPARATION

In recognizing a separate genus for each of the four species of Scomberesocidae we are cognizant of the circumstance that we are in a period when lumping is prevalent. We hold, however, that the grounds for the recognition of the four genera are compelling, and consistent with other generic recognitions on similar grounds. The distinctive features stand out sharply in the generic comparisons (Table 1).

The complete lack vs. strong development of the gas gladder and the single vs. paired ovaries, supplemented by a series of minor characters, primarily the striking differences in body musculature (Figure 7), and bolstered by the vast difference in body size, seem to provide fully adequate grounds for distinguishing both *Elassichthys* and *Nanichthys* from either *Cololabis* or *Scomberesox*.

The sagittal sections of the four genera of scomberesocid fishes (Figure 7A-D), taken from close behind the bases of the pelvic fins, portray these striking differences. The 59 mm SL adult of *Elassichthys* and 60 mm SL adult of *Nanichthys* clearly show the lack of the gas bladder; also, there is no evidence of even a weak septum that might indicate a paired condition of the ovaries. Even in the young of *Cololabis* (59.4 mm SL) and of *Scomberesox* (59.7 mm SL) the roughly triangular gas bladder is plainly evident just above the liver and gut; these young specimens are too immature to have recognizable gonads.

Also evident and notable is a difference in the arrangement of the myotomes; those of the young *Cololabis* and *Scomberesox* (and of adults) are separated by distinct septa. However, in the adults of the dwarf forms the myotomes are much more massive and the dividing septa are greatly reduced in number in *Nanichthys* (virtually nonexistent in *Elassichthys*). Perhaps this reduction is a reflection of the weak-swimming, surface-pelagic habits of these small fishes.

The development of filaments of a peculiar well-formed type on the egg of *Cololabis* strengthens the basis for the separation of that genus from *Scomberesox*, with unfilamented eggs. The large literature on *Cololabis* and its great commercial importance are additional incentives for retaining the familiar and well-established nomenclature; *Scomberesox* now approximates qualification in both categories.

The generic separation of the two dwarf forms also seems to be well justified. The feature of the well-developed beak in *Nanichthys* vs. its lack in *Elassichthys* (Figure 2) calls for generic separation, as it does for retaining *Cololabis* distinct from *Scomberesox*. The apparent total lack of an external lateral line in *Elassichthys* and its considerable development in *Nanichthys* provides sustaining evidence. Furthermore, the high probability that *Nanichthys* and *Elassichthys* are of separate origin (Figure 3), owing their resemblances to convergent evolution, seems to us clinching reason for generic separation.

Description of Gonads

The one ovary and the two testes of *Nanichthys* are essentially like those of *Elassichthys* (Figures 8, 9). Instead of being pendant from the dorsolateral walls of the coelom, they form, as they develop, a coherent median mass, occupying, with maturity, a very large proportion of the coelom from the middorsal line to the ventrally displaced liver, intestine, and other visceral organs. In the specimen figured for this discussion, the length of the ovary composes 38% of the standard length of the fish; the greatest depth of the ovary 20% of its length; and its greatest width 60% of its greatest depth.

The development of a single functional ovary in "*Scomberesox* sp" [= *Nanichthys simulans*] has been noted by Dudnik (1975b), who, however, mentioned that "the second [ovary] is rudimentary and can barely be discerned" [a translation]. We, however, have found not even a rudimentary

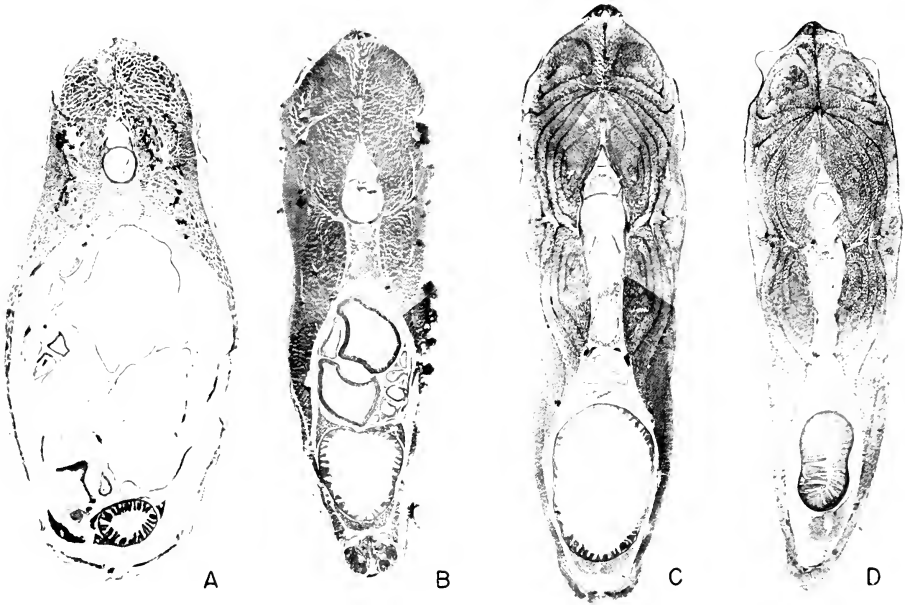


FIGURE 7.—Sagittal sections, taken from slightly behind origin of pelvic fin, of gravid females: (A) *Elassichthys adocetus*, 59.0 mm SL; (B) *Nanichthys simulans*, 60.0 mm SL; and of juveniles: (C) *Colalabis saira*, 59.4 mm SL; (D) *Scomberesox saurus*, 59.7 mm SL.

FIGURE 8.—Gravid single ovaries in situ: Upper—*Nansichthys simulans*, 85.5 mm SL; Lower—*Elassichthys adocetus*, 62.3 mm SL. Note the great range in sizes of ova.

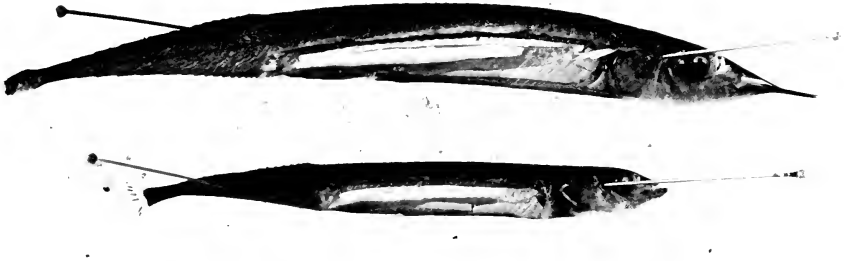


FIGURE 9.—Mature paired testes in situ: Upper—*Nansichthys simulans*, 90.0 mm SL; Lower—*Elassichthys adocetus*, 59.0 mm SL.

ovary in this species (nor in the other dwarf, *Elassichthys adocetus*).

In cross section the maturing and mature ovaries of both dwarfs are rather ovate in section. They very nearly fill the whole coelom between the much expanded body walls, particularly in *Elassichthys* (Figure 8). As they ripen, the ova fill the entire ovary so tightly that many of the ripe ova and even some of those in developmental stages are compressed into angular forms throughout the ovary. Forward, the ovary narrows dorsoventrally where the liver broadens to fill much of the coelom. Gentle probing readily discloses that the ovary lacks any structural connection with the coelom wall (except at the genital opening), although, with development, the ovary completely fills the body cavity above the visceral organs and lies closely appressed to the body wall, both dorsally and laterally. Dislodging the ova by probing discloses no trace of any internal septum.

The ova in the mature ovary of *Nanichthys* and *Elassichthys* appear on gross examination to represent at least four stages of development, but a major difference in size exists between the largest category (readily visible in Figure 8) and the next largest, as though an acceleration in growth precedes the extrusion of the brood. Since the ova of the largest category are usually markedly irregular in shape (presumably due to crowding), measurements are approximations. However, after discharge the ova are probably normally spherical rather than ovoid in shape, as the eggs of *Cololabis saira* have been described to be (Mito 1958; Mukacheva 1960). The largest egg size in the *Nanichthys* series studied ranged in diameter from 2.0 to 2.5 mm. The smaller and presumably younger size groups seemed to group around 0.80, 0.40, and 0.10 mm. Similar size groupings appeared to hold for *Elassichthys*.

The positioning of the largest eggs in the ovaries of the dwarfs seems to be quite random among the smaller ones (Figure 8). These large eggs were noted to be arranged generally mostly two abreast (three abreast once in *Elassichthys*). The random distribution of the large eggs within an ovary otherwise filled with smaller eggs invites speculation on how the anteriormost eggs of the largest size category move past the smaller ones to become extruded.

None of the eggs of the dwarfs, even of the largest and presumably soon-to-be-extruded category, show any sign of bearing filaments. Their surfaces, however, are sculptured with closely set, round, and extremely minute tubercles which are colorless (in preservative) and produce, under strong magnification, a finely pebbled effect.

It has not been determined whether the single ovary of the two dwarfed scomberesocids is the result of the fusion of bilateral primordia or is due to the failure to develop, or to the atrophy, of one ovary. The presence of but one gonad in synentognath fishes has been reported. Collette (1968) indicated that in the Belonidae *Strongylura marina* differs from a closely related species, *S. timucu*, in having only the right gonad developed. Collette (1974) reported that in the freshwater needlefish, *S. hubbsi*, 48 males had both testes developed but 2 apparently lacked the left one, and of 45 females, 2 had a tiny left ovary but all others lacked any trace of a left ovary.

In contrast with the ovary, the testis of both *Nanichthys* and *Elassichthys*, at apparent maturity, occupies only about one-third instead of about three-fourths of the height of the fleshy body (Figure 9). The testis agrees with the ovary, however, in occupying virtually the entire (limited) width of the coelom, forming from body wall to body wall a compact and compressed organ of seemingly homogeneous reproductive tissue. However, close inspection and some probing with a fine dissecting needle clearly discloses that the dorsally rounded mass comprises both testes. As seen from the right side, on removing the body wall (Figure 9), a fine, somewhat wavy longitudinal line, nearer top than bottom, indicates that the essentially homogeneous structure comprises the paired testes, and gentle probing confirms the indication. The left testis is definitely the larger, but both are well developed and are obviously functional. The two are essentially coterminal along the ventral edge, but the left testis definitely and sharply overtops the right. Ventrally the two organs form, at about the same level, symmetrical ridges on a rather broad base. At front, the paired testes are clearly distinct as lobes, of which the right one ends distinctly as a point, at that side of the left one. Anterior to the end of the right organ, the left one broadens on the ventral surface and forms a pair of bilaterally paired ridges, the left one of which seems to structurally replace the lost end of the right testis.

Mucus Pores and Canals of the Head

Numbers and arrangement of mucus pores and canals of the head vary notably among the scomberesocids (Figure 10, items 1-6). Adults of the two

larger forms, *Scomberesox* and *Cololabis* (Figure 10, items 1, 4), have a much greater number and complexity of pores and canals on the side and particularly on the top of the head, than do adults of the dwarfed forms, *Nanichthys* and *Elassichthys* (Figure 10, items 3, 6). Also juveniles of the larger forms (Figure 10, items 2, 5) show a greater pore-canal development than do the adult dwarfs, although they are of virtually identical size. This reduction of pores and canals in the dwarfs may be interpreted as an arrested state of development, perhaps neotenic or paedomorphic in character, as very small (20-24 mm SL) specimens of the larger forms bear a pore-canal structure similar to those of the adult dwarfs (Figure 10, items 3, 6); or, it may be that neither numbers nor complexity of pores is necessary at such small sizes and (perhaps) less active habits.

López (1957) provided the first figure of the pores and canals of the head of an adult (size not stated) *Scomberesox saurus* (= *S. s. scombroides*) from near Nechochea, Argentina. Our specimen, from the Perú-Chile area, bears a much greater profusion of pores and complexity of canals, particularly dorsally, than shown by López.

Collette (1966) illustrated interorbital canals and pores of four species of belonid fishes. These canals, rather simple and unbranched, which he reported to be representative of the Belonidae, are basically like those of *Elassichthys* and *Nanichthys*, although those of the latter show slight branching (Figure 10, item 3). Collette (his figure 7D) figured a complete joining of the left and right canals dorsally on *Belonion dibranchodon*, with both median and lateral pores present. He reported this condition to be unlike that of any other synentognath. Despite the profusion of pores and canals atop the heads of *Scomberesox* and *Cololabis* (Figure 10, items 1, 4), no joining of the left and right canals is apparent, although some canals very closely approach the median line.

Lateral Line Scales

The lateral line scales of *Scomberesox* and *Cololabis* are basically similar, but those of the dwarfed *Nanichthys* differ notably, both in shape and in numbers and development of circuli (Figure 11A-C). We have found no trace of lateral line scales in *Elassichthys*. All scales were removed from within 1 cm anterior to the pelvic fin. The basic similarity in the scales of the three genera involves the secondary tube on each scale that leads posteroventrally from the main tube and opens to the external surface of the scale. The primary (main) tube of each scale, in contrast, overlies the lateral line canal which extends along the body.

The lateral line scale of the adult *Scomberesox* (270 mm BL (body length); Figure 11A) lacks circuli, but they are present, though very weakly developed, on fish about 200 mm BL. Development of circuli appears to decrease as the fish grows; the circuli on scales on a 100 mm fish are notably better defined than on the 200 mm specimen. These early developed circuli occur in areas rather similar to those that are better developed in *Cololabis*. A principal feature distinguishing the *Scomberesox* scale from that of *Cololabis* is a well-developed baselike structure on the ventral aspect of the scale (Figure 11C). As the *Scomberesox* scale is much more tenacious than that of *Cololabis*, perhaps this structure serves as an anchor to the body. Another difference between the scales of *Scomberesox* and *Cololabis* is a narrow median band of tissue at about the center of the scale (and main tube) that does not absorb the weak solution of alizarin red S stain. When removing it, the highly tenacious scale usually breaks at this band. The *Scomberesox* scale figured is about 0.9 mm thick at the main tube.

The lateral line scale of the adult of *Cololabis* (262 mm BL; Figure 11B), in addition to differing in form from that of *Scomberesox*, differs in having at least weakly formed circuli on the anterodorsal and anteroventral aspects (these circuli do not show clearly, probably due to a slight canting of the scale during mounting and to the extremely short depth of focal field inherent in photomicroscopy). The scale has a thickness at the main tube of about 0.4 mm. The circuli are better developed on smaller fish and extend farther posteriad along both the ventral and dorsal aspects of the scale in about the same areas as in the adult scale. Some, but not all, lateral line scales of adults of *Cololabis* bear the nonstaining band of tissue found in *Scomberesox*, but it is much less strongly developed.

The lateral line scale of *Nanichthys* (106 mm BL; Figure 11C, from the 121.2 mm Funchal "giant") differs notably from that of its two larger relatives. The shape is quite different and the circuli are much more numerous and more strongly developed and extend over most of the scale, being absent only on the central portion of the basal (exposed) area. The thickness of the scale at the

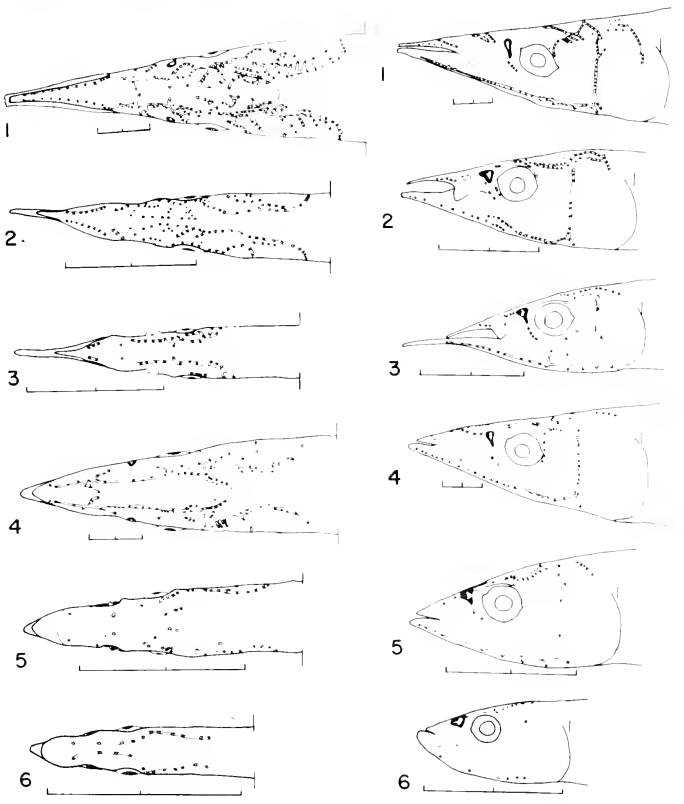


FIGURE 10.—Dorsal and lateral views of mucus pores and canals of heads of adults and young of scomberesocid fishes: (1) adult *Scomberesox saurus scombroides*, 240 mm BL; (2) young of *S. s. scombroides*, 70.8 mm BL; (3) adult of *Nanichthys simulans*, 70.0 mm BL; (4) adult of *Cololabis saira*, 243 mm BL; (5) young of *C. saira*, 54.0 mm BL; (6) adult of *Elassichthys adocetus*, 54.6 mm BL. Each scale line represents 1 cm

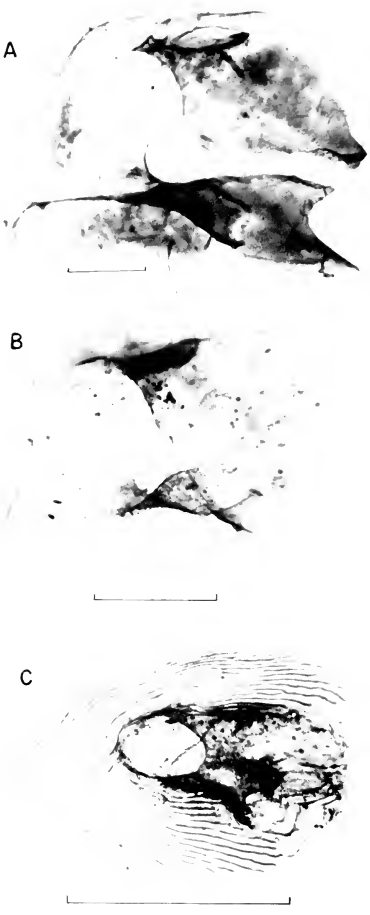


FIGURE 11.—Lateral line scales of adults: (A) *Scomberesox saurus scombroides*; (B) *Cololabis saira*; (C) *Nanichthys simulans*. The apical (covered) portion is to the left. All scale lines represent 1 mm. No lateral line scales have been found on *Elassichthys adocetus*.

main tube is about 0.1 mm. The tube is relatively more fragile than it is in the larger forms, and there is only a hint of the stain-resisting band of tissue.

Pharyngeal Bones and Teeth

The first pair of upper pharyngeal arches (bones) is absent in all the scomberesocid fishes. Also, the second pair of upper bones are so closely appressed as to appear as a single unit and are not notably larger than the third pair, which are not closely appressed; the lower pharyngeal bones are fused into one, as in the Synentognathi. Absence of the first upper pair of pharyngeals in synentognathous fishes has been reported by Collette (1966) who figured the pharyngeal bones and teeth of six species of the Belonidae: *Belonion dibranchodon*, *B. apodion*, *Potamarraphis guianensis*, *Strongylura notata*, *Pseudostylus angusticeps*, and *Xenentodon cancila*. Of these six, only *B. apodion* and *X. cancila* lack the first (lower) pair of upper pharyngeals; they also lack the second pair, retaining only the third (uppermost) pair. As figured by Collette, but not discussed, the pharyngeal teeth of these belonid species appear to have only a conical type of tooth, with no cuspate or lobate features. In apparent contrast, many of the pharyngeal teeth of the scomberesocid species treated below have more or less well-developed lateral lobes or cusps, or are distinctly tricuspid.

Cololabis saira, 281 mm SL, 225 mm BL, from the Gulf of Alaska (SIO 57-198). The greatest length of the lower pharyngeal arch is 12.8 mm, the greatest width 8.6 mm. The teeth are moderately strong and curved. The marginal ones are all slender and unicuspid but those within the margin in the wider part are definitely widened, slightly to greatly, medially, with usually on each side a marginal lobe grading from rudimentary to, rarely, a rather definite cusp. There is only a trace of alignment (the arrangement is more nearly quite indefinite). Along the interior, greatly narrowed half of the length, the teeth, reduced in size, are very roughly in three or four rows. The lateral teeth do not form a definite row and are not markedly enlarged. Toward the posterior margin the teeth are large and irregularly crowded. Most of the larger teeth bear a more or less well-developed median, lengthwise, rather rounded ridge.

Each bone of the second pair of upper pharyngeals is 11.8 mm long and 3.0 mm wide. Anteriorly and marginally the teeth are slender, moderately curved, and almost strictly unicuspid. Over the major portion of each bone, however, the teeth are, for the most part, definitely tricuspid, with the lateral cusps submedian and occasionally represented by weak to strong lobes. Between the left and right arches there is, posteriorly, a triangle of dermal ridges, medially a low ridge, and anteriorly a high ridge reaching to the surface with a strong fimbriation. As in the lower pharyngeal, the teeth are crowded and irregularly show just a trace of oblique seriation.

Each bone of the third pair measures about 2.3 · 6.7 mm. The teeth are nearly concealed in the strong fimbriation of the surface, and all are small, irregularly arranged, moderately curved, and unicuspid.

Elassichthys adocetus, 58.0 mm SL, 49 mm BL, from off Perú at 08°07′S, 84°58′W (SIO H 52-380). The lower pharyngeals are about 2.6 mm long and 1.1 mm wide. The teeth are relatively few, not more than about 10 across at the widest part of the arch. Most of the relatively large teeth in the median portion of the broad posterior region are broadened and to a varying degree tricuspid, with the central cusp much stronger than the lateral ones. The teeth along the posterior edge are rather broadly lanceolate rather than very slender as in *Cololabis*. Anteriorly, where the arch narrows, the teeth become weak. In the rows along the outer margins the teeth are relatively conical and moderately curved. The teeth across the posterior field are much larger than others and bear a median lengthwise ridge. Near the middle of the arch are only about four teeth in cross section.

Each bone of the second pair measures approximately 0.6 · 1.5 mm. The teeth are relatively robust and uniformly the sharp, definitely unicuspid tip is bent sharply. On the broad part of the bone there are only about five teeth in cross section. A membranous septum, very weakly patterned, extends the whole length between the two bones.

Each of the third pair of bones measures about 0.4 · 0.9 mm. The relatively few teeth are all unicuspid with the tips bent backward.

Scomberesox saurus scombroides, 290 mm SL, 205 mm BL, from off Chile, 34°30′S, 79°30′W (SIO 58-263). The lower pharyngeal has a midline length of 11.4 mm, a maximum width of toothed area (at posterior edge) of 7.3 mm, and a width

over teeth at midlength of 1.0 mm. The teeth are strongly heterodont and are rather definitely aligned, especially marginally, in rows. The teeth along the posterior margin number 41; those near the middle on each side are in nearly a single series alternating in proximity to the edge, whereas those toward either end tend to be arranged in oblique, separate rows of 2-4 teeth. All of these teeth are essentially erect, fairly stout, and pointed, with the tips not bent backward. The teeth along the two margins tend to form a rather even row; they are all sharply pointed, rather strongly bent backward, tend to flare outward, and are, in general, especially forward, larger and stronger than the teeth within; toward the anterior angles of the arch the marginal teeth tend to have a rather weak lobe on each side below the tip, and thus intergrade toward the median teeth. In the anterior half of the length of the arch the whole set of teeth grade from nearly triserial to uniserial, with only the very strong marginal teeth of each side occupying much of this space. After some intergradation, both anteriorly and laterally, the teeth occupying the major triangular part of the arch are dilated and bear on each side, well below the tip, a lobe or a cusp; they are strongly bent backward. Anteriorly the margins of the arch are rather strongly concave.

The length of each dental surface of the second pair is 8.9 mm; the maximum width of each, near the posterior end, is 2.7 mm. The teeth are arranged on each bone in about 16 rather regular rows extending from near the midline outward and backward in a weak curve. Teeth of reduced size, but otherwise similar, also curved, are found on a fimbriate pad immediately behind each bone. All of the teeth are bent backward. A number of teeth at the anterior end are simply conical, and especially strong. Virtually all of the other teeth, including those along the median and lateral edges, are tricuspid, with the median cusp very much stronger than the lateral pair, which arise well below the tip. The two bones are narrowly separated and a strongly fimbriate compressed membranous ridge intervenes, grading both forward and backward into several papillate rows.

The length of each bone of the third pair is 5.8 mm, the width of each 1.9 mm. The small teeth arise from a strongly papillate surface. They are directed mesiad and are strongest on the median margin, but definitely weakening laterally. They are all conical, without any trace of marginal enlargement.

Nanichthys simulans, 85.0 mm SL, 68.0 mm BL, from the central South Atlantic, 24°02.5′ S, 15°32.0′ W (SIO 63-546). The lower pharyngeal measures 1.9 × 3.3 mm. As in *Elassichthys*, but contrasting with the two large species, the arch is less attenuate forward and the posterior border is definitely convex instead of being slightly concave. There is no definitive alignment of the teeth, and a band about three or four teeth wide extends virtually to the front tip. The teeth rather regularly and strongly increase in size backward. About 20 teeth in one very irregular row, or in two rows, occur along the posterior margin; these are essentially erect, mostly very large, relatively, and show barely a trace of the lateral enlargements. Toward the front end the teeth are conical and less curved backward than the following teeth (excluding the posterior marginal ones). Most of the other teeth bear on each margin, well below the tip, either a lateral swelling or a definite cusp.

Each second pharyngeal measures 0.9 × 3.1 mm, with the greatest width well behind the middle. The teeth are scattered without definite alignment. Those in the narrow front end of the arch and those along the outer margin are conical or nearly so, with the tips bent backward, somewhat as in the other species. The remaining teeth, however, are vastly different, actually submolar. These rather lobular teeth seem to have been built on a much swollen and rounded version of the corresponding teeth in the other series, sometimes showing a trace of the lateral enlargements or cusps; but essentially they are irregularly rounded domes, but grading forward, outward, and backward into the more conventional, weakly tricuspid type.

Each third pharyngeal measures approximately 0.6 × 1.6 mm. The arch is widest behind the middle. The teeth are rather hidden in the papillae and all are simply conic, weakly curved backward. They are quite strong along the inner margin but grade into extremely minute ones on the outer margin.

DISTRIBUTION

The distributions of the scomberesocid fishes have been depicted by various Russian and Japanese authors. The Russian data are summarized by Parin (1968a, b, 1969a). Parin (1968a, b) received from us many of his data on "*Scomberesox* sp" (= *Nanichthys simulans*) and on *Collabis adocetus* (= *Elassichthys adocetus*). Dudnik

(1975a) charted the distribution of *Scomberesox saurus* (= *S. s. scombroides*) in the South Atlantic Ocean, and (1975b) of *Scomberesox* sp. in the North and South Atlantic. Ueyanagi and coauthors have reported many captures of all the scomberesocid species, primarily juveniles and postlarvae, in the Pacific and Atlantic Oceans and the Mediterranean Sea.

In Figures 12-17 we attempt to show the known captures of all four species of scomberesocid fishes. In each figure the solid circles represent material examined by us. The large open circles in the North Atlantic and southwestern Pacific Oceans refer to literature records (specimens not seen by us); we have not used this symbol for literature records from the Pacific coasts of North and South

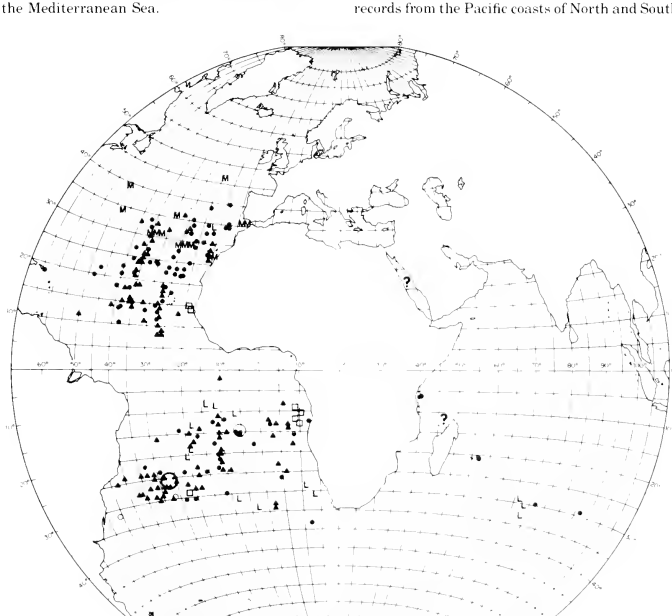


FIGURE 12.—Distribution of *Nanichthys simulans*. Solid circles represent material examined by us, solid triangles represent localities mapped by Ueyanagi et al. (1972); the large open circle in the southwestern Atlantic indicates 18 closely spaced collections (111 specimens), and the small open circles represent unpublished localities furnished by Parin, open squares refer to records mapped by Dudnik (1975b); letters L and M refer to records from Lampe (1914) and by Murray and Hjort (1912). The question mark near Madagascar represents Smith's 1955 record of *Scomberesox saurus* from Aldabra Island, which seems to represent this species. The query in the Red Sea refers to Borodin's 1930 record of a young "*Scomberesox saurus*."

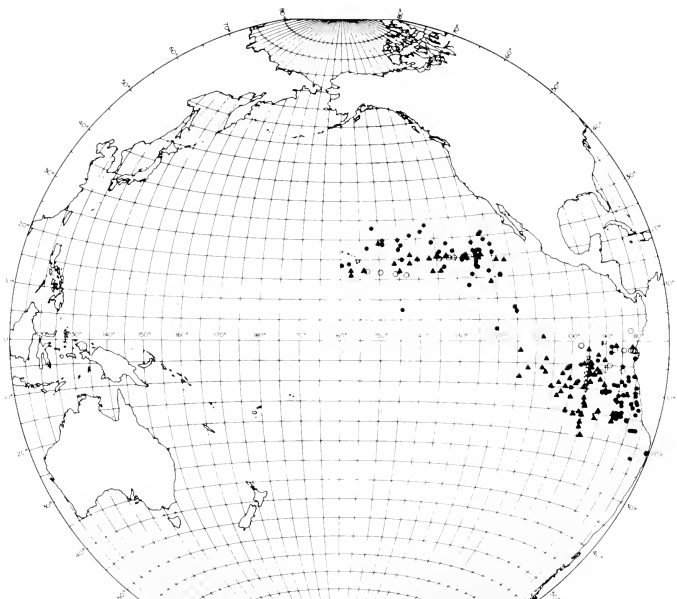


FIGURE 13.—Distribution of *Elassichthys adocetus*. Solid circles represent material examined by us; solid triangles, records mapped by Ueyanagi et al. (1972); open triangles, localities by Ahlstrom (1972); small open circles, unpublished records furnished by Parin.

America because either we have seen many of these specimens or have numerous captures from closely adjacent localities.

The sauries are essentially antitropical in distribution. This is particularly true for two larger forms, *Scomberesox* and *Cololabis*, which mostly inhabit cold to warm-temperate waters (Figures 14, 15). The dwarf genera *Nanichthys* and *Elassichthys* occupy much more tropical waters and occur much nearer the Equator than do their larger congenors. The one exception to this generalization is that of the northerly extension of juveniles and young of *S. s. scombroides* along the coast of Ecuador to about 02° S (Figure 15), where these young stages and the adults and young of *Elassichthys* have been taken together. This far northern extension of the young of *S. s. scombroides* is interpreted as due to transport by the northerly flowing Perú Current. Along the coast of Perú and northern Chile the ranges of *Elassichthys* and *S. s. scombroides* overlap to about 22° S (Figure 17).

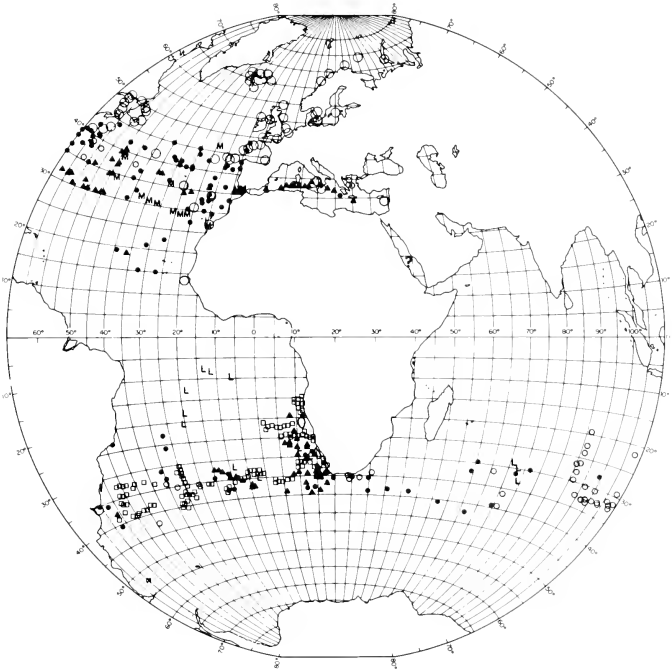


FIGURE 14.—Distribution of the northern and southern populations of *Scomberesox saurus* in the Eastern Hemisphere. Solid circles represent material examined by us; small open circles, records published by Parin (1968a); large open circles represent other published records (specimens not examined by us); solid triangles, records mapped by Ueyanagi et al. (1972); small open squares, localities mapped by Dudnik (1975a), additional and closely spaced records by Dudnik off southwestern Africa are indicated by two open ellipses. Letters L and M refer to records published by Lampe (1914) and Murray and Hjort (1912).

The far-southern locality off Chile for *S. s. scombroides*, at 47° S, 81° W (Figure 15), is based on seven juveniles (56-67 mm SL) in the Hamburg Museum (No. 10601) examined by us. This southern occurrence is not readily explained. It lies well within the portion of the West Wind Drift that forms the northerly flowing Perú Current; perhaps these specimens were waifs carried south into the edge of this current by the counterclockwise southeastern eddy of subtropical water that extends to between about 20° to 40°-45° S and 120°-80° W. The southern localities listed by Parin (1968a) to 48° S, about 110° W, are apparently attributable to a similar extension of subtropical water (Figure 15).

The questioned locality near the Straits of

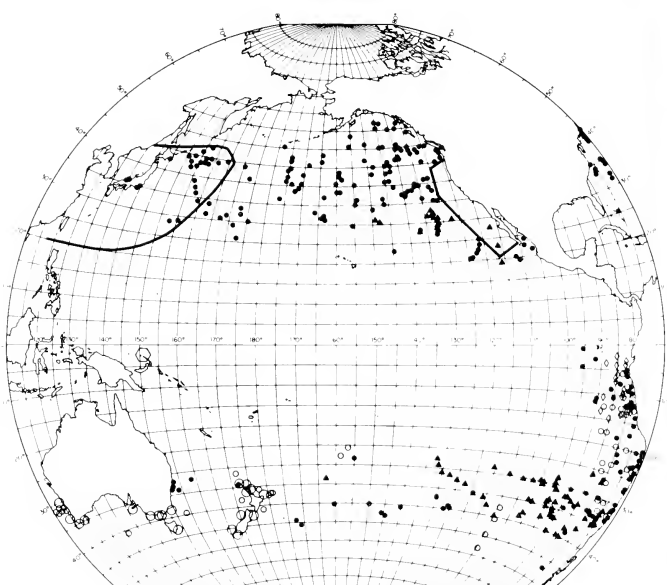


FIGURE 15.—Distribution of *Cololabis saira* and of *Scomberesox saurus* in the Western Hemisphere. Solid circles represent material of *C. saira* in the North Pacific, *S. saurus scombroides* in the South Pacific, and *S. s. saurus* in the extreme northeastern Atlantic Oceans examined by us. For the two areas bounded by heavy lines the records for *C. saira* would virtually blacken the areas and are omitted. Solid triangles refer to mapped records by Ueyanagi et al. (1972) for *C. saira* in the North Pacific and for *S. s. scombroides* in the south; small open circles represent both published and unpublished records of *S. s. scombroides* by Parin; large open circles are for other published records; open diamonds refer to records by Ahlstrom (1972). The question mark near Straits of Magellan refers to Lönnberg's (1907) record for a scomberesocid. The large open hexagon near New Guinea refers to the record of *C. saira* by Kailola (1974).

Magellan (Figure 15) refers to a statement by Lönnberg (1907) in a report on fishes from the Straits (Smyth Channel, Eden Harbor): "In der Sammlung befanden sich ausser den oben aufgeführten Spezies [*Macruronus magellanicus* n. sp.] noch Junge von mehreren Arten, die sich wegen der Jugend der Examplare nicht bestimmen liessen. Unter diesen fanden sich auch einige Repräsentanten für *Scomberesocidae*, so dass sich die Zugehörigkeit dieser Familie zu der magalhaensischen Fauna als sicher annehmen lässt." We question Lönnberg's identification of "Scomberesocidae" at a locality so far south, but we are at a loss to know with what other species his-

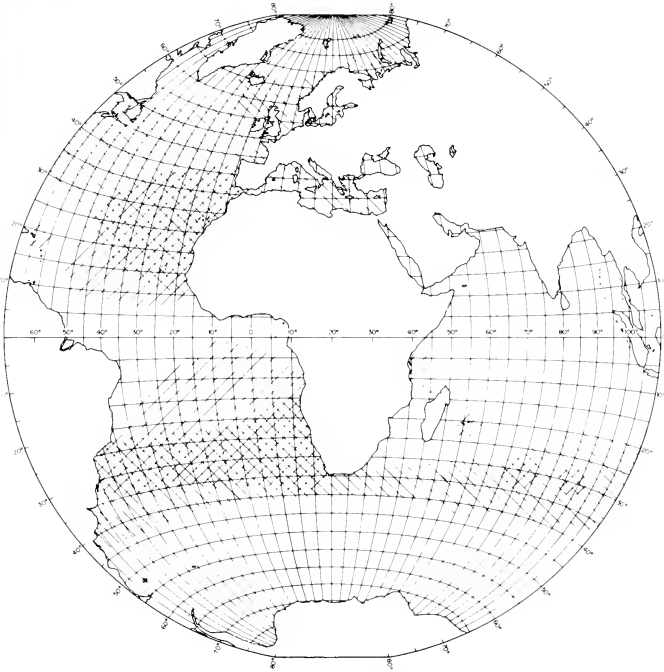


FIGURE 16.—Overlapping distributions of Scomberesocidae in the Eastern Hemisphere. Lines sloping downward to the left refer to *Nanichthys simulans*; lines sloping downward to the right refer to *Scomberesox saurus* in the Atlantic and Indian Oceans.

"young" specimens could have been confused. Mann (1954b, 1960) listed no scomberesocids or beloniforms from the Patagonian area. Also, there appears to be confusion as to the locality of the capture stated by Lönnberg: Smyth Channel and Eden Harbor appear to be about 240 mi apart. According to Defense Mapping Agency Chart 22ACO 22390, Eden Harbor (now Puerto Eden) lies on a narrow channel along the east side of Isla Wellington, about 49 09′ S, 74 24′ W. This is far inland from the open sea and is a seemingly improbable place to find a synentognath fish. Smyth Channel (Defense Mapping Agency Chart 22XHA 22404) opens to the Pacific Ocean at about 52 50′ S, 73 50′ W (about the center of its wide mouth) and extends northerly to about 52 23′ S, where it merges with Mayne and Gray Channels. If scomberesocid fishes of any size occur in the area, the mouth of Smyth Channel is a more probable place than the inland Eden Harbor. The taking of seven young of *S. s. scombroides* at 47° S, 81° W, cited above, lends some credence to the possibility of the

FIGURE 17.—Overlapping distributions of Scomberesocidae in the Western Hemisphere. Lines sloping downward to the right refer to *Cololabis saira* in the North Pacific and near New Guinea, and to *Scomberesox* ssp. in the South Pacific and extreme northwestern Atlantic; lines sloping downward to the left refer to *Elassichthys adocetus*.

species being taken in the wide oceanic mouth of Smyth Channel some 400 mi farther south.

Our findings on the distribution of *S. s. scombroides* westward across the South Pacific differ little from that shown by Parin (1968a).

The northern subspecies, *S. s. saurus*, occurs widely in the North Atlantic Ocean, north of about 30° N, but rather sparsely in the central area, where it is very largely replaced by *Nanichthys* (Figures 12, 14, 16). It ranges along North America from Florida (rarely) to Newfoundland, and well into the Gulf of St. Lawrence (Vladykov and McAllister 1961) and to Iceland (Saemundsson 1949). The species occurs uncommonly along the eastern shores of the United States south of New Jersey. It occurs at the oceanic islands of the eastern North Atlantic, throughout the Mediterranean, Aegean, and Adriatic Seas, the British Isles, and along Norway to near Nordkapp. It has been reported from the Barents Sea, and from the

White Sea in Kandalaksha Bay, about 67° N, 32°45' E (Andriashev 1954, after Novikov). Berg (1939) reported it from the western entrance to the Strait of Matochkin Shar, Novaya Zemlya Island (about 73°16' N, 56°27' E); Andriashev (1954) gave the length of this specimen as 25 cm. Presumably the species is rare that far north and is a summer migrant. However, it has been reported (Anonymous 1970) that four Russian vessels captured 7 to 10 metric tons per vessel per day of "saury" in late September 1969 near Novaya Zemlya. W. L. Klawe[16] feels that these large catches of *Scomberesox* so far north actually represented either "saida" (*Pollachius virens*, the Atlantic pollock) or "saika" (*Boreogadus saida*, the Arctic cod), and that the use of the Russian vernacular "saira" (= saury) was either a misprint or misinterpretation.

The southern extension of *S. s. saurus* into the central North Atlantic, to 15° N (Figure 14) is probably due to the southeasterly flowing currents of the huge gyre that extends across the ocean between about 40° and 20° N; the southern border of this gyre forms the northern boundary of the west-flowing North Equatorial Current; its southerly boundary reaches to about 5° N.

Nanichthys is common in the more central parts of the North and South Atlantic Ocean but is not common in the Indian Ocean (Figure 12). We enter on the distributional chart (Figure 12) a question mark in the Red Sea on the dubious basis of Borodin's (1930) record of "*Scomberesox saurus*, young" from the "Red Sea" (accepted by Fowler 1956). The record is questioned because Borodin's identifications have proved to be commonly inaccurate, and we have not seen the specimen (which has been reported to us as no longer extant in the Vanderbilt Museum). If the record was not based on a juvenile hemiramphid or other nonscomberesocid synentognath, it may have been based on *Nanichthys*, which we have seen from Zanzibar. We also enter a question mark (Figure 12) in reference to the record of *S. saurus* reported by J. L. B. Smith (1955). Smith[17] has stated: "With regard to the Aldabra record, I regret that we cannot find the specimen. In our field notes this species is entered as 'Juvs. in stomach of Tunny.' Neither my wife nor I can remember whether that material was kept or not; it probably was in a bad state."

The records of capture of *Nanichthys* in the Indian Ocean are too few to warrant more than conjecture as to limits of distribution there; it is either uncommon or has been very infrequently taken. No specimens resulted from the broad station coverage of the International Indian Ocean Expedition, 1963-64. N. V. Parin[18] did not encounter any specimens of *Nanichthys*, although he did report many captures of *S. s. scombroides* (Figure 14). Sauvage (1891) listed "*Scombresox saurus*" from near Madagascar, within a rather broad area bounded by "3° et 26° parallèles et les 42° et 65° méridiens." Misidentification is possible as Sauvage included species of Belonidae, Hemiramphidae, and Exocoetidae in his "Scombresocidae"; no size or number of specimens was given.

In most of the records of *Nanichthys* from the North Atlantic Ocean, the greatest number of captures lie within the large eddy system and easterly of about 40° W, extending to the African coast. The southern border of the range, ca. 10° N, is at about the middle of the North Equatorial Current, and the northern border, at ca. 35° N, at the northern margin of the eddy and the southern margin of the Gulf Stream and of its continuation—the North Atlantic Current. There is little difference in current structure between winter and summer in the southern portion of the North Atlantic (Anonymous 1965), and the currents are relatively slow during both periods. Oddly, *Nanichthys* is infrequently taken west of about 40° W, the most westerly occurrence being near St. Thomas Island, West Indies (Figure 12). *Nanichthys* appears to be more antitropical in distribution than does *Elassichthys*. Ueyanagi et al. (1972) mapped the occurrence of a juvenile at about 02° S, 10° W (Figure 12).

In the Atlantic, in both hemispheres, this dwarfed form has often been confused by authors with the young of *Scomberesox*. The material reported by Murray and Hjort (1912) ("M" in Figures 12 and 14), and by Lütken (1880) from the North Atlantic in part represent *Nanichthys*. Each author stated that the young of *Scomberesox* were taken in great numbers in collections from the open Atlantic; each figured (as young of *Scomberesox saurus*) the distinctive beak structure of

[16]W. L. Klawe, Inter-American Tropical Tuna Commission, La Jolla, Calif., pers. commun. 20 March 1970.

[17]J. L. B. Smith, Department of Ichthyology, Rhodes University, Grahamstown, South Africa, pers. commun. 20 November 1964.

[18]N. V. Parin, P. P. Shirshov Institute of Oceanology, Akademia 117218 Moscow, Krasikowa 23, U.S.S.R., pers. commun. 14 September 1978.

adult or semiadult *Nanichthys*—the upper beak notably shorter than the lower. We have examined most, if not all, of these specimens and found them to be referable to *Nanichthys*. Also, most of the reports of *Scomberesox saurus* from the South Atlantic and Indian Oceans by Lampe (1914) ("L" in Figure 12) may, on the basis of geographical evidence, be referable to *Nanichthys*. We have, however, not seen the specimens, but many of Lampe's collections occurred in the area of overlap (Figure 16). Dudnik (1975a) reported on an extensive collection of "*Scomberesox saurus*" from the South Atlantic (about 3,000 specimens, from 8 to 460 cm). In general his data agree well with ours and with Parin's (1968a, b) but he shows (Dudnik 1975a, fig. 2) the species to extend northward to about 18° S along the coast of Africa. This is notably farther north of the expected range but is well within that of *Nanichthys*. He did not discuss the dwarf ("*Scomberesox* sp") in his study (Dudnik 1975a), submitted for publication on 20 January 1974, nor did he compare it with its larger relative, although presumably he was aware of the form and of Parin's (1968a) study for he submitted his own (Dudnik 1975b) concerning it on 20 November 1974. As no tabular or descriptive morphological data were offered in the first study (on *Scomberesox saurus*), it is not entirely clear whether or not Dudnik (1975a) dealt only with the larger form, for he indicated that only smaller specimens, larvae to juveniles up to 100 mm (a size range encompassing most adults of *Nanichthys*), occurred north of 20° S. Also, in his later work on *Scomberesox* sp. (= *Nanichthys simulans*), Dudnik (1975b) showed collections of the dwarfed form between about 10° and 15° S in this same area off Africa.

The dwarfed form, *Elassichthys adocetus*, of the eastern Pacific Ocean also has been confused with the young of *Cololabis saira*. Roedel (1953) and Chirichigno F. (1962) reported *C. saira* (as young) from off northern Perú. Schaefer and Reintjes (1950) reported (as young of *C. saira*) specimens of *E. adocetus* from between the Hawaiian Islands and the western coast of North America.

Elassichthys adocetus appears to be less antitropically distributed than is *Nanichthys simulans* in the Atlantic Ocean. A few specimens have been taken between the two principal areas of occurrence north and south of the Equator (Figure 13); perhaps these are strays from the main groups (presumably from the southern) and transported there by the complex current systems of the area and/or associated with oceanic fronts, as reported by Knauss (1957) in the vicinity of 03° N, 120° W.

An interesting aspect of the distributions of the northern population of *E. adocetus* is its absence from the large area bounded by about 115° W and the Equator. Also, it has not been taken within hundreds of miles of the coast of Baja California, México. In contrast, the species is very common in the coastal waters of Ecuador and Perú. One reason for the avoidance (or absence) of the area westerly of Baja California may be the still cool water of the California Current, between 18° and 25° N. This broad current is evident out to about 120° W and flows southerly to about 22° N between January and June-July before turning westerly and mixing with the North Equatorial Current; from August to December these two currents merge at or north of 20° N. Temperatures within this large area range between 25° and 29° C (Wyrtki 1964) and are probably above the optimum tolerated by the species. Also, this area is one of very low oxygen content (0.05 ml l), but this may not be a factor in the distribution of *E. adocetus* as it is an entirely surface form and probably remains well above the upper depth limit of the O_2 minimum layer, between 50 and 200 m (Wyrtki 1967).

The occurrence of *E. adocetus* (and *S. saurus scombroides*) near the coasts of Ecuador and Perú, and its westward extension of range to about 115° W near the Equator, are no doubt due to the still cool water of the Perú Current; the temperatures range to about 20°-26° C in summer and 16°-24° C in winter, between about 0° and 22° S (Wyrtki 1964).

In the northeastern Pacific Ocean the ranges of *C. saira* (again mostly juveniles and young) and the northern population of *E. adocetus* overlap in an extensive area roughly bounded by about 20° to 30° N, 115° to 155° W (Figure 17); perhaps the overlap is primarily seasonal but often the two have been taken together in the northern portion of the overlap area. King and Iversen (1962:320, app. table 8) reported one specimen (86 mm) of "Scomberesocidae" from the Equatorial Counter Current (ECC) in 1955-56. No coordinates were given but the collection was made between about 108° and 160° W within the ECC, the boundaries of which these authors indicated to be between about 5° and 10° N (p. 286, fig. 12). The stated size ("86 mm") is notably longer than the largest of hundreds examined by us (about 68 mm SL), but it can scarcely be other than *Elassichthys*, which is

common within the ECC. The southernmost known occurrence of *C. saira* is some hundreds of miles to the north.

Cololabis saira apparently does not occur south of about 20° N (Figure 15), based on our data and those of Parin (1960). North of this latitude it ranges throughout the North Pacific to the Aleutian chain, but apparently not into the eastern and central Bering Sea. In the far western area it occurs in the eastern portion of the Yellow Sea, the entire Sea of Japan to well along Sakhalin, into the southern Okhotsk Sea, and northerly along the Bering Sea coast of Kamchatka to Olyutorsky Bay, at about 60° N (Parin 1968a, b) (Figure 17). Along the North American coast *C. saira* is very common from Alaska to at least central California, but only sporadically so to about the Cedros Island region of Baja California, Mexico; it is relatively uncommon south of that region, particularly adults, but young and juveniles have been taken at about 19° N in the eastern Pacific.

Cololabis saira juveniles (8-30 mm) were reported from 180 mi east of Port Macquarie (New South Wales, Australia) by Fourmanoir (1971); however, we have examined these small fishes and determined them to be *S. s. scombroides*. One apparently valid capture of *C. saira* near New Guinea (kindly communicated to us by N. V. Parin, 14 September 1978) was reported by Kailola (1974): ". . . one specimen. East of Kavieng [New Ireland] (2°34′ S, 150°49′ E) Dipnetted by night light, 1967.—205 mm SL." The count of dorsal and anal finlets (5 each) indicates the specimen is a scomberesocid, and certain proportions listed can pertain only to *Cololabis*: "Eye 5, 1.8 in snout. Snout 2.7 in head," falling far outside the range for *Scomberesox* of similar size. The stated size, 205 mm, is far too large for *Elassichthys*. This locality (Figure 15, large hexagon) is about 1,800 miles south of any other known occurrence of *C. saira* in the western Pacific. Parin believes, and we concur, that this specimen was very probably lost from a Japanese longline vessel; Fourmanoir and Laboute (1976) describe the use of frozen sauries (*C. saira*) as bait by longliners operating in the area.

Intriguing questions arise concerning this apparently valid capture in the Southern Hemisphere. We assume that the specimen was alive (at least it was not stated otherwise). Kailola (1974) postulated that "abnormal extensions of cold currents south of the Equator may thus account for the southern record of the species." An alternative explanation is that the specimen was transported alive from northern waters in a bait tank aboard a vessel. However, *C. saira* does not keep well in live-bait tanks; they are "wild" and dash themselves to death against the walls, particularly of small tanks. And, to our knowledge, there are no recorded instances of a Japanese longline vessel carrying large live-bait tanks.

ACKNOWLEDGMENTS

Our efforts have been aided by many persons—so many that no doubt we will fail to list at least a few; in that event we hereby express our great appreciation for any effort made to further our work. We are deeply indebted to our Russian colleague Nikolai Parin for deferring to us the naming of his "*Scomberesox* sp" and for persuading his fellow workers also to refrain; also, we are indebted to him for providing many unpublished capture localities for all four species of the family. Our Japanese colleagues, Shoji Ueyanagi, Shigeru Odate, Keiichiro Mori, Hiroshi Hiyama, and Tokiharu Abe, have provided information on distribution of *Cololabis saira*; Ueyanagi, in addition, provided much information on *Scomberesox*, *Nanichthys*, and *Elassichthys*. We are very grateful to Philip Sloan, formerly a student at Scripps Institution of Oceanography, for his efforts on the Scripps expedition LUSIAD in gathering the nucleus of the material on which we base the new genus and species, *Nanichthys simulans*.

Specimens and information have been provided by Bruce B. Collette and Robert H. Gibbs, Jr. (USNM), G. Palmer (BMNH), Enrico Tortonese (Museo Civico di Storia Naturale, Genoa), W. Ladiges (ZSZM), P. Fourmanoir (New Caledonia), Frank Talbot (AMS), Frederick H. Berry (TABL), Myvanwy Dick (MCZ), E. Bertelsen and Jørgen Nielsen (ZMUC), and Marie-Louise Bauchot (Paris). Leslie W. Knapp (SOSC) and Leonard P. Schultz (USNM) have kindly provided much study material. We are grateful to Camm C. Swift (LACM) and Peter U. Rodda (CAS) for the loan of fossils that have been referred to the Scomberesocidae.

Bruce B. Collette critically reviewed the manuscript and offered valuable suggestions. Elizabeth N. Shor typed the final manuscript and otherwise provided assistance. To all these persons (and those we have forgotten) we offer our very great appreciation and deep thanks.

ADDENDUM

Fossil Fishes from California Referred to Scomberesocidae

We are uncertain of the synonymic status of the nominal genus *Scomberessus*, based on a fossil from the Miocene (Monterey) formations, introduced by Jordan (1920). By context, Jordan proposed *Scomberessus* as a new genus, as follows: "**Scomberessus** Jordan, 571 [referring to the same item in *The Genera of Fishes*], orthotype SCOMBERESOX ACUTILLUS J. & G. (fossil). Differs from the living genus SCOMBERESOX in the much larger dorsal, of 16 rays." But an examination of the text and figures of the two fossil specimens described by Jordan and Gilbert (1919: 37-38, pl. XIV, fig. 2, and XVIII—*Scomberesox acutillus* and *S. edwardsi*) indicate a serious confusion. The one item of diagnosis (dorsal fin) was obviously drawn not from the account and figure of *Scomberesox acutillus* Jordan and Gilbert (1919:37-38, pl. XIV, fig. 2 [the paratype]), but from the description and figure of *Forfex hypuralis* Jordan and Gilbert (1919:36-37, pl. XIV, fig. 3). The description of *S. acutillus* states only "dorsal obliterated," also, the paratype (a complete skeleton examined by us) shows no remaining trace of a dorsal fin. The description of *F. hypuralis* lists the dorsal rays as "apparently I, 16 in number" and the figure shows a long-based dorsal of approximately the stated number of rays and beginning before the middle of the body (without head). The juxtaposition of the two figures on the plate presumably led the aged master astray. Despite the nonapplicability of the one stated character, the generic name *Scomberessus* must, we assume, rest on the designated type-species, *Scomberesox acutillus*.

Regardless, we are more concerned with the reference of these fossils to the family Scomberesocidae. We have examined the paratype of *Scomberesox acutillus* (a complete skeleton but with crushed head), and five essentially complete skeletons referable (presumably) to *S. edwardsi* (the holotype is a head and anterior few vertebrae) and have failed to find any finlets—a key character of the family—this despite the listing by Jordan and Gilbert (1919) of ". . . traces of five finlets" for *S. acutillus* (the paratype); under high magnification these traces proved to be isolated scales.

David (1943) may have inferred the presence of finlets by listing counts for *S. edwardsi* of "Dorsal fin 14, V; anal fin 18, VI. . . ." As Roman numerals have long been used to designate spiny or unsegmented rays, and as living scomberesocids and related fishes all have segmented rays, we assume that David was referring to finlets. However, on examination of David's and other material labelled *S. edwardsi*, we find nothing to substantiate a count including any "V" or "VI," particularly for finlets.

Each finlet of the Scomberesocidae and Scombridae (mackerels and tunas) arises from a single base (ray) that branches into a fanlike structure that is much more robust than a slender, single ray of the dorsal and anal fins proper. Since the individual rays of these fins are distinctly evident on some of these fossils, it is reasonable to expect the heavier finlets also to be preserved or that an imprint at least would have remained.

The lack of imprint of finlets is substantiated by the absence of any (or imprint) of the supporting bones associated with them. In present scomberesocids these supporting bones are robust, flattened laterally, and lie embedded somewhat parallel to the surfaces of the caudal peduncle rather than extending more or less vertically between the neural and haemal spines, as do those of the rays of the main portions of the fins. Thus, since the supporting rays of the main portions of the fins are often visible in the fossils, it is reasonable to expect such rays of the finlets also to be visible, if present.

In addition to the apparent lack of finlets on these fossils (labeled as of Clarendonian stage), there are notable differences in proportions in lengths of anal bases and caudal peduncle between them and present *Scomberesox*. In two fossils on which the anal fins appear to be entire (none have complete dorsal fins) the length of this fin is slightly shorter than the length of caudal peduncle (23.7 vs. 26.5 and 28.5 vs. 33.2 mm). In present *Scomberesox* the caudal peduncle is about 2.5 times the length of either the dorsal or anal fin base, exclusive of finlets. In this regard the fossils approach the condition found in the Belonidae, wherein the length of the caudal peduncle is one-half or less as long as the fin bases; in *Ablennes hians* the peduncle is scarcely more than one-fourth the length of these bases. Thus, among known marine fishes with both jaws greatly prolonged into beaks, these fossils are about midway between present belonids and *Scomberesox* in the ratio of lengths of caudal peduncle to the base of either dorsal or anal fins (exclusive of finlets in the latter group). An additional difference is a notable

reduction in numbers of vertebrae in those fossils with complete skeletons, 54-58 vs. 64-70 in present *Scomberesox*, and 62-69 in *Cololabis*.

Due to the apparent absence of finlets and the discrepancy in lengths of caudal peduncle and anal fin base, and the many fewer vertebrae, it seems justifiable to remove these fossils from the family Scomberesocidae. To retain them therein would require acceptance of development of finlets and drastic modification of the peduncular region since the Miocene period (7-26 million years BP [Before Present]) and a gain of at least six vertebrae; we hold these to be improbable occurrences. In any event, the name *Scomberessus* appears to have no bearing on the new generic names proposed herein.

Furthermore, we find no sound basis for even the doubtful reference of *Praescomberesox pacificus* David (1946:58-59, pl. 2, fig. 3, and pl. 3, fig. 2) to the Scomberesocidae on the basis of isolated scales found in a core from oil-well drilling at a depth between 3,895 and 3,907 feet (holotype).

LITERATURE CITED

AHLSTROM, E. H.
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull., U.S. 70:1153-1242.

ALLEN, G. R., D. F. HOESE, J. R. PAXTON, J. E. RANDALL, B. C. RUSSELL, W. A. STARCK II, F. H. TALBOT, AND G. P. WHITLEY.
1976 Annotated checklist of the fishes of Lord Howe Island. Rec. Aust. Mus. 30:365-454.

ANDRIASHEV, A. P.
1954. Fishes of the northern seas of the USSR. Izd. Akad Nauk SSSR 53, 617 p.
1961. A list of ichthyological stations [Obj], with a preliminary characterization of the collections. [In Russ.] Tr Sov. Antarkt. Exped. 2:227-234.
1962. Bathypelagic fishes of the Antarctic I, Family Myctophidae. [In Russ.] Exploration of the fauna of the seas, biological results of the Soviet Antarctic Expedition (1955-1958). Acad. Sci. USSR, Zool. Inst. 1(IX):216-294

ANONYMOUS.
1965. Oceanogrpahic atlas of the North Atlantic Ocean. Section 1. Tides and currents. U.S. Nav. Oceanogr. Off., Wash., D.C., 75 p.
1970. USSR fishes saury in the northern Barents Sea. Commer. Fish. Rev. 32(2):44.

ARNOULT, J., F. D'AUBENTON, M. L. BAUCHOT, AND M. BLANC
1966. Compagne de la Calypso dans le Golfe de Guinée et aux îles Principe, São Tomé et Annabon (1950). 15 Poissons Téléostéens (primière partie). Ann. Inst Océanogr., New Ser. 44:3-22.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3d ed. Am. Fish. Soc. Spec. Publ. 6, 149 p.

BARNARD, K. H.
1925. A monograph of the marine fishes of South Africa. Ann. S. Afr. Mus. 21:1-418.
1950. A pictorial guide to South African fishes marine and freshwater. Askew Miller Ltd., Cape Town, 222 p.

BEN-TUVIA, A.
1971. Revised list of the Mediterranean fishes of Israel. Isr. J. Zool. 20:1-39.

BERG, C.
1895. Enumeración sistemática y sinonímica de los peces de las costas argentina y uruguaya. An. Mus. Nac. Buenos Aires 4:1-120.

BERG, L. S.
1939. Appearance of boreal fishes in the Barents Sea. [In Russ.] *In* Miscellaneous papers dedicated to the memory of the scientific worker, the honorable member of the Academy of Sciences, Nikolai Michailovich Knipovitch (1855-1939), M.-L. 207-208. [Reprinted *in* Selected works by Academician L. S. Berg, 4, 1961, Ichthyology 654-655, quoted from 1961 reprint.]
1940. Classification of fishes, both recent and fossil. (In Russ. and Engl.) Trav. Inst. Zool. Acad. Sci. URSS 5:85-517.

BERMAN, I. S., AND V. I. RYZHENKO.
1968. Peculiarities of the distribution and biology of the mackerel-pike. [In Russ.] Commer. Fish. (Moscow) 44:10-12.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BIGELOW, H. B., AND W. W. WELSH.
1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(1), 567 p.

BLEEKER, P.
1860. Over eenigie Vischsoorten van de Kaap de Goede Hoop. Natuur. Tijdschr. Ned. Indië 21:49-80.

BLOCH, M. E., AND J. G. SCHNEIDER.
1801. Systema ichthyologiae iconibus cx illustratium. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider Saxo, Berl., 584 p.

BOHLKE, J. E.
1951. A new Pacific saury (genus *Cololabis*) from off the coast of Peru. Trans. Kans. Acad. Sci. 54:83-87.

BORODIN, N. A.
1930. Scientific results of the yacht "Ara" expedition during the years 1926 to 1930, while in command of Wilham K. Vanderbilt. Fishes (collected in 1929). Bull. Vanderbilt Mar. Mus. 1:39-64.

BREDER, C. M., JR.
1932. On the habits and development of certain Atlantic Synentognathi. Carnegie Inst. Wash. Publ. 435:1-35.
1938. A contribution to the life histories of Atlantic Ocean flyingfishes. Bull. Bingham Oceanogr. Collect., Yale Univ. 6:1-126.

BREVOORT, J. C.
1856 Notes on some figures of Japanese fish taken from recent specimens by the artists of the U. S. Japan Expedition. *In* Narrative of Commander M. C. Perry's Expedition to Japan 2:253-288.

BRIGGS, J. C.
1958 A list of Florida fishes and their distributions. Bull. Fla. State Mus. 2:223-318.

BUEN, F DE
1950 El Mar de Solis y su fauna de peces (2 a Parte). Publ Cient , Serv Oceanogr Pesca (Montevideo) 2 47-144
1955 Pelagic fishes and oceanographic conditions along the northern and central coast of Chile. Proc UNESCO Symp Phys Oceanogr , Tokyo
1959 Notas sobre ictiologia chilena, con descripcion de dos especies nuevas [In Span] Rev Biol. Mar 9 257-270
1963a Los peces de la Isla de Pascua Bol Soc Biol Concepcion, Chile 35-36 (for years 1960-61) 3-80
1963b. Peces chilenos Beloniformes, Syngnathiformes y Gobiidae Bol Soc Biol Concepción, Chile 35-36 (for years 1960-61) 1-133

CADENAT, J
1950 Poissons de Mer du Senegal Initiations afric. 3 Inst Fr d'Afr Noire, 345 p

CHIGIRINSKY, A I
1972 Size and age class composition of Atlantic saury in the South-Eastern Pacific. [In Russ.] Trans Pac Sci Res Inst Fish Oceanogr 81 150-165
1973 The main aspects of biology and stock assessment of skipper in the southeast Pacific [In Russ] Tr Vses Nauchno-Issled Inst Morsk Rybn Khoz Okeanogr 93 198-215

CHIRICHIGNO F , N
1962 Algunos peces nuevos y poco conocidos de la fauna marina del Peru Serv Pesq Perú, Serv Divulg Cient 17 1-29
1969. Lista sistematica de los peces marinos communes para Ecuador, Peru, Chile Conferencia sobre explotacion y conservacion de los riquezas marítimas del Pacifico Sur — Chile-Ecuador-Perú, Secretaria General, 108 p
1974 Clave para identificar los peces marinos del Perú Inst Mar Perú, Inf 44 1-185

CHYUNG, M K
1961 Hankook dongmool dokam, uryu [Illustrated encyclopedia, the fauna of Koreal Central Publ Co , Seoul, 861 p

CLEMENS, H B
1955 Fishes collected in the tropical eastern Pacific, 1952-53 Calif Fish Game 41 161-166

CLEMENS, H B , AND J C NOWELL
1963 Fishes collected in the eastern Pacific during tuna cruises, 1952 through 1959 Calif Fish Game 49 240-264

COLLETTE, B B
1966 *Belonion*, a new genus of fresh-water needlefishes from South America Am Mus Novit. 2274, 22 p
1968 *Strongylura timucu* (Walbaum) a valid species of western Atlantic needlefish Copeia 1968 189-192
1974 *Strongylura hubbsi*, a new species of freshwater needlefish from the Usumacinta Province of Guatemala and Mexico Copeia 1974 611-619

COSTA, A
1862 Di un novello genere di pesci Esocetidei Ann Mus Zool Napoli 1 54-57

DAVID, L R
1943 Miocene fishes of southern California Geol Soc Am Spec Pap 43, 193 p
1946 Some typical Upper Eocene fish scales from California Contrib Paleontol IV, Carnegie Inst Wash Publ 551 45-79

DELFIN, F. T.
1900 Catálogo de los peces de Chile. Rev Chil. Hist. Nat. 4 4.
1901. Ictiólogia Chilena. Catálogo de los peces de Chile Republished from Rev. Chil. Hist. Nat. 3 (1899) and 4 (1900), Valparaiso, 133 p.

DEVINCENZI, G J
1924 Peces del Uruguay. II Nuestra fauna ictiológica segun nuestras colecciones. An Mus Hist Nac Montevidéo 2:139-293.

DEVINCENZI, G J., AND L P BARATINI.
1928 Album ictiológico del Uruguay. An Mus Hist. Nac. Montevideo 2:pls. 14-24

DUDNIK, Y I
1975a Some characteristic features of the geographical range of Atlantic saury *Scomberesox saurus* (Walb) in the South Atlantic in winter [In Russ] Vopr. Ikhtiol 91 203-210
1975b On the biology of dwarf *Scomberpike Scomberesox* sp Parin (Pisces, Scomberesocidae) of the Atlantic Ocean [In Russ , Engl summ.] Okeanologia 15 738-743

EBELING, A W
1967 Zoogeography of tropical deep-sea animals. Stud Trop Oceanogr (Miami) 5 593-613

EHRENBAUM, E
1936 Naturgeschichte und wirtschaftliche Bedeutung der Seefische Nordeuropas *In* H Lubbert and E Ehrenbaum, Handbuch Seefischerei Nordeuropas, band 2, 337 p E Schweizerbart'sche Verlagsbuchhandlung, Stuttgart

FOURMANOIR, P
1971 Notes ichtyologiques, IV Cahiers ORSTOM, sér Oceanogr 9 491-500

FOURMANOIR, P , AND P LABOUTE
1976 Poissons de Nouvelle Caledonie et des Nouvelles Hebrides Les Editions Pacifique, Papeete, 376 p

FOWLER, H W
1936 The marine fishes of West Africa based on the collection of the American Museum Congo Expedition, 1909-1915 Bull Am Mus Nat Hist 70 1-605
1940 The fishes obtained by the Wilkes Expedition, 1838-1842 Proc Am Philos Soc 82 733-800
1942a A list of the fishes known from the coast of Brazil Arq Zool Estado São Paulo 3 115-184
1942b The coastal fishes of Brazil Proc 8th Am Sci Congr , Biol Sci , Zool 3 381-387
1944a Results of the fifth George Vanderbilt Expedition (1941) The fishes Acad Nat Sci Phila Monogr 6 57-583
1944b Fishes of Chile systematic catalog Rev Chil Hist Nat [2d part] 46 (for 1942) 37-102
1951 Analysis of the fishes of Chile Rev Chil Hist Nat 51-53 263-326
1956 Fishes of the Red Sea and southern Arabia Vol 1 Branchiostomida to Polynemida Weizmann Sci Press Isr , Jerusalem, 240 p

GILCHRIST, J D F
1901 Catalogue of fishes recorded from South Africa Mar Invest S Afr 6 97-179
1904 Development of South African fishes, part II Mar Invest S Afr 3 131-152

GILL, T
1895 The families of synentognathous fishes and their nomenclature Proc U S Natl Mus 18 167-178

GOLVAN, Y.-J
1962 Catalogue systematique des noms de genres de poissons actuels. Ann. Parasitol. Hum. Comp. 37:1-227.
1965. Catalogue systematique des poissons actuels Ann Parasitol. Hum Comp , 277 p

GOSLINE, W A
1959 Four new species, a new genus, and a new suborder of Hawaiian fishes. Pac Sci. 13 67-77.
1971 Functional morphology and classification of teleostean fishes Univ Hawaii Press. Honolulu, 208 p

GOSLINE, W A., AND V. E. BROCK.
1960 Handbook of Hawaiian fishes Univ Hawaii Press. Honolulu, 372 p

GREENWOOD, P H , D E. ROSEN, S H. WEITZMAN, AND G S MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus Nat. Hist. 131:339-455.

GUICHENOT, A.
1848 Fauna chilena Peces *In* C Gay, Historia fisica y politica de Chile Zoologia (Paris) 2:137-372

GUNTHER, A
1866. Catalogue of the fishes in the British Museum, London Vol. 6, 368 p
1889. Report on the pelagic fishes collected by H M S Challenger during the years 1873-76 Voyage of H M S Challenger, Zool 31 1-47.

HAECKEL, E
1855 Ueber die Eier der Scomberesoces Arch Anat Physiol Wiss.-Med., p 23-31

HARTMANN, J.
1970. Juvenile saury pike (*Scomberesox saurus* Walb.), an example of ichthyoneuston J Cons 33 245-255

HEATH, E , AND J M MORELAND
1967. Marine fishes of New Zealand. A H & A W Reed Wellington, 56 p

HECTOR, J
1872. Notes on the edible fishes of New Zealand Colon Mus Geol Surv Dep , p 95-133

HILDEBRAND, S F , AND W C SCHROEDER.
1928. Fishes of Chesapeake Bay Bull. U S Bur Fish 43(1), 388 p

HOTTA, H
1964 Biological studies and fisheries of the saury, *Cololabis saira* (Brevoort). Jpn. Fish Prot Assoc , Fish Res Ser , 96 p

HUBBS, C L
1916 Notes on the marine fishes of California Univ Calif Publ Zool 16 153-169
1933 Observations of the flight of fishes, with a statistical study of the flight of the Cypselurinae and remarks on the evolution of the flight of fishes Pap Mich Acad Sci., Arts Lett. 17 575-611

HUBBS, C L , AND C HUBBS
1953 An improved graphical analysis and comparison of series of samples Syst Zool 2 49-57

HUBBS, C L., AND A PERLMUTTER
1942. Biometric comparisons of several samples, with particular reference to racial investigations Am Nat 76 582-592

HUTTON, F W
1872 Fishes of New Zealand, catalogue, with diagnosis of the species Colon Mus Geol Serv Dep , p. 1-93
1889 List of the New Zealand fishes Read before Philos Inst Canterbury, p 275-288
1904 Index faunae Novae Zealandiae Dulau & Co , Lond , 372 p

JORDAN, D S
1917 The genera of fishes from Linnaeus to Cuvier, 1758-1833, seventy-five years, with the accepted type of each A contribution to the stability of scientific nomenclature Stanford Univ Publ , Univ Ser , 161 p
1920 The genera of fishes Part IV From 1881 to 1920, thirty-nine years, with the accepted type of each Stanford Univ Publ , Univ Ser , p 411-476
1921 The fish fauna of the Cahfornia Tertiary Stanford Univ Publ., Univ Ser , Biol Sci 1 233-300
1923 A classification of fishes including families and genera as far as known Stanford Univ Publ , Univ Ser , Biol Sci. 3 79-243

JORDAN, D S , AND B W EVERMANN
1896 The fishes of North and Middle America, part 1 U S Natl Mus Bull. 47, 1240 p

JORDAN, D S , B W EVERMANN, AND H W. CLARK
1930 Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia Rep U S Comm Fish 1928, part II 1-670

JORDAN, D S., AND J Z GILBERT
1919 Fossil fishes of southern California II Fossil fishes of the Miocene (Monterey) formations Stanford Univ Publ , Univ Ser , p. 13-60

KALLOLA, P J
1974. Additions to the fish fauna of Papua New Guinea III Dep Agric , Stock Fish (Papua New Guinea) Res Bull 12 54-89

KAWAMURA, A
1974 Food and feeding ecology in the southern sei whale Sci Rep Whales Res Inst 26 25-144

KENDALL, W C , AND L RADCLIFFE
1912 The shore fishes Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U S Fish Commission steamer "Albatross" from October, 1904, to March, 1905 XXV Mem Mus Comp Zool. 35:77-172

KING, J E , AND R T B IVERSEN
1962 Midwater trawling for forage organisms in the central Pacific, 1954-1956 U S Fish Wildl Serv , Fish Bull 62 271-321

KNAUSS, J A
1957 An observation of an oceanic front Tellus 9 234-237

KOEPCKE, H -W
1962. Lista de los peces marinos conocidos del Peru con datos de su distribucion geografica Tercera Parte Boeta 4 193-204

KUSAKA, T
1974 The urohyal of fishes Univ Tokyo Press, Tokyo. 320 p

LACEPEDE, B G E V
1803 Histoire naturelle des poissons Vol 5 Plassan, Paris, 401 p

LAMPE, M
1914 Die Fische der Deutschen Sudpolar-Expedition 1901-1903 III Die Hochsee-und Kustenfische Dtsch Sudpolar-Exped 15:201-256

LEIM, A H , AND W B SCOTT
1966 Fishes of the Atlantic coast of Canada Fish Res Board Can , Bull. 155, 485 p

LESUEUR, C A
1822 Observations on several genera and species of fish, belonging to the natural family of the Esoces. J Acad Nat Sci Phila , New Ser , 2 124-138
LINDBERG, G U , AND M I LEGEZA.
1965. Fishes of the Sea of Japan and the adjacent areas of the Sea of Okhotsk and the Yellow sea. Part 2, Teleostomi, XII. Acipenseriformes - XXVIII Polynemiformes Akad Nauk SSSR, 391 p
LÖNNBERG, E.
1907 Fische Hamburger magalhaensische sammelreise L Friederichsen & Co., Hamburg, 15 p
LOPEZ, R. B
1957. Pex aguja, "Scomberesox saurus" (Walbaum) pescado en Necochea Univ Nac de la Plata, Notas Mus 19(Zool. no. 1976):145-151.
LOZANO REY, L.
1947 Peces ganoideos y físostomos. Mem R Acad. Cienc. Exactas Fis. Nat. Madr., Ser. Cienc. Nat. 11, 839 p.
LÜTKEN, C F
1880. Spolia Atlantica. Bidrag til Kundskab om Formforandringer hos Fiske under deres Vaext og Udvikling, saerligt hos nogle af Atlanterhavets Højsøfiske. Vidensk Selsk Skr. (5) 12 409-613.
MACLEAY, W
1881 Descriptive catalogue of the fishes of Australia. Part IV Proc Linn Soc N S W 6 202-387.
MAIS, K F , AND T JOW
1960 Exploratory longline fishing for tunas in the eastern tropical Pacific, September, 1955 to March, 1956. Calif. Fish Game 46.117-150.
MANN, F G
1950. Peces de Chile. Clave de determinación de las especies importantes Chile Minist Agric , 84 p.
1954a Vida de los peces en aguas chilenas. Minist. Agric , Santiago de Chile, 342 p
1954b. El mar chileno y sus regiones biogeograficas. Invest Zool Chil 2 75-86
1960 Regiones biogeograficas de Chile Invest Zool Chil 6 15-49
MAYR, E , E G LINSLEY, AND R L USINGER
1953 Methods and principles of systematic zoology McGraw-Hill Book Co , N Y , 336 p
MCCOY, F
1888 Prodromus of the zoology of Victoria. *In* Natural history of Victoria J Ferres, Gov Printer, Melbourne [Not seen]
MCKENZIE, M K
1964 Tuna bait Kai Moana, Food of the waters 3 11-15
MEDINA, W
1965 Los peces marinos conocidos del Callao con referencia de su distribución geografica. Biota 5:245-287.
MIRANDA RIBEIRO, A DE
1915 Fauna Brasiliense—Peixes (Eleutherobranchios aspirophoros)—Physoclisti Arch Mus Nac Rio de J 17, 833 p
1918 Fauna Brasiliense (Peixes) Tomo V Eleutherobranchios aspirophoros, Physoclisti Arch Mus Nac Rio de J 21, 227 p
MITO, S
1958 Eggs and larvae of *Cololabis saira* (Brevoort) (Scomberesocidae) [In Jpn] *In* K Uchida S Imai, S Mito, S Fujita, M Ueno, Y Shojima, T Senta, M Tahuku, and Y Dotu, Studies on the eggs, larvae, and juveniles of Japanese fishes, ser. 1, p 22-23. Fish. Dep. Fac. Agric., Kyushu Univ
MOREAU, E.
1881. Histoire naturelle des poissons de la France. Paris, 697 p.
MORELAND, J.
1963. Native sea fishes. Nature in New Zealand. A H & A. W. Reed, Wellington, 64 p
MOSELEY, H. N.
1879. Notes by a naturalist on the "Challenger," being an account of various observations made during the voyage of H. M. S. "Challenger" round the world, in the years 1872-1876. MacMillan & Co., Lond , 620 p
MUKHACHEVA, V. A.
1960 Some data on the breeding, development and distribution of saury. [In Russ.] Tr. Inst Okeanol. 41:163-174.
MUNRO, I. S. R.
1938 Handbook of Australian fishes. Aust. Fish. Newsl. 16(1):15-18.
MURRAY, J., AND J. HJORT.
1912 The depths of the ocean MacMillan and Co., Lond , 821 p
NELSON, J. S
1976. Fishes of the world. Wiley, N Y , 416 p
NICHOLS, J. T , AND C. M. BREDER, JR.
1928 An annotated list of the Synentognathi with remarks on their development and relationships. Zoologica (N Y.) 8:432-448.
ORTON, G. L.
1964 The eggs of scomberesocid fishes. Copeia 1964.144-150.
PARIN, N. V.
1960. The area of the saury (*Cololabis saira* Brev.—Scomberesocidae, Pisces) and the influence of oceanographic factors upon its distribution. [In Russ.] Doklady Akad Nauk USSR 130:649-652.
1961. Principles of classification of flying fishes (Oxyporhamphidae and Exocoetidae). [In Russ.] Tr. Inst. Okeanol. Akad Nauk USSR 43:92-183.
1963. Results of studying pelagic ichthyofauna of the Pacific and Indian oceans by use of electric light for attracting fishes. [In Russ.] Tr. Inst. Okeanol. 62:128-144.
1967a. Chapters 1, 2, 3, 5. *In* V. G. Kort (editor in chief), Biology of the Pacific Ocean, 7(3). Acad. Sci. Inst. Oceanol. USSR. [In Russ.]
1967b. Diurnal variations in the larval occurrence of some oceanic fishes near the ocean surface. [In Russ.] Okeanologia 7 148-156
1968a. Scomberesocidae (Pisces, Synentognathi) of the eastern Atlantic Ocean. Atlantide Rep. 10:275-290.
1968b. Ichthyofauna of the epipelagic zone. [In Russ.] Nauka, Moscow, 185 p.
1969a. Die Fischwelt der Hochsee. Ideen des Exakten Wissens, p 713-722
1969b Ichthyological investigations during the fourth cruise of R.V *Akademik Kurchatov* in southeastern Pacific [In Russ] Vopr Ikhtiol 56:575-579
1973 Scomberesocidae. *In* J C Hureau and Th. Monod (editors), CLOFNAM 1, Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, p. 261-262 UNESCO, Paris
1975 Change of pelagic ichthyocoenoses along the section at the equator in the Pacific Ocean between 97° and

155 W. [In Russ.] Akad. Nauk USSR, Tr. Inst. Okeanol. 102:313-334.

PARIN, N. V., AND A. P. ANDRIASHEV
1972. Ichthyological studies during the 11th cruise of the R.V. *Akademik Kurchatov* in the southern Atlantik Ocean. [In Russ.] Vopr. Ikhtiol. 76:960-964.

PARIN, N. V., AND N. N. GORBUNOVA
1964. On the reproduction and development of some Indian Ocean synentognathous fishes (Beloniformes, Pisces) (based on materials of the r/s "Vityaz" expeditions). [In Russ.] *In* T. S. Rass (editor), Fishes of the Pacific and Indian Oceans, biology and distribution. Tr. Inst. Okeanol. 73:224-234.

PENRITH, M. J.
1967. The fishes of Tristan da Cunha, Gough Island and the Vema Seamount. Ann. S. Afr. Mus. 48:523-548.

PHILLIPPS, W. J.
1921. Notes on the edible fishes of New Zealand, with a record of fishes exposed for sale in Wellington during 1918. N. Z. J. Sci. 4:114-125.

POZZI, A. J., AND L. F. BORDALE.
1935. Cuadro sistemático de los peces marinos de la Republica Argentina. An. Soc. Cient. Argentina 120:145-191.

QUIJADA B., B.
1912. Catálogo de la colección de los peces chilenos i estranjeros del Museo Nacional. Bol. Mus. Nac. Chile 4:69-109.
1913. Catálogo ilustrado descriptivo de la colección de peces chilenos i estranjeros. Bol. Mus. Nac. Chile 5:1-139.

RAFINESQUE, C. S.
1810. Caratteri di alcuni nuovi generi e nuovi specie di animali e Piante della Sicilia. San Filippo, Palermo, 105 p.

RAMIREZ HERNANDEZ, E., AND A. GONZALEZ PAGES
1976. Catálogo de peces marinos mexicanos. Secretaria de Industria y Comercio, Subsecretaria Nacional de Pesca, 462 p.

RASS, T. S. (editor).
1967. Fishes of the open waters. Akad. Nauk SSSR, Inst. Okeanol., 275 p.

REED, E. C.
1897. Catálogo de los peces chilenos. Ann. Universidad, p. 1-24.

REGAN, C. T.
1911. The classification of the teleostean fishes of the order Synentognathi. Ann. Mag. Nat. Hist., Ser. 8, 7:327-335.
1916. British Antarctic ("Terra Nova") Expedition, 1910. Larval and post-larval fishes. Br. Mus. (Nat. Hist.) Zool. 1:125-156.

RENDAHL, H.
1921. The fishes of the Juan Fernandez Islands. *In* C. Skottsberg (editor), The natural history of Juan Fernandez and Easter Island, 3:49-58. Almqvist & Wiksells Boktryckeri-A.-B., Uppsala.

RICHARDSON, J.
1842. Report on the present state of the ichthyology of New Zealand. Rep. 12th Meet. Br. Assoc. Adv. Sci. 1842:12-30.

ROBERTSON, D. A.
1975. A key to the planktonic eggs of some New Zealand marine teleosts. Fish. Res. Div., Wellington, Occas. Publ. 9:1-19.

RODRIGUEZ-RODA, J.
1960. Nombres vulgares y cientificos de las principales especies comerciales de peces de la region sudatlántica española. Invest. Pesq. 17:109-125.

ROEDEL, P. M.
1953. Common ocean fishes of the California coast. Calif. Dep. Fish Game, Fish Bull. 91, 184 p.

ROSEN, D. E.
1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bull. Am. Mus. Nat. Hist. 127:217-267.

SAEMUNDSSON, B.
1949. Marine Pisces. Zoology of Iceland 4, part 72:1-150.

SANZO, L.
1940. Sviluppo embrionale a larva appena schiusa di *Scomberesox saurus* (Flem.). Mem. R. Comm. Talassogr. Ital. 276, 6 p.

SAUSKAN, V. I., AND G. N. SEMENOV
1969. Results of research on *Scomberesox saurus* in the north-east Atlantic in 1968. Annal. Biol. (for 1968), 25:250-252.

SAUVAGE, M. H.
1891. Histoire physique, naturelle et politique de Madagascar. Vol. 16, Histoire naturelle des poissons. l'Imprimerie Nationale, Paris, 543 p.

SCHAEFER, M. B., AND J. W. REINTJES.
1950. Additional records confirming the trans-Pacific distribution of the Pacific saury, *Cololabis saira* (Brevoort). Pac. Sci. 4:164.

SCHLESINGER, G.
1909. Zur Phylogenie und Ethologie der Scombersociden. Verh. Zool.-Bot. Gesellsch. Wien 59:302-339.

SCHREINER, C., AND A. DE MIRANDA RIBEIRO.
1902. A collecção de peixes do Museu Nacional do Rio de Janeiro. Arch. Mus. Nac. Rio de Janeiro 12:1-41.

SCHULTZ, L. P.
1940. The Pacific saury, *Cololabis saira* Brevoort, from the North Pacific Ocean. Copeia 1940:270.

SCORDIA, C.
1936. Intorno alla accertata presenza dello *Scomberesox saurus* (Walb.) nel Mediterraneo. Boll. Zool. 7:217-220.
1938. Sulla specie di *Scomberesox* del Medio Tirreno. Boll. Zool. 9:17-18.

SCOTT, T. D.
1962. The marine and fresh water fishes of South Australia. W. L. Hawes, Gov. Printer, Adelaide, 338 p.

SCOTT, T. D., C. J. M. GLOVER, AND R. V. SOUTHCOTT.
1974. The marine and freshwater fishes of South Australia. 2d ed. A. B. Jaems, Gov. Printer, South Australia, 392 p.

SHERRIN, R. A. A.
1886. Handbook of the fishes of New Zealand. Wilsons and Horton, Printers, Auckland, 307 p.

SIVERTSEN, E.
1945. Fishes of Tristan da Cunha with remarks on age and growth based on scale readings. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937-38, 12:1-44.

SMITH, J. L. B.
1949. The sea fishes of southern Africa. Central News Agency, Ltd., Cape Town, South Africa, 550 p.
1953. The sea fishes of southern Africa. Revised. Central News Agency, Ltd., Cape Town, South Africa, 580 p.
1955. The fishes of Aldabra, part 1. Ann. Mag. Nat., Hist., Ser. 12, 8:304-312.

SMITH, M M
1975 Common and scientific names of the fishes from southern Africa J L B Smith Inst Ichthyol Spec Publ. 14(part I):1-178

STEAD, D G
1906 Fishes of Australia A popular and systematic guide to the study of the wealth within our waters Wm Brooks and Co , Ltd , Sydney. 278 p
1908 The edible fishes of New South Wales Their present importance and their potentialities W A Gullick, Gov Printer, Sydney, 117 p

STORER, D H
1853 A history of the fishes of Massachusetts Mem Am Acad Arts Sci (New Ser) 5 49-92, 122-168, 257-296
1867 A history of the fishes of Massachusetts (Reprinted from Mem Am Acad Arts Sci) Cambridge and Boston, Welch & Bigelow and Dakin & Metcalf. 284 p

SUDA, A
1973 Development of fisheries for non conventional species J Fish Res Board Can 30:2121-2158

SUPINO, F
1935 Osservani sul *Behone acus* Natura, Revista di Scienze Naturali Milano 26 1-9

TE WINKEL, L E
1935 A study of *Mistichthys luzonensis* with a special reference to conditions correlated with reduced size J Morphol 58 463-535

TORTONESE, E
1970 Fauna d'Italia X Osteichthyes (Pesci ossei) Parte prima Edizioni Calderini Bologna, 565 p

UEYANAGI, S , AND S DOI
1971 Spawning area of sauries in the eastern Pacific Div Pelagic Fish Resourc , Far Eastern Fish Res Lab Ecological study of offshore pelagic fish resources, p 17-21

UEYANAGI, S , G IMAKOJI, AND S DOI
1972 Ecological studies on the resources of the offshore pelagic fishes Div Pelagic Fish Resour , Far Seas Fish Res Lab , p 15-19

UEYANAGI, S , K MORI, AND Y NISHIKAWA
1969 Tuna spawning ground and potential resources of pelagic fishes based on distribution of larvae Div Pelagic Fish Resour , Far Seas Fish Res Lab , p 1-9

VALENCIENNES, A
1846 *In* Cuvier and Valenciennes, Histoire naturelle des poissons P Bertrand, 18, 505 p

VLADYKOV, V D , AND D E MCALLISTER
1961 Preliminary list of marine fishes of Quebec Nat Can (Que) 88 53-78

WHITE, E R
1921 Illustrated catalogue of the fishes of South Australia G Hassell & Son, Adelaide. 208 p
1923 The fishes of South Australia R R E Rogers, Gov. Printer, Adelaide, 243 p.

WHEELER, A
1975 Fishes of the world An illustrated dictionary Macmillan Publ Co , N Y , 366 p

WHEELER, A C , AND M N MISTAKIDIS
1960 The skipper (*Scomberesox saurus*) in the southern North Sea and the Thames estuary Nature (Lond) 188 334-335

WHITLEY, G P
1948 A list of the fishes of Western Australia W Aust Fish Dep Fish Bull 2 1-35
1962 Marine fishes, vol 2 Jacaranda Press, Brisbane, p. 145-288
1968 A check-list of the fishes recorded from the New Zealand region Aust Zool 15 1-102

WILHELM, O E , AND A L HILLOT
1957 Peces y pesces de la Isla de Pascua (notes ictiologicas de Chile) Bol Soc Biol Concepcion, Chile, Bol 32 139-152

WISNER, R L
1977 FAO species identification sheets, fish, area 31 (W Central Atlantic), Scomberesocidae, p 1-2

WYRTKI, K
1964 The thermal structure of the eastern Pacific Ocean Dtsch Hydrogr. Z Ergän, A, no. 6 6-84
1967 Circulation and water masses in the eastern equatorial Pacific Ocean Int J Oceanol Limnol 1 117-147

ZILANOV, V K , AND S I BOGDANOV
1969 Results of research on *Scomberesox saurus* in the north-eastern Atlantic in 1968 Annal Biol (for 1968) 25 252-255

EFFECTS OF TEMPERATURE AND SALINITY ON PRODUCTION AND HATCHING OF DORMANT EGGS OF *ACARTIA CALIFORNIENSIS* (COPEPODA) IN AN OREGON ESTUARY

JOHN KENNETH JOHNSON[1]

ABSTRACT

Experimental results indicate that induction of dormancy in *Acartia californiensis* eggs is temperature dependent and occurs below 15° C in two ways: 1) Cold adapted females spawn true resting eggs which exhibit major differences in hatching and survival rates from nondormant eggs under similar conditions. 2) Nondormant eggs spawned above 15° C may become dormant and have short-term viability at temperatures below 15° C. Salinity does not induce dormancy.

Hatching results of field-collected resting eggs at naturally occurring temperature-salinity combinations demonstrate that termination of dormancy is also primarily temperature dependent. Salinity, however, regulates rate and success of hatching. In addition, heavy naupliar mortality occurs following hatching at low salinities. Substantial hatching must occur in the field over much of the year. Since subsequent survival and population growth depends on the presence of favorable temperature and salinity conditions, naupliı which hatch during the low salinity winter and spring months in Yaquina Bay must be lost. This phenomenon is viewed as a "leaky" population diapause.

Resting eggs were also demonstrated for *Epilabidocera longipedata* and *Eurytemora affinis*, an occurrence previously undescribed in the literature.

Resting eggs have been known to be a common adaptation in freshwater zooplankton since the turn of the century (see reviews in Hutchinson 1967 and Elgmork 1967). The existence of a comparable resting egg phase in the life cycle of marine neritic species was postulated for many years to explain the seasonal disappearance of coastal species from the water column (e.g., Fish and Johnson 1937; Barlow 1955; Conover 1956). Preliminary evidence of marine calanoid resting eggs was first reported by Sazhina (1968) for the species *Pontella mediterranea* and *Centropages ponticus*.

Zillioux and Gonzalez (1972) conclusively demonstrated with laboratory and field evidence that the seasonal disappearance of *Acartia tonsa*, a common coastal species, coincides with the production of overwintering eggs as water temperatures fall below 14.5 C. Subsequent research has shown that egg dormancy is an important adaptation in many boreal and temperate neritic calanoids, including both summer-fall species (e.g., *Tortanus forcipatus*, Kasahara, Onbé, and Kamigaki 1975; *Labidocera aestiva*, Grice and Gibson 1975) and winter-spring species (e.g., *A. clausi*, Uye and Fleminger 1976; *C. abdominalis*, Pertzova 1974). Egg dormancy probably enables most coastal species to survive periods during which conditions in the water are unfavorable.

Environmental factors such as temperature or photoperiod usually govern the induction of dormancy in arthropods (Lees 1955). Both the adult and/or the egg may be responsive to adverse environmental changes. Egg dormancy may result from a physiological response of the female to a changing milieu which modifies the eggs. Conversely, dormancy may develop as a response of the egg to changes in conditions as it sinks through the water column into the bottom sediments. There is evidence for both mechanisms in marine copepods. Zillioux and Gonzalez (1972) demonstrated that the production of resting eggs by *A. tonsa* is a response of the female to low temperatures. However, Uye and Fleminger (1976) examined egg development of four *Acartia* species (including *A. tonsa*) from southern California waters at various temperature and salinity combinations and concluded that dormancy is primarily a response of the egg to the milieu. Their results led them to hypothesize that exposure of the eggs to abnormal salinities may be necessary to induce dormancy in at least two of the species of *Acartia*. Once buried in the sediments,

[1]School of Oceanography, Oregon State University, Corvallis, OR 97331

Manuscript accepted March 1979
FISHERY BULLETIN VOL. 77, NO. 3, 1980

egg dormancy is maintained by low oxygen levels (Kasahara, Onbé, and Kamigaki 1975; Uye and Fleminger 1976). Light is also required to break dormancy in at least one species, *A. clausi* (Landry 1975a; Uye and Fleminger 1976).

Further work is required to fully demonstrate the factors regulating dormancy in coastal calanoids. A localized summer-fall population of *A. californiensis* in Yaquina Bay, Oreg., affords an excellent opportunity to examine this phenomenon, since the entire winter-spring period is passed in the resting egg stage. A field research program provided data for the correlation of population dynamics with temperature and salinity. Laboratory experiments were carried out to determine the relative importance of temperature and salinity in the formation and subsequent hatching of dormant eggs of *A. californiensis*. Analysis of the data provides additional information on the role of the female versus that of the egg in development of dormancy.

Acartia californiensis, a newly described species (Trinast 1976), is useful for comparative studies in egg dormancy since it displays close affinities to *A. tonsa* in both physiological and morphological features. Earlier studies in Yaquina Bay (Zimmerman 1972; Frolander et al. 1973; Johnson and Miller 1974; Miller et al. 1977) identified the species as *A. tonsa* in the belief that it represented a smaller, ecophenotypic variant of the larger, offshore, *A. tonsa* present in the northerly Davidson Current during the winter months. Furthermore, the unidentified "*Acartia* sp. I" discussed by Uye and Fleminger (1976) has been recently identified as *A. californiensis* Trinast by A. Fleminger,[2] thus permitting comparison of egg dormancy in northern and southern populations.

METHODS

The seasonal population cycle of *A. californiensis* in Yaquina Bay was determined by the collection of plankton samples twice weekly at Stations 21, 29, 39, 45, and 57 (Figure 1). Sampling was done from June to November in 1972-74 with a Clark-Bumpus sampler (mouth diameter 12.5 cm) fitted with a 112 μm mesh net which quantita-

[2]Abraham Fleminger, Scripps Institution of Oceanography, University of California, La Jolla, CA 92037, pers. commun. June 1978.

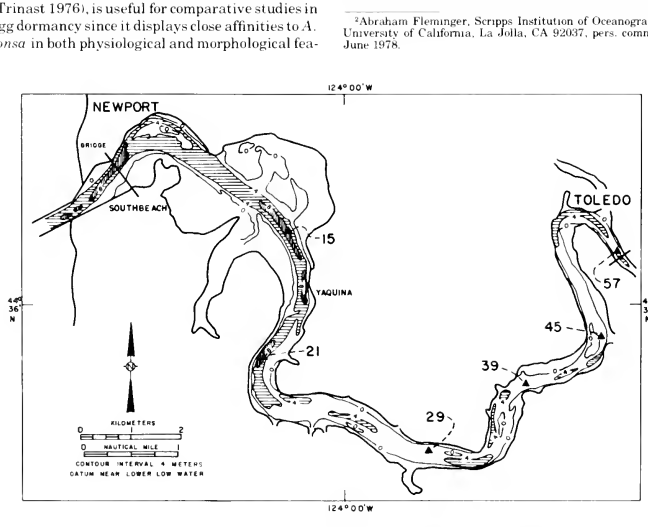


FIGURE 1.—Sampling stations for *Acartia californiensis* in Yaquina Bay estuary, Oreg.

tively retained all copepodite stages. Tows were oblique in a stepwise pattern from just above the bottom to near surface at midchannel. A calibrated propeller flowmeter in the mouth of the net was used to estimate the quantity of water filtered. Volumes filtered were typically 5-6 m^3. Temperature measurements and salinity samples were taken at the surface and just above the bottom at each station. Salinities were later determined by inductive salinometer in the laboratory.

RESTING EGG PRODUCTION

October Experiment

Adult *A. californiensis* were collected at Station 39 (Figure 1) on 9 October 1975, using a 239 μm mesh net towed slowly at 1-2 m depth. Surface temperature and salinity were 14.9 C and 26.8‰, respectively. Laboratory cultures were established the same day by sorting 50 female and 25 male adults into each of eight 1,400 ml beakers containing 1,200 ml of Millipore[3]-filtered water (25‰). Water temperature increased to room temperature (16.8 C ±0.3) during this time. Upon completion of sorting, all newly spawned eggs were removed by screening and discarded. Replicate cultures were then transferred to water baths and maintained at 21, 17, 13, and 9 C (±0.1). Continuous overhead lighting (low level) was used throughout the experiment.

Adults were fed daily with a mixture of *Pseudoisochrysis* sp., *Isochrysis galbana*, and *Thalassiosira fluviatilis* at a concentration of approximately 200,000-250,000 cells · ml^{-1}. Phytoplankton cultures were maintained in log-phase at 16.8 C. Viability of the algal species over the temperature range of 9-21 C was not determined but assumed to be unimportant in the experimental design since *A. californiensis* adults were provided excess food daily. In addition, adult mortality was moderately low (estimated at ~20%) during the acclimation and spawning period with similar losses observed in all cultures. Thus, selection of adults in response to temperature or food during the acclimation period was not likely a factor in influencing the type of egg spawned.

After the third day of adult acclimation, accumulated eggs were removed by gentle screening. The eggs were used in a preliminary experiment on hatching success which differed from the main experiment in that fewer hatching temperatures were tested for eggs produced at each acclimation temperature.

The main experiment was established with eggs collected on the eighth day of adult acclimation. Maximum egg age ranged from 5 days at 9 C to 1 day at 21 C because of differences in egg development rate as a function of temperature. Eggs from replicate cultures at a given acclimation temperature were mixed together in a Petri dish for sorting by pipette. Water temperature was maintained as close as possible to acclimation temperature during sorting. Depending on the number of eggs available, 10-15 replicate batches of 50 eggs each were placed in small 6 ml Petri dishes (1 cm depth, 3.5 cm in diameter) containing 4-5 ml of Millipore-filtered water (25‰). Dish bottoms were marked in a grid for ease in counting at 25× with a dissecting scope. Salinity changes caused by evaporation were prevented by floating the small dishes in transparent, tightly capped 100 ml beakers filled with 80 ml of water (also 25‰). Two and usually three or more replicate dishes of 50 eggs were then placed in each of five water baths at 21, 17, 13, 9, and 5 C, respectively. This procedure was repeated for eggs produced at all four acclimation temperatures (21, 17, 13, 9 C), resulting in an experimental design (Table 1) using over 2,500 eggs.

Hatching success was determined daily by making separate counts of eggs remaining and hatched nauplii. Nauplii were captured and removed daily with a pipette. Every 5th day, water was changed by pipette with minimum disturbance to the remaining eggs. Unhatched eggs were maintained at the experimental temperature well past the time expected for normal hatching (Table 2) and then transferred to a favorable temperature (21 C) to determine subsequent hatching success.

November Experiment

Animals collected on 4 November 1975 at Station 39 (12° C, 21‰) were used to repeat the experiment at the prevailing field temperature and salinity conditions. By this time, the field population of *A. californiensis* was greatly reduced and egg production was assumed to be primarily resting eggs. Females were kept at 12 C and 21‰ during transfer to the laboratory and subsequent culturing. Eggs were collected on the fourth day of

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

TABLE 1.—Production of resting eggs and summer eggs by female *Acartia californiensis* collected for the October experiment, 9 October 1975. Hatching results at each temperature-salinity combination expressed as a mean percentage for two and usually three replicates of 50 eggs each.

Cumulative time (days)	Event	Conditions																					
0	Collection	14.9 °C, 28.8‰, Station 39, Yaquina Bay, Oreg.																					
0-1	Preliminary acclimation	14.9 °C, 25‰, temperature increasing to 16.8 °C)																					
5-9	Spawning	21 °C						17 °C						13 °C						9 °C			
	Main experiment	25‰						25‰						25‰						25‰			
	Adjusted time	Hatching temp. (°C)	21	17	13	9	5	21	17	13	9	5	21	17	13	9	5	21	17	13	9	5
9	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1		92	84	70	5	3	98	93	39	8	2	12	7	1	0	0	30	1	0	0	0	0
11	2		96	100	79	12	6	99	99	63	17	2	18	11	3	1	0	42	25	0	0	0	0
12	3	Results in cumulative percentage hatched	97		89	23	8	99	100	66	25	4	42	15	4	1	0	53	27	2	0	0	0
13	4		97		90	32	9	99		80	28	5	65	23	4	1	0	66	29	2	0	0	0
14	5		97		90	35	9	99		87	31	5	75	32	4	1	0	72	31	3	0	0	0
17	8				90	34	9			71	34	5	91	54	4	1	0	82	47	3	0	0	0
20	11				90	35	9			71	35	5	97	76	4	1	0	89	64	3	0	0	0
24	15					35	9				35	5	97	92		1	0	89	79		0	0	0
29	20						9					5	97	99			0	89	87			0	0
129	120						9					5					0					0	0
		Warming (21 °C) on day		11	15	120		11	15	120						11	15	120				11	15	120
		Subsequent hatch (%)		0	39	0		19	61	0						91	96	30				76	81	71
		Final hatch (%)	97	100	90	74	9	99	100	90	96	5	97	99	96	97	30	89	87				79	81	71

spawning at 12 °C and sorted into replicate batches of 50 eggs each. Hatching rate and success were determined at 21, 17, 15, 13, 9, and 5 °C in 25‰ water. Other procedures were as described above.

TABLE 2.—Nondormant egg development time for *Acartia tonsa* and *A. clausi* as a function of temperature, and time that unhatched eggs of *A. californiensis* were initially held at the same experimental hatching temperature (October experiment).

Temp (°C)	Egg duration (days)		Incubation time (days)	
	A. tonsa[1]	*A. clausi*[2]	*A. californiensis* 21-17 °C[3]	*A. californiensis* 13-9 °C
21	1.3	1.2	5	20
17	1.9	1.5	3	20
13	3.1	2.2	11	11
9	8.5	3.8	15	15
5	45.1		120	120

[1]Data based on prediction of Belehradek function (Zilioux and Gonzalez 1972).
[2]Data from experimental observations of Landry (1975b).
[3]Temperatures at which *A. californiensis* eggs were spawned.

HATCHING OF RESTING EGGS COLLECTED IN THE FIELD

A series of preliminary experiments (J. K. Johnson, unpubl. data) had demonstrated that resting eggs of *A. californiensis* and *A. clausi* occur in similar numbers in the surface sediments in the vicinity of Station 39 (Figure 1). Unfortunately, the resting eggs of the two species are not distinguishable from each other on the basis of diameter, shape, or color. Therefore, the following hatching experiments include resting eggs of both species at unknown ratios. Much information and insight were gained in spite of this serious experimental limitation.

Salinity Experiment

Resting eggs were obtained by collecting mud with an Eckman-Birge grab 500 m upstream of Station 39 on 7 February 1976 during low tide. The upper 1-2 cm of sediments were saved for later screening. Temperature and salinity values near the bottom were 9.8 °C and 4.1‰. An accompanying series of plankton tows from Station 21 to Station 45 verified that no copepodite stages of *A. californiensis* were present in the upper estuary, as expected from earlier field work. *Acartia clausi* was present in low numbers only at Stations 21 and 29 ($<50 \cdot m^{-3}$). It does occur at Station 39 during January to April but only at extremely low densities (ca. $5\text{-}20 \cdot m^{-3}$) during periods of high tides (Zimmerman 1972). Thus, few recently spawned eggs were likely to be present in the sediments collected at Station 39.

Sediment samples were maintained at field temperature (10 °C) during transport to the

laboratory and storage in the dark for 1 mo. Resting eggs were removed (10 March 1976) by first sieving the sediments through 119 μm and 64 μm mesh nylon screens. This size fraction was diluted with water (5‰), stirred well, and allowed to settle. Approximately 5-6 ml of the surface sediments were then slowly introduced by pipette onto the surface of 8-10 ml of a 2.8 M aqueous sucrose solution (suggested by Brewer 1964) in each of several 15 ml centrifuge tubes. Following centrifugation at 1,000-2,000 rpm for 1-2 min, resting eggs of *Acartia* spp. and other species (including calanoids, harpacticoids, and rotifers) were removed by pipette from the water-sucrose interface. These eggs were nearly free of detritus. A thorough rinse with Millipore-filtered water (5‰) on a 64 μm mesh screen removed the sucrose solution. No evidence of egg distortion or crushing was found to result from the high osmotic gradient. In contrast, eggs centrifuged from surface sediments collected in September collapsed under similar conditions.

Following rinsing, *Acartia* spp. eggs were sorted from extraneous material and then mixed in a Petri dish in 5‰ water. Approximately 2,000-2,500 eggs were collected in 3-4 h of work. Most eggs had a clear, outer layer which surrounded a dark inner mass, similar to that reported for resting eggs of *Labidocera aestiva* (Grice and Gibson 1975). A moderate number of eggs (ca. 10-20%), lacking the clear layer, had ended diapause and progressed to various stages of embryogenesis. These latter eggs were most likely undergoing development in the uppermost sediment layer when collected in February. Only those eggs with a clear outer layer were used for the experiment.

Thirty-five resting eggs were sorted by pipette into each of 43 small (6 ml) Petri dishes. The accompanying water at 5‰ (ca. 1 ml) was removed by pipette. Water of 11 salinities, ranging from 0‰ (glass distilled) to 23.5‰, was then added to batches of three or more of these dishes. Three complete rinses of appropriate salinity were added and removed before the final addition. The Petri dishes with eggs were maintained at 17° C (±0.1°) in covered beakers as described above. Continuous overhead lighting was provided. Water was replaced every 5th day.

Egg and naupliar counts were usually made daily. There were some 2-day intervals. Naupliar mortality between observations was also recorded. Salinity was increased in some replicates at various time intervals to determine viability of remaining dormant eggs. Hatched nauplii were captured and reared to copepodite stages (17° C, 20‰) for positive species identification because of uncertainty in distinguishing between *A. californiensis* and *A. clausi* nauplii.

Salinity and Temperature Experiment

The effect of salinity on hatching of resting eggs was later evaluated at three more temperatures (15°, 12.5°, 10° C) to obtain hatching rates at temperature-salinity combinations normally present in the upper estuary during later fall and early spring months. Resting eggs were obtained by 2.8 M sucrose centrifugation of sediments collected at Station 39 on 18 February 1978. Water conditions were 9.4° C and 7.6‰. Transport to the laboratory, storage (2 days), screening, centrifuging, and sorting were all done at 10° C. Two or three replicates of 35 resting eggs (clear-layer type) were prepared at 5‰, 10‰, 15‰, and 25‰ for each temperature. Other details were as described in the salinity experiment.

Additional beakers were established at all temperature-salinity combinations to determine the approximate ratio of *A. californiensis* to *A. clausi* resting eggs by rearing hatched nauplii to copepodites. These beakers contained the unsorted mixture of resting eggs of *Acartia* spp. and other accompanying species plus detritus which collected at the water-sucrose interface during centrifugation. The number of eggs in each beaker was variable, ranging between 50 and 250. Hatched nauplii were removed daily and transferred to new beakers at the next higher salinity (+5‰) and temperature (+2.5° C). Salinity and temperature were increased every 5th day to maxima of 15° C and 25‰. This was done to improve survival while avoiding abrupt change. Ratios were determined when most individuals had molted into the copepodite stages. Hatched nauplii from the Petri dishes were also reared when practical to the copepodite stages.

RESULTS

Field Population Cycle

The twice-weekly sampling program was adequate to follow the seasonal cycle and distribution of *A. californiensis* in upper Yaquina Bay. Only field data for 1972 are presented, since the population had similar cycles in 1973 and 1974.

The population range extended from Station 21 to Station 57 (Figure 1) during the months of maximum abundance (August, September). However, few adults or copepodites were ever present at these two boundary stations. The bulk of the population was restricted to the region from the vicinity of Station 29 to Station 45 with an approximate population center at Station 39. Location of the population center was not static at Station 39 because of the diurnal tides. It was occasionally found during sampling cruises downstream at Station 29 or upstream at Station 45.

The maximum density of *A. californiensis* observed on a given sampling day was considered to be the center of the population, regardless of location in the upper estuary. A plot of maximum density values for adults and copepodites I-V on successive sampling dates represents the seasonal cycle of the population (Figure 2). The persistent alternation between peak abundance of adults and copepodites is evidence that successive generations remain distinct. The fact that successive density estimates at the population center show such a refined feature creates confidence that the approach is valid.

Physical factors such as temperature and salinity can be correlated with population growth and decline on the premise that optimal conditions at a given time coincide with maximum spatial population abundance. Thus, given the population concentration from Station 29 to Station 45, mean temperature and salinity data (surface and bottom) at Stations 29 and 45 (Figure 3) can be considered to represent the lower and upper range of the most favorable physical conditions possible for growth of *A. californiensis* in the estuary at any given time. The means closely reflect the entire water column (4-6 m depth) as the upper estuary is well-mixed (Type D; Burt and McAlister 1959) during June to October with a maximum vertical gradient of 1-2° C and 1-3‰. The fortnightly periodicity seen in the data is an effect of the progression of tidal stage upon twice-weekly sampling conducted during the fixed hours from 0900 to 1400. A sharp decline in salinity during late November and December (Figures 3, 4) occurred as a result of the beginning of the winter rains and resulting heavy runoff. Salinity in the upper estuary remained extremely low (Figure 4) until the following spring when rainfall and runoff decreased, and the salt wedge intruded up the bay.

The appearance in early June of *A. californiensis* copepodites occurred when water temperatures were between 15° and 18° C and salinities were 10-20‰ (Figure 3). Abundance gradually increased throughout June and much of July. A population explosion began in late July and continued throughout August, a period when water temperature and salinity were 17°-22° C and 20-31‰. The subsequent population crash in early

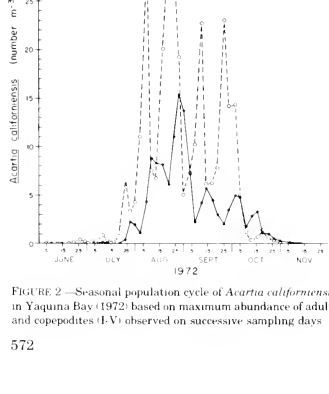


FIGURE 2.—Seasonal population cycle of *Acartia californiensis* in Yaquina Bay (1972) based on maximum abundance of adults and copepodites (I-V) observed on successive sampling days

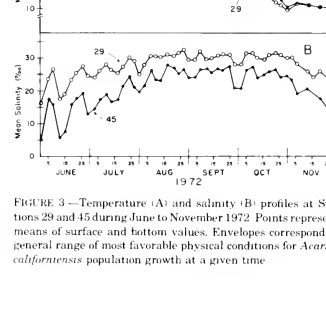


FIGURE 3.—Temperature (A) and salinity (B) profiles at Stations 29 and 45 during June to November 1972. Points represent means of surface and bottom values. Envelopes correspond to general range of most favorable physical conditions for *Acartia californiensis* population growth at a given time

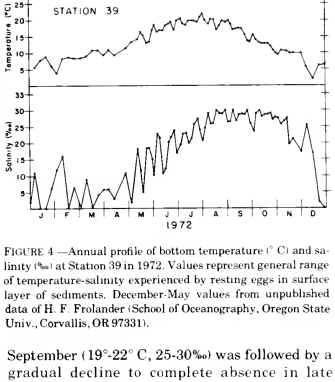


FIGURE 4.—Annual profile of bottom temperature (° C) and salinity (‰) at Station 39 in 1972. Values represent general range of temperature-salinity experienced by resting eggs in surface layer of sediments. December-May values from unpublished data of H. F. Frolander (School of Oceanography, Oregon State Univ., Corvallis, OR 97331).

September (19°-22° C, 25-30‰) was followed by a gradual decline to complete absence in late November. Production of nondormant eggs remained important throughout September, as evidenced by the large numbers of copepodites present in the water column. However, copepodite recruitment nearly ceased by the first week of October, indicating that most reproduction was likely in the form of resting eggs. Some nondormant eggs were still produced, however, since a small pulse of copepodites was seen in the last half of October. Mean temperature had dropped to 13°-15° C at the end of September when recruitment began to fail. The population was gone by December at a field temperature of 9°-10° C. Salinity remained high, relatively stable, and presumably in a favorable range (25-30‰) during the September-October decline and disappearance. Salinity began to drop only in November when *A. californiensis* was essentially absent from the water column.

Resting Egg Production

October Experiment (Preliminary)

Eggs collected on the third day of adult acclimation to 21°, 17°, 13°, or 9° C had essentially similar hatching rates and cumulative hatching success at a given temperature to eggs collected on the eighth day. The similarity in results indicates that *A. californiensis* can shift from production of nondormant eggs to production of resting eggs in only 1-2 days in response to a significant lowering of water temperature. The absence of significant changes in egg hatching time and viability with increasing adult acclimation time demonstrates that the eggs produced were not adversely affected by the rapid change in water temperature (2-4 h) at the beginning of the acclimation period. The only effect observed was an initially lower fecundity in those females which experienced the largest temperature changes (16.8° C to 21° C or 9° C). In these latter two cultures, fecundity increased with acclimation time.

October Experiment (Main)

Hatching successes of eggs spawned over the range of 9°-21° C give evidence that the type of egg spawned is a function of ambient temperature (Figures 5, 6). Experimental conditions and results are also summarized in Table 1. Females which spawned at 21° and 17° C (typical midsummer temperatures at Stations 29-45) produced nondormant summer eggs that developed normally at 21° and 17° C (Figure 5A, B). Development time was <36 h with nearly 100% of the eggs hatching. Lower hatching temperatures (13°, 9°, 5° C), however, were found to arrest development of summer eggs which then entered dormancy. The incidence of dormancy increased with decreasing hatching temperature: eggs spawned at 17° C had a total hatching success of 71% at 13° C compared with 35% at 9° C (Figure 5C, D) and 5% at 5° C (Figure 6). Thus dormancy in summer eggs is a response to low, unfavorable temperatures and may occur independently of parental influence.

More than adequate time (Table 2) was allowed in these experiments for "normal" hatching, given the prediction from a Bělehradek function for *A. tonsa* (Zillioux and Gonzalez 1972) and the observed development rates for *A. clausi* (Landry 1975b). A subsequent increase in water temperature to 21° C broke the dormancy of the summer eggs previously incubated at 13° and 9° C (Figure 5C, D). Hatching resumed within a few hours at a rate similar to that observed earlier at 17° and 21° C (Figure 5A, B).

Mortality of summer eggs spawned at 17° C was low during the 11- and 15-day "holding" periods at 13° and 9° C (Figure 5C, D), evidenced by a final hatching success of 90-96% after increase to 21° C. However, dormant 21° C summer eggs experienced substantial mortality during the 15-day

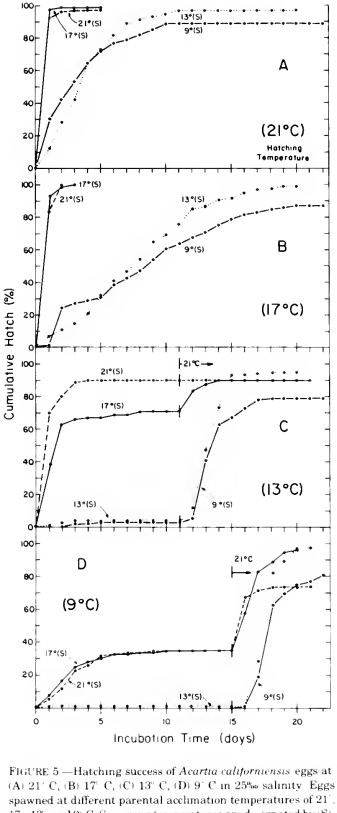


FIGURE 5.—Hatching success of *Acartia californiensis* eggs at (A) 21° C, (B) 17° C, (C) 13° C, (D) 9° C in 25‰ salinity. Eggs spawned at different parental acclimation temperatures of 21°, 17°, 13°, and 9° C. Spawning temperatures are designated by (S). Hatching temperatures increased to 21° C on day 11 (C) and 15 (D).

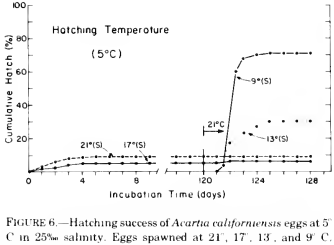


FIGURE 6.—Hatching success of *Acartia californiensis* eggs at 5° C in 25‰ salinity. Eggs spawned at 21°, 17°, 13°, and 9° C. Spawning temperature is designated by (S). Hatching temperature increased to 21° C on day 120.

holding period at 9° C (Figure 5D). Only 60% of the remaining eggs hatched following the temperature rise, resulting in a cumulative total of 74%.

Long-term survival of summer eggs was negligible at low temperature (120 days at 5° C). Only 1% of the 17° C spawned eggs subsequently hatched at 21° C. Many of the eggs remained normal in appearance, being greenish yellow, throughout the 120-day period. However, within 3-4 days at 21° C, nearly all dormant summer eggs had disintegrated. Most eggs probably died long before day 120, given the high mortality of 21° C spawned eggs after 15 days at 9° C (Figure 5D).

In comparison with dormant summer eggs, the eggs spawned at 13° and 9° C appear to be true resting eggs with an overwintering capacity. The final cumulative hatch of the two types of eggs was similar over the temperature range of 21°-9° C. However, there were major differences in hatching rates between eggs spawned at 9°-13° C and 17°-21° C at all five hatching temperatures tested (Figures 5, 6). For example, the 9°-13° C spawned eggs required 11 and 20 days at 21° and 17° C, respectively, to reach the final comparable hatch of 87-99%. This period was 10-20 times longer than that required by summer eggs.

While none of the 9°-13° C spawned eggs exhibited dormancy at 17° and 21° C, few hatched at the lower incubation temperatures. Only 3-4% hatched at 13° C in contrast to 70-90% for the summer eggs. Likewise only 0-1% at 9° C and 0% at 5° C hatched versus 35% and 5-10%, respectively, for the summer type (Figures 5D, 6).

Temperature was increased to 21° C on days 11, 15, and 120 for the 13°, 9°, and 5° C hatching treatments, respectively. Hatching resumed in all cases at a rate and with success similar to those of summer eggs. However, a 1-1.5 day delay occurred in each case before hatching resumed (Figures 5C,

D; 6). This delay, absent from the data on hatching of summer eggs following an identical temperature increase, is evidence of a difference in the character of dormancy in the two types of eggs.

Resting egg mortality was low during the 11- and 15-day incubation periods (Figures 5C, D). Approximately 96% and 80% final hatch occurred for eggs spawned at 13° and 9° C, respectively. The somewhat lower viability of the 9° C spawned eggs was also seen at hatching conditions of 17° and 21° C (Figure 5A, B). Survival remained high (71%) for 9° C spawned eggs following 120 days incubation at 5° C (Figure 6). In comparison, the 13° C spawned eggs had only 30% survival. This substantial difference in survival may not be important, as opposite results were found for the hatching success of resting eggs from the preliminary experiment under equivalent conditions (9° C spawn = 45%; 13° C spawn = 60% survival). The implication is that resting egg survival is about 50% after a 4-mo dormant period.

In most cases, hatching success at a given temperature was similar for eggs of a given type (summer or resting) spawned at different temperatures (Figures 5, 6). For example, 21° C spawned eggs displayed little difference in hatching time or success from 17° C spawned eggs at 21°, 17°, and 9° C. The discrepancy in summer egg hatching times and cumulative totals at 13° C was likely an experimental artifact since it was absent in the results of the preliminary experiment. Uye and Fleminger (1976) similarly reported finding no difference in hatching success at a given temperature for *A. clausi* eggs spawned at 17.5° and 13.5° C.

A notable exception to this pattern occurred for 13° and 9° C spawned eggs which were incubated at 21° and 17° C (Figure 5A, B). In both cases, the 9° C spawned eggs had a higher initial rate of hatching than 13° C spawned eggs. By day 5, this was reversed, and the rate for 13° C spawned eggs exceeded that for 9° C spawned eggs. It is possible that some of the 9° C spawned eggs had an enhanced metabolic rate relative to 13° C spawned eggs, caused by cold acclimation (suggested by Landry 1975b). Uye and Fleminger (1976) also found evidence that cold-acclimated eggs of *A. tonsa*, spawned at 6.5° C, tended to hatch more quickly at temperatures below 12.5° C than eggs spawned at 17.5° C.

Long-term exposure to low temperature resulted in abnormal development for some resting eggs. This was only seen in 5-12% of the 9° C spawned eggs incubated at 9° or 5° C for 120 days. Abnormalities of the newly hatched NI nauplii ranged from mild to strong structural deformation. Some nauplii possessed an enlarged labrum or fused appendages (e.g., second antennae and mandible); some lacked appendages of one side of the body. One nauplius had two severe constrictions which divided the body into three lobes. Many of the abnormal nauplii were alive, though weak, at the time of observation. Uye and Fleminger (1976) also reported finding deformed NI nauplii and postulated that osmotic stress from abnormal salinities may have caused the deformations. In this case, however, deformation must have resulted from long exposure to low temperatures, since salinity was maintained at a favorable concentration of 25‰.

November Experiment

Different hatching results were obtained using eggs spawned by females acclimated at the November field temperature of 12° C. Hatching patterns (Figure 7) indicate that both nondormant and resting eggs were produced concurrently in the population. This is in contrast to production of resting eggs only in the 13° and 9° C treatments of females collected in October for the main experiment (Figures 5, 6). The evidence for the presence of both egg types is the two different hatching rates which occurred at summer temperatures (Figure 7). The initial hatching at 21° and 17° C occurred within the first day, similar to summer eggs at identical temperatures (Figure 5A, B).

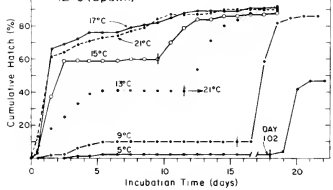


FIGURE 7.—Hatching success of *Acartia californiensis* eggs spawned by November-collected females at the field acclimation temperature of 12° C. Hatching temperatures varied from 21° C to 5° C; salinity was 25‰. Temperature increased to 21° C (denoted by vertical line) after variable periods of incubation below 17° C.

However, after reaching a total of 61-66% hatched, the rate decreased sharply with hatching continuing at a low, constant rate to a final total of 90-91% at day 16. The latter pattern resembles that found for resting eggs (13°, 9° C spawn) hatched at summer temperatures (Figure 5A, B). A comparable 56% hatch also occurred at 15° C within the first 2.5 days. However, development then ceased until temperature was increased to 21° C. Thus, at all three temperatures, approximately 60% of the eggs behaved as nondormant summer eggs, while the remaining 40% had characteristics of resting eggs.

Dormancy increased from 40% at 15° C to 98% at 5° C (Figure 7), presumably as a result of dormancy induced by low temperatures in otherwise nondormant eggs. This result is similar to that seen for summer eggs hatching at the lower temperatures (Figures 5C, D; 6).

Egg viability during short- and long-term dormancy was determined by increasing temperature to 21° C on days 9, 11, 15, and 102 for the 15°, 13°, 9°, and 5° C hatching treatments, respectively (Figure 7). Mortality was low during the 9-15 day incubation period at 15°, 13°, and 9° C with a final cumulative hatch of 85-91%. In contrast, only 45% of the dormant eggs incubated for 102 days at 5° C completed development into NI nauplii following temperature elevation. Probably few dormant summer-type eggs survived the long holding period at 5° C, given that about 40% of the eggs exhibited characteristics of resting eggs in 21°, 17°, and 15° C water. This conclusion is supported by the high mortality (99-100%) found for summer eggs incubated at 5° C for 120 days in the October experiment (Figure 6).

Hatching of Resting Eggs Collected in the Field

Salinity Experiment

The effect of salinity on hatching of resting eggs collected from field sediments was initially determined at 17° C, a temperature favorable for egg hatching (Figure 5) and population growth of *A. californiensis* (Figures 2, 3). Results presented in Figure 8 are the combined data for both *A. californiensis* and *A. clausi*, since their respective overwintering eggs could not be separated.

Hatching occurred at all salinities from 23.5‰ to 0‰ (Figure 8). Rates decreased only slightly with decreasing salinity from 23.5‰ (37% •day^{-1}) to 12.5‰ (31% •day^{-1}; day 2.5). Final hatch in this salinity range was 91-96%. Initial hatching rates below 12.5‰ decreased markedly, ranging from 26% •day^{-1} at 10‰ to 1.8% •day^{-1} at 0‰. These latter rates, while reduced, were nevertheless substantial over a 2-wk span. Overall hatching success by day 12 was 21%, 61%, and 88% of the resting eggs at 0‰, 5‰, and 8‰, respectively. Furthermore, hatching was continuing, even in freshwater, as indicated by the slopes of the curves, when the experiment was ended. In comparison, resting eggs of *Tortanus forcipatus* do not hatch in freshwater when temperature is favorable (Kasahara, Onbé, and Kamigaki 1975).

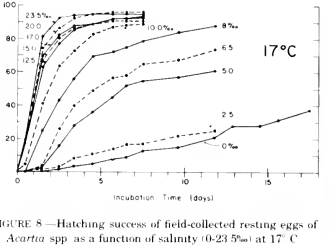


FIGURE 8.—Hatching success of field-collected resting eggs of *Acartia* spp. as a function of salinity (0-23.5‰) at 17° C.

The retarding effect of low salinity on hatching appeared to be limited to the actual process of naupliar escapement from the eggshell. Embryogenesis proceeded at similar rates (subjective observations) in all treatments (0-23.5‰), apparently independent of external salinity concentration. Developmental arrest, when present, normally occurred after the fully formed nauplius was visible inside the eggshell.

Exposure to low salinity (0-5‰) for varying periods during dormancy was not fatal for the majority of prehatch nauplii. In each case, high rates of successful hatching (Figure 9) quickly followed a salinity increase to 23.5‰. However, prehatch mortality of "holding" nauplii increased substantially as a function of salinity reduction when compared at equal time. This is seen in a final hatch of 79%, 71%, and 59%, following a salinity increase (day 12) to 23.5‰ for eggs previously incubated at 5‰, 2.5‰, and 0‰, respectively. Thus, an approximate 10% increase in mortality occurred for each 2.5‰ decrease in salinity below 5‰.

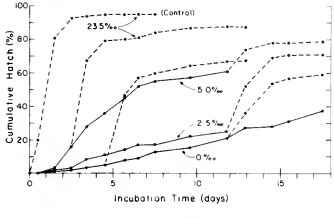


FIGURE 9.—Hatching success and viability ("holding" success) of *Acartia* spp at 23.5‰ salinity (dashed line), following variable periods of exposure to low salinities (0-5‰) at 17° C. Initial hatching results at 23.5‰ used as a control.

Prehatch mortality also increased gradually with increasing time at low salinity (Figure 9). Total hatch in 23.5‰ after 2.5 and 12 days exposure to 5‰ was 87% and 79%, respectively. This corresponds to a loss of 8% viability within the first 2.5 days and 16% by day 12 as measured against the control hatch at 23.5‰. A comparable trend and loss rate occurred for 0‰ salinity-exposed eggs later hatching in 23.5‰. Losses in viability on days 4.5 and 12 were 27% and 36%, respectively.

The cause of death in prehatch nauplii is unknown, but presumably is related to exhaustion of energy reserves during the holding period. Mortality may also be partially caused by increased osmotic stress at progressively lower salinities. Eggs that died prior to hatching usually disintegrated with 2-3 days at 17° C.

The occurrence of naupliar mortality during the actual hatching process or within the following 24 h substantially increased at salinities below 12.5‰. This is shown by a comparison of cumulative hatching and subsequent naupliar mortality as a function of salinity on days 4.5 and 12 (Figure 10). Naupliar losses on day 4.5 increased from 1% at 12.5‰ to 73% at 5‰. Mortality was 100% at 2.5‰ and 0‰. Corresponding losses were 5-10% higher on day 12, indicating that survival following hatching decreased gradually with increasing time required to hatch.

Observation of hatching success in salinities below 8‰ revealed that many nauplii died during the hatching process or immediately thereafter. At 5‰, many of the dead nauplii were found only partially freed from the cracked-open eggshell. More typically, the nauplius was found lying next to the empty eggshell, indicating immediate death followed hatching. Some nauplii successfully hatched, but never unrolled. Others escaped the outer egg membrane, but died while still inside the osmotically swollen inner membrane. Eggs which had obviously cracked open prior to full development, and exhibiting an extrusion of cellular debris, were also occasionally seen at 0‰ and 2.5‰.

The specific effects of salinity on resting eggs of *A. californiensis* cannot be separated from those of *A. clausi* in the results above. However, supportive evidence indicates that eggs of both *Acartia* species hatched at substantial rates at all salinities from 0‰ to 23.5‰. For instance, 41% of the copepodites reared from viable nauplii during the course of the experiment were *A. californiensis*. While there is no information on possible differential mortality during culturing, an estimate of 41% is probably low for the percentage of *A. californiensis* resting eggs in the experiment. Initial rearing conditions actually favored *A. clausi*, a species that is much more euryhaline in Yaquina Bay. Thus, even when considering the lowest hatching rate at 0‰ salinity on day 17 (Figure 7), it is clear that the 37% hatch (100% mortality) had to include at least some *A. californiensis* eggs. Approximately another 40-50% of the holding eggs at 0‰ were no longer viable. Therefore, one can conclude that prolonged exposure of *A. californiensis* resting eggs to extremely low salinities at 17° C will result in death for the majority, whether it be from prehatch or posthatch salinity stresses.

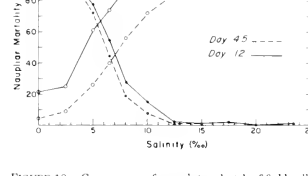


FIGURE 10.—Comparison of cumulative hatch of field-collected resting eggs of *Acartia* spp (open circles) and subsequent mortality within first 24 h (solid circles) at salinities from 0‰ to 23.5‰. Results on day 4.5 (dashed line) and 12 (solid line) based on 3 replicates of 35 eggs at each salinity.

Salinity and Temperature Experiment

The effect of salinity on hatching of resting eggs was reexamined (Figure 11) at lower temperatures (15°, 12.5°, 10° C) which are marginal to unfavorable for growth of the *A. californiensis* population (Figures 2, 3). The basic intent was to determine, if possible, the lowest termperature-salinity combination(s) which could break diapause of the overwintering eggs.

General hatching patterns as a function of salinity (Figure 11) were similar to those observed at 17° C (Figure 8) in that hatching rates decreased with decreasing salinity at all three temperatures.

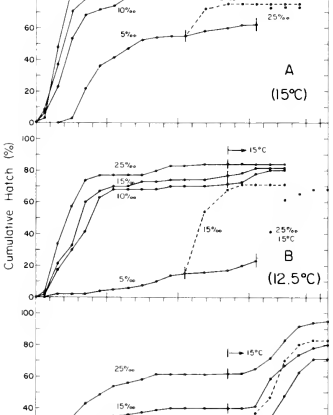


FIGURE 11.—Hatching rate and cumulative success of field-collected resting eggs of *Acartia* spp. in various salinities at: (A) 15° C, (B) 12.5° C, and (C) 10° C. Lower temperatures and salinities increased to 15° C and 15‰, respectively, after variable periods of incubation to determine short-term "holding" success at suboptimal conditions.

Lower temperatures similarly reduced hatching rates and final hatches at a given salinity. However, the interactive effect of temperature with salinity increased nonlinearly as temperature decreased (Figure 11). As a result, the percentage of resting eggs remaining in a state of dormancy became progressively larger with decreasing temperature.

Few *Acartia* spp. resting eggs incubated at 15° or 12.5° C (Figure 11A, B) failed to terminate diapause and begin development. As observed at 17° C, embryogenesis progressed to the final prehatch stage, apparently independent of external salinity. Subsequent holding time (pseudodormancy) depended on the interaction of salinity and temperature. For example, hatching rates at 25‰, 15‰, and 10‰, while progressively reduced, were still relatively high with very little dormancy evident. The majority of eggs hatched within 3-4 days. Final hatches were high and in a narrow range from 91-81% at 15° C to 84-71% at 12.5° C. However, some prehatch holding did occur at these higher salinities since an increase in salinity (10‰ to 15‰; Figure 11A) or temperature (12.5° to 15° C; Figure 11B) resulted in an additional 5-9% hatch.

Prehatch holding at 5‰ was increasingly more important with decreasing temperature (Figure 11A, B). At 15° C, the 5‰ hatching rate was greatly reduced, but was still substantial and similar to that seen at 17° C (Figure 8). Over 50% hatch was attained by day 7, with hatching continuing to 62% on day 15. Viability of the remaining eggs (38%) was low since a salinity increase to 25‰ only yielded an additional 11% hatch. In comparison, prehatch holding in 5‰ at 12.5° C (Figure 11B) was pronounced since the hatching rate was reduced to only 1-2% $\cdot$ day^{-1}. However, the holding dormancy was only a temporary condition since hatching continued throughout the 15-day exposure to 5‰. Viability was reduced but still substantial as seen in a final hatch of 68% in 25‰. Thus, hatching in 5‰ water at 12.5° C or 15° C would have probably continued until all eggs either hatched or died from exhaustion of energy reserves during the holding state.

Hatching results at 10° C (Figure 11C) were considerably different from results at 12.5° C and 15° C in that dormancy was a major factor at all salinities. For example, final hatches (prior to changes) at 25‰, 15‰, and 10‰ were 61%, 40%, and 33%, respectively. This represented a 23-38% increase in dormancy from that at 12.5° C. Persis-

tence of dormancy at 5‰ was nearly complete with only 2% hatch achieved.

The nature of continued dormancy at 10° C (Figure 11) was unusual in that both diapause and prehatch holding cooccurred. Dormant eggs remaining on day 13 at 25‰, 15‰, and 10‰ appeared to still be in diapause since no apparent change in coloration or internal structure occurred during incubation at 10° C. A subsequent 1-3 day delay in hatching after temperature was increased to 15° C is also indicative that the eggs were still in diapause (as seen in the October temperature experiments; Figure 5C, D). Copepodites reared from nauplii hatched at 15° C in the 25‰, 15‰, and 10‰ treatments after day 13 were found to be mainly *A. californiensis* (87%; $n = 23$). As a result, most of the eggs remaining in diapause at 10° C over the 25-10‰ range were probably those of *A. californiensis*.

In contrast to results at 25-10‰ (Figure 11C), diapause did not persist in eggs of either *A. californiensis* or *A. clausi* exposed to 5‰ at 10° C. The reason for this difference is not known. While only 2% of the eggs had hatched, nearly all remaining eggs had broken diapause and were in the final prehatch holding state many days before the temperature increase on day 13. The difference in the nature of dormancy is reflected by the rapid hatching rate with no delay period following the temperature increase. In spite of high viability seen after day 13, the termination of diapause and the failure to hatch at 5‰ and 10° C demonstrate that egg survival of both *Acartia* species was short-term and limited by available energy reserves.

Posthatch naupliar mortality within the first 24 h as a function of salinity at 15°, 12.5°, and 10° C was very similar to that shown for 17° C (Figure 10). The mortality range in 15‰, 10‰, and 5‰ water, for example, was 2-7%, 12-22%, and 80-100%, respectively, as compared with 2%, 15%, and 78% at 17° C. Typically, the percent survival decreased slightly at a given salinity as temperature decreased. Therefore, at salinities 10‰, survival was high with mortality primarily increasing with decreasing temperature. Below 10‰, the NI naupliі experienced increasingly heavy mortality primarily as a function of decreasing salinity.

Additional information on hatching behavior and fraction of *A. californiensis* resting eggs were obtained by a comparison of the proportions of copepodites reared from nauplii which initially hatched from unsorted egg mixtures at each temperature-salinity combination (Table 3). Hatching at the most optimal of the given experimental conditions for both species (15° C, 25-15‰) resulted in copepodite proportions of 51% and 62% *A. californiensis*. A similar percentage (54%) was observed at 12.5° C and 25‰. As these estimates are based on independent rearing treatments, it is reasonable to conclude that roughly 55% of the field resting eggs were those of *A. californiensis*. This result corresponds very well with other estimates of percent abundance determined in earlier unpublished experiments.

Copepodites of *A. californiensis* were absent in the cultures which initially hatched in 10‰ and 5‰ at both 15° and 12.5° C (Table 3). As nearly all resting eggs were previously found to terminate diapause at these lower salinities (Figure 11A, B), the absence of *A. californiensis* is the result of mortality during either prehatch holding or subsequent naupliar stages. This is verified, in part, by the increasing mortality of NI nauplii (*Acartia* spp.) below 12.5‰ (Figure 10). Furthermore, hatching rate differences over the range of 25-10‰ were small as shown in Figure 11A, B. For example, at 15° C, a total hatch of 86% and 81% was observed at 15‰ and 10‰, respectively. Yet, the proportion of *A. californiensis* copepodites was 62% at 15‰ and 0% at 10‰ (Table 3). Similarly at 12.5° C, only 6% survived to copepodites when hatched at 15‰ as compared with 54% at 25‰. It must be reemphasized that the temperature and salinity values referred to here and in Table 3 are hatching conditions only. Rearing was under more favorable conditions (see Methods). Therefore, as

TABLE 3.—Proportion of *Acartia californiensis* and *A. clausi* copepodites that survived following hatching at 12 temperature-salinity combinations. Temperature and salinity levels for rearing to copepodite stages were gradually increased to 15° C and 25‰ to increase posthatch survival (see text for further details).

	10° C			12.5° C			15° C		
Salinity (‰)	n	*A. clausi* (%)	*A. calif* (%)	n	*A. clausi* (%)	*A. calif* (%)	n	*A. clausi* (%)	*A. calif* (%)
5	0	0	0	4	100	0	0	0	0
10	16	100	0	24	100	0	119	100	0
15	15	100	0	71	94	6	40	38	62
25	235	100	0	28	46	54	183	49	51

diapause was ended at all salinities at 12.5°-15° C, it is evident that individuals hatching from resting eggs of *A. californiensis* exposed to salinities below 15‰ experienced early death, even when temperature and salinity were increased to more favorable levels following hatching. As a result, these data can be used to define minimal hatching conditions for growth to maturity and can be correlated with the fall disappearance and summer repopulation of *A. californiensis* in Yaquina Bay.

Acartia californiensis copepodites were absent at all salinities at 10° C (Table 3). Absence over the range of 25-10‰ was probably the result of continued diapause of the resting eggs of *A. californiensis*, as previously demonstrated (Figure 11C). Some of the latter eggs may have hatched at 25‰, given the likelihood of a 62% hatch (Figure 11C) and an estimated resting egg ratio of 55% (Table 3). However, egg hatching at 15‰ and 10‰ (40-33%; Figure 11C) can be completely attributed to *A. clausi* since it composed ca. 45% of the resting eggs.

An unrelated but important observation concerns the hatching of a few *Epilabidocera longipedata* Sato (= *E. amphitrites* McMurrick) 10° C, 25‰) and *Eurytemora affinis* (Poppe) (10 -15 C, 5-25‰) from the unsorted resting egg mixtures used to obtain *Acartia* spp. ratios. Identification was made at the late copepodite stages. Neither species has previously been reported as possessing a resting egg stage. Both species are absent at Station 39 in Yaquina Bay during the winter months, insuring that the eggs were in diapause when collected.

DISCUSSION

Environmental Conditions Resulting in Egg Dormancy

Many shallow-water neritic and estuarine calanoid species with multivoltine life cycles are now known to survive long periods of adverse environmental conditions by facultative production of resting eggs. Field observations and laboratory results have demonstrated that this is true for *A. californiensis* in Yaquina Bay. After 4 or 5 successive generations with substantial recruitment (July-September 1972; Figure 2), the planktonic population declined rapidly and was gone by mid-November. The failure of recruitment in early October coincided with a decline in temperature below 15° C. Salinity remained relatively high and stable at 25-30‰, during the population disappearance, implying temperature dependence for the production of resting eggs (Figures 3, 4).

Experimental results confirmed the hypothesis that diapause in *A. californiensis* eggs is essentially a response of the spawning females to low temperatures, similar to that shown for *A. tonsa* (Zillioux and Gonzalez 1972), *Tortanus forcipatus* (Kasahara, Onbé, and Kamigaki 1975) and possibly *Pontella meadi* (Grice and Gibson 1977). The shift from summer egg to resting egg production occurred between 15° and 13° C (Figure 5), a temperature range comparable to that observed in the field. Salinity was not a factor, since it was maintained at a constant and favorable level (25‰) in all treatments. Food quantity and quality were excluded as factors by daily providing the adults with an ample ration consisting of three prey species. Photoperiod is known to influence induction of diapause in some cladocerans (cf.: *Daphnia magna*, Bunner and Halcrow 1977; *D. pulex*, Stross and Hill 1965). However, it was eliminated as a possible extrinsic factor by the use of continuous lighting.

The production of overwintering eggs was most likely initiated by changes, possibly hormonal, within the female in response to the extrinsic stimulus of adverse temperature. Extensive research on the physiology of insects has confirmed the regulation of diapause by hormones (e.g., Lees 1955; Sláma et al. 1974). Moreover, Carlisle and Pittman (1961) found differences in forebrain neurosecretions between summer and overwintering "dormant" CV copepodites of *Calanus finmarchicus* that resembled diapause in insects. Watson and Smallman (1971) similarly reported significant changes in small tissue patches in the head region of the cyclopoid copepod, *Diacyclops navus*, that correlated with induction and cessation of diapause. Since dormant egg production can be rapidly induced in *A. californiensis* by lowering water temperature, it is probable that the controlling physiology is somewhat different.

The temperature-dependent maternal role in the induction of dormancy in *A. californiensis* eggs is contrary to results reported by Uye and Fleminger (1976) for *A. californiensis* (= *Acartia* sp. I) in a southern California lagoon. They concluded that egg dormancy in *A. californiensis* must occur independently of maternal influence since 90-100% of the eggs hatched at all temperatures in the annual field range (10°-25° C). Expo-

sure to salinity extremes was suggested as a possible cause of induced dormancy. Their conclusion, however, was based upon the hatching behavior of *A. californiensis* eggs which were spawned at 17.5° C. On the basis of my observations (Figure 5), these latter eggs were most likely all summer eggs which exhibited increasing dormancy below 10° C. It is likely that female-induced dormancy would have been observed if a spawning temperature below 15° C had been used.

Summer eggs of *A. californiensis* possess the capacity for short-term facultative dormancy when exposed to temperature below 15° C (Figure 5). Hatching resumed within hours following temperature elevation above 15° C. This type of arrested development, temporarily induced by unfavorable external conditions and ended with the return of a favorable environment, represents a state of "quiescence" as the term is used by Andrewartha (1952), Lees (1955), and Wigglesworth (1972) for other arthropod groups.

Quiescence of nondormant eggs at low temperatures is probably a characteristic of most calanoid species which inhabit highly variable environments such as estuaries and lagoons (Uye and Kasahara 1978). For example, Uye and Fleminger (1976) found that *A. tonsa* eggs which were spawned at 17.5° C (a favorable temperature) exhibited dormancy only at 7.5° and 5° C, a result which they also demonstrated for *A. californiensis*. In both species, survival during dormancy at 7.5° and 5° C was of short duration, since no hatching occurred following a temperature elevation after 28-30 days. The lack of long-term viability is supporting evidence that the respective eggs were in a quiescent state and not true resting eggs.

In each species, the percentage of quiescent summer eggs increased as temperature decreased. However, quiescence occurred at significantly higher temperatures in eggs of *A. californiensis* from Yaquina Bay, shown by a 35% hatch at 10° C (Figure 5D), as compared with 100% for the southern California population (Uye and Fleminger 1976). Both sets of eggs were spawned at 17° or 17.5° C. The considerable difference in thermal induction of quiescence in summer eggs may represent a genetic gradient reflecting the latitudinal separation of the two populations. Selection for quiescence in this warmwater species is probably more important in Oregon estuaries because of lower water temperatures (2°-22° C range) and longer winters (Figure 4). Less of a selective advantage would exist in California estuarine and lagoonal waters with a narrower annual range of 10°-25° C (from Uye and Fleminger 1976). Furthermore, any genetic gradient caused by differential selective pressures would be reinforced by the localized confinement of populations within estuaries or lagoons, which must greatly reduce gene flow.

The adaptive value of quiescence may be greatest in temperate estuaries (e.g., Yaquina Bay) where eggs in the bottom sediments typically experience large variations in temperature over successive tidal cycles. However, since viability of *A. californiensis* eggs in the quiescent state at low temperatures is limited to 1-2 mo, as shown above (Figures 5, 6) and in figure 5F of Uye and Fleminger (1976), the importance of quiescence in overwintering must be considered negligible.

Summer and resting eggs of *A. californiensis* may cooccur in equal proportions in the cumulative spawn at temperatures below 15° C as shown in the November experiment with females which spawned at their field acclimation temperature of 12° C (Figure 7). Zillioux and Gonzalez (1972) reported similar spawning results for *A. tonsa* females at acclimation temperatures of 9°, 11.4°, and 14.5° C. In each case, approximately 50-60% of the eggs were nondormant and hatched. It is not known from these data if the same female can produce both egg types at once. It is likewise not known if a female producing only resting eggs at lower temperatures can switch back to summer egg production if temperature increased above 15° C. These questions will need to be resolved by observations on individual females.

There is an apparent discrepancy between the November and October observations. Females collected from 15° C water in October produced exclusively dormant eggs when rapidly cooled to 13° or 9° C. It is reasonable to have expected all of the November eggs spawned at the field acclimation temperature of 12° C to have also been dormant, given the October results. Perhaps there are effects upon the initiation of dormant egg production from both low temperature to which a female is fully acclimated and from sudden temperature reductions. Response to the latter stimulus would protect against more than usually moderate cooling rates in the fall. Given normal field conditions, however, there probably is considerable variation between individual females in the population in the threshold temperature which induces dormant egg production. As a result, cooccurrence of both egg types would be expected during a significant

portion of the fall population decline. Some field evidence of this is seen in the weak pulse of copepodites found in late October, indicating that substantial hatching did occur below 15° C earlier in the month (Figures 2, 3).

Termination of Diapause and Population Reappearance

Hatching of field-collected resting eggs of *Acartia* spp. at various temperature-salinity combinations indicates that termination of dormancy is essentially temperature dependent. However, hatching rates and survival are regulated by salinity. My conclusions with respect to *A. californiensis*, based on the often disparate observations, are:

1. Approximately half of the experimental resting eggs were *A. californiensis*.

2. Embryogenesis and hatching occurred at all salinities tested at 12.5 -15° C (5-25‰) and 17° C (0-23.5‰).

3. Diapause persisted at 10° C over the range of 10-25‰, while embryogenesis occurred at 5‰.

4. Hatching was retarded at low salinities, particularly below 10‰.

5. Developmental arrest in low salinity normally occurred at the last stage of embryogenesis. Viability of "holding" prehatch nauplii was limited to 1-2 mo, depending on temperature.

6. Mortality losses were increasingly severe below 10‰ for hatched nauplii and substantial for "holding" eggs.

7. No nauplii survived to reach the copepodite stages at salinities below 15‰ at 12.5° C or at any salinity at 10° C.

Exposure to low temperatures over a prolonged period (comparable to cold stratification for seeds of many temperate, deciduous plants) is unnecessary for the release of diapause in *A. californiensis* overwintering eggs. This is probably the normal condition for most *Acartia* species (see Zillioux and Gonzales 1972 and Uye and Fleminger 1976). It is not universal, however, as the resting eggs of *Pontella meadi*, a neritic species, require a chilling period before hatching can occur (Grice and Gibson 1977). A similar requirement is implied but not conclusively demonstrated for resting eggs of *P. mediterranea* and *Centropages ponticus* (Sazhina 1968). Overwintering eggs of some freshwater calanoids (e.g., *Diaptomus oregonensis*, Cooley 1971) are also known to require exposure to low temperatures prior to hatching.

While chilling is unessential for termination of diapause in *A. californiensis* resting eggs, some effects from chilling were observed. For example, all field-collected eggs were found to commence development at 12.5° C (Figure 11) while laboratory-spawned eggs terminated diapause only above 15° C (Figures 5, 6, 7). Thus, exposure to winter temperatures appears to lower the hatching threshold. The time required is unknown but may be quite short. Newly spawned resting eggs initially hatched at very low rates when incubated at 17° or 21° C (Figure 5). However, after 11 and 14 days of chilling, hatching rates approached those of summer eggs when placed in favorable temperatures.

The "holding" phenomenon induced by low salinities represents a second type of short-term quiescence in *A. californiensis* resting eggs. It differs from the temperature-induced quiescent state seen in summer eggs in that quiescence does not set in until the final stage of embryogenesis. In addition, salinity-induced quiescence is much weaker, since hatching continues at low levels. In these aspects, it closely resembles the dark inhibition of summer egg hatching of *A. clausi* (Landry 1975a). Development of *A. clausi* eggs in the dark proceeds to the prehatch naupliar stage before "holding" occurs. Viability of eggs in this darkness-induced quiescence is even shorter than that of *A. californiensis* in low salinity-induced quiescence. Uye and Fleminger (1976) and my own data (unpubl.) indicate it is 20-25 days.

On the basis of field collections in February, experimental results and the temperature and salinity cycles in the field, significant hatching (or embryogenesis followed by holding) of resting eggs must occur over much of the year. Low oxygen tension in sediments, while important in inhibiting hatching (Kasahara, Onbé, and Kamigaki 1975), is probably not a critical factor, since resting eggs in the bottom sediments are continually exposed to oxygenated surface layers by turbulence and erosion. Termination of diapause does not always coincide with the presence of favorable environmental conditions for naupliar growth. Those resting eggs which undergo development and then either enter quiescence or hatch during the winter-spring months, a period of very low salinities, must be soon lost. Such a process would partially account for the seasonal decline in resting egg numbers in the sediments with

increasing time as observed by Kasahara, Uye, and Onbé (1975). Successful repopulation is possible at any point in spring that daily mean salinity is in excess of 10‰, which usually occurs in early June. Production of resting eggs in the annual cycle of *A. californiensis* is thus viewed as a "leaky" population diapause that is consistent with the opportunistic nature of estuarine copepod species.

It is possible that the leaky character of the diapause is retained because of the occasional success of the early-hatching portion of the population in years with early termination of winter rains. In those years, this fraction of the population would be strongly favored by the end of the growing season because of its early start. In years with prolonged spring rains, the late-hatching fraction would be favored. Variations in the weather cycle, thus, may prevent development of absolute and restrictive requirements for termination of diapause.

ACKNOWLEDGMENTS

I wish to thank Charles B. Miller for the invaluable assistance provided in discussions of the experimental results and in reviewing the manuscript. Special thanks are also due Abraham Fleminger and Peter Sertic for their aid in resolving the taxonomic status of *Acartia* populations from Los Penasquitos Lagoon, La Jolla, Calif., and upper Yaquina Bay.

This research was supported by the Oregon State University Sea Grant College Program, under the Office of Sea Grant (NOAA), #04-6-158-44094.

LITERATURE CITED

ANDREWARTHA, H. G.
1952. Diapause in relation to the ecology of insects. Biol. Rev. (Camb.) 27:50-107.

BARLOW, J. P.
1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. Biol. Bull. (Woods Hole) 109:211-225.

BREWER, R. H.
1964. The phenology of *Diaptomus stagnalis* (Copepoda: Calanoida). The development and the hatching of the egg stage. Physiol. Zool. 37:1-20.

BUNNER, H. C., AND K. HALCROW.
1977. Experimental induction of the production of ephippia by *Daphnia magna* Straus (Cladocera). Crustaceana 32:77-86.

BURT, W. V., AND W. B. MCALISTER.
1959. Recent studies in the hydrography of Oregon estuaries. Res. Briefs Fish Comm. Oreg. 7(1):14-27.

CARLISLE, D. B., AND W. J. PITMAN.
1961. Diapause, neurosecretion and hormones in Copepoda. Nature (Lond.) 190:827-828.

CONOVER, R. J.
1956. Oceanography of Long Island Sound, 1952-1954. VI. Biology of *Acartia clausi* and *A. tonsa*. Bull. Bingham Oceanogr. Collect., Yale Univ. 15:156-233.

COOLEY, J. M.
1971. The effect of temperature on the development of resting eggs of *Diaptomus oregonensis* Lill. (Copepoda: Calanoida). Limnol. Oceanogr. 16:921-926.

ELGMORK, K.
1967. Ecological aspects of diapause in copepods. *In* Symposium on Crustacea, p. 947-954. Mar. Biol. Assoc. India, Symp. Ser. 2.

FISH, C. J., AND M. W. JOHNSON.
1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. J. Biol. Board Can. 3:189-322.

FROLANDER, H. F., C. B. MILLER, M. J. FLYNN, S. C. MYERS, AND S. T. ZIMMERMAN.
1973. Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. Mar. Biol. (Berl.) 21:277-288.

GRICE, G. D., AND V. R. GIBSON.
1975. Occurrence, viability and significance of resting eggs of the calanoid copepod *Labidocera aestiva*. Mar. Biol. (Berl.) 31:335-337.
1977. Resting eggs in *Pontella meadi* (Copepoda: Calanoida). J. Fish. Res. Board Can. 34:410-412.

HUTCHINSON, G. E.
1967. A treatise of limnology. Vol. II. Introduction to lake biology and the limnoplankton. Wiley, N.Y., 1115 p.

JOHNSON, J. K., AND C. B. MILLER.
1974. Dynamics of isolated plankton populations in Yaquina Bay, Oregon. Proc. 3d Annu. Tech. Conf. Estuaries Pac. Northwest, p. 27-35. Oreg. State Univ. Eng. Exp. Stn. Circ. 46.

KASAHARA, S., T. ONBÉ, AND M. KAMIGAKI.
1975. Calanoid copepod eggs in sea-bottom muds. III. Effects of temperature, salinity and other factors on the hatching of resting eggs of *Tortanus forcipatus*. Mar. Biol. (Berl.) 31:31-35.

KASAHARA, S., S. UYE, AND T. ONBÉ.
1975. Calanoid copepod eggs in sea-bottom muds. II. Seasonal cycles of abundance in the populations of several species of copepods and their eggs in the Inland Sea of Japan. Mar. Biol. (Berl.) 31:25-29.

LANDRY, M. R.
1975a. Dark inhibition of egg hatching of the marine copepod *Acartia clausi*. Giesbr. J. Exp. Mar. Biol. Ecol. 20:43-47.
1975b. Seasonal temperature effects and predicting development rates of marine copepod eggs. Limnol. Oceanogr. 20:434-440.

LEES, A. D.
1955. The physiology of diapause in arthropods. Camb. Univ. Press, Engl., 151 p.

MILLER, C. B., J. K. JOHNSON, AND D. R. HEINLE.
1977. Growth rules in the marine copepod genus *Acartia*. Limnol. Oceanogr. 22:326-335.

PERTZOVA, N M
1974 Life cycle and ecology of a thermophilous copepod *Centropages hamatus* in the White Sea. [In Russ.] Zool Zh. 53:1013-1022

SAZHINA, L I
1968. Hibernating eggs of marine Calanoida. Zool. Zh 47:1554-1556 (Transl., 1969, Fish. Res. Board Can Transl. Ser. 1259.)

SLAMA, K., M ROMANUK, AND F. ŠORM.
1974 Insect hormones and bioanalogues. Springer-Verlag, N Y., 477 p.

STROSS, R G , AND J C. HILL
1965 Diapause induction in *Daphnia* requires two stimuli. Science (Wash., D C.) 150:1462-1464

TRINAST, E M
1976. A preliminary note on *Acartia californiensis*, a new calanoid copepod from Newport Bay, California Crustaceana 31:54-58

UYE, S., AND A FLEMINGER
1976 Effects of various environment factors on egg development of several species of *Acartia* in southern California Mar. Biol. (Berl.) 38:253-262

UYE, S., AND S. KASAHARA.
1978 Life history of marine planktonic copepods in neritic region with special reference to the role of resting eggs Bull Plankton Soc Jpn 25:109-122

WATSON, N H F , AND B N SMALLMAN
1971. The physiology of diapause in *Diacyclops navus* Herrick (Crustacea, Copepoda). Can. J Zool. 49:1449-1454

WIGGLESWORTH, V B
1972 The principles of insect physiology 7th ed Chapman and Hall, Lond , 827 p.

ZILLIOUX, E. J., AND J G GONZALEZ.
1972 Egg dormancy in a neritic calanoid copepod and its implications to overwintering in boreal waters. *In* B. Battaglia (editor), Fifth European Marine Biology Symposium, p. 217-230. Piccin Editore, Padova, Italy.

ZIMMERMAN, S T
1972. Seasonal succession of zooplankton populations in two dissimilar marine embayments on the Oregon coast Ph D Thesis, Oregon State Univ , Corvallis, 212 p

AERIAL CENSUS OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN A REGION OF THE TEXAS COAST

ERIC G. BARHAM,[1] JAY C. SWEENEY,[2] STEPHEN LEATHERWOOD,[3] ROBERT K. BEGGS,[4] AND CECILIA L. BARHAM[5]

ABSTRACT

On five replicate aerial surveys in late March 1978, the bottlenose dolphin, *Tursiops truncatus*, herds were sighted and their numbers estimated in 21 strip transects flown across bays and channels between barrier islands and the coast from Port Aransas northeast to Matagorda, Texas. The transects were spaced at 4 63 km intervals and herds were scouted in about 800 m wide strips totaling 436 km in length, providing approximately 17% coverage of the area. On surveys 1-4 (survey 5 was excluded from population calculations because it was conducted in adverse weather) 133 bottlenose dolphin herds were sighted, containing an estimated 916 animals. Within these strips the mean heard size was 6.95 animals and mean herd density was 0.0947/km², extrapolating to a population estimate of 1,319 dolphins and a density estimate of 0.752/km² for the entire area. These figures are relatively high in contrast to recent studies in other environments. About half the herds were feeding and approximately one-third were traveling. Sightings were most frequent in ship channels, shallow areas inside barrier islands, and near shore. There were several sources of bias in our measurements, and we consider the results to be conservative.

In the waters under jurisdiction of the United States, live capture of marine mammals is now limited by law to those species that are used for public exhibition and scientific research. With the exception of certain pinnipeds, the greatest demand is for the bottlenose dolphin, *Tursiops truncatus* Montagu, the most tractable of the smaller cetaceans.

This recent management regime has generated a need for assessment of marine mammal stocks that consider population size and reproductive rates of potentially impacted species (Odell et al.[6]). Obviously, rigorous density estimates are an essential starting point for such studies, but despite the long history of a live fishery for bottlenose dolphins (Townsend 1914) there are scant population data on which to base management decisions (Odell 1975).

The majority of bottlenose dolphins that are readily available for capture dwell in the coastal and inland waterways of Florida and the other states bordering the Gulf of Mexico. In such environments several factors make *T. truncatus*, in contrast to pelagic odontocetes, ideally suited for synoptic studies from aircraft: many of the environments are semienclosed waters of limited dimensions, the herds are usually small thus individuals can be relatively accurately counted, and *T. truncatus* is generally the only small cetacean in the area and therefore easily identified. Accordingly, recent studies of bottlenose dolphins off the northern Gulf of Mexico and the Indian River area of Florida have used and refined aerial survey tactics and methods (Leatherwood et al. 1978; Leatherwood 1979; Leatherwood and Platter[7]; Odell and Reynolds[8]). Using similar procedures

[1]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.
[2]Dinnes Memorial Veterinary Hospital, 16133 Ventura Boulevard, Encino, CA 91436.
[3]Biomedical Branch, Naval Ocean Systems Center, San Diego, Calif.; present address: Hubbs-Sea World Research Institute, 1700 South Shores Road, San Diego, CA 92109.
[4]Sea Arama Marineworld, P.O. Box 3068, Galveston, TX 77552.
[5]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.
[6]Odell, D. K., D. B. Siniff, and G. H. Waring (editors). 1975. *Tursiops truncatus* assessment workshop. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021, 141 p. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

[7]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* assessment workshop, p. 49-86. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.
[8]Odell, D. K., and J. E. Reynolds III. 1978. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Draft - Final Report, Marine Mammal Commission, Contract MM5AC026, 55 p. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

Manuscript accepted March 1979
FISHERY BULLETIN VOL. 77, NO. 3, 1980

we report here on the size and density of the bottlenose dolphin population in the Port Aransas Pass-Matagorda Peninsula region of the Texas coast as observed in late March 1978 and compare the density figures with those obtained in the previous studies. Observations on *T. truncatus* distribution, behavior, sighting cues, and the perpendicular distances of the sightings, and alternative procedures and results are also presented and discussed.

STUDY AREA AND METHODS

Based on previous research (Leatherwood et al. 1978), a strip transect was designed (Eberhardt 1978). The dolphin herds were sighted and their numbers estimated within strips theoretically 804.5 m wide (0.435 n.mi.). All sightings, regardless of the numbers of animals, were statistically considered as a herd, and the term is used here in the general sense of a grouping of animals without implying more complex behavior. To achieve precision the same area was surveyed during five replicate flights. The extent of the area surveyed was limited to dimensions that could be covered in 7-8 h of flying time and that would provide approximately 17% coverage of the area on any one replicate survey.

The surveyed territory extended along 160 km (86 n.mi.) of the central Texas coast from Port Aransas at the northern end of Corpus Christi Bay to the base of the Matagorda Peninsula (Figures 1-3). This terrain is a complex of bays, bayous, lakes, and channels bordered seaward by long, low barrier islands. Convoluted arms of the larger bays extend inland into river deltas surrounded by agricultural lands. Marshes fringe much of the barrier and outer bay shorelines and numerous sand and shell reefs, small islands, and spoil dumps interrupt the water areas. Extensive shoals are covered by water of < 1 m, and the deeper parts of the bays are limited to about 4 m depths. Oil well platforms and well heads are numerous in some parts of the bays and man-made

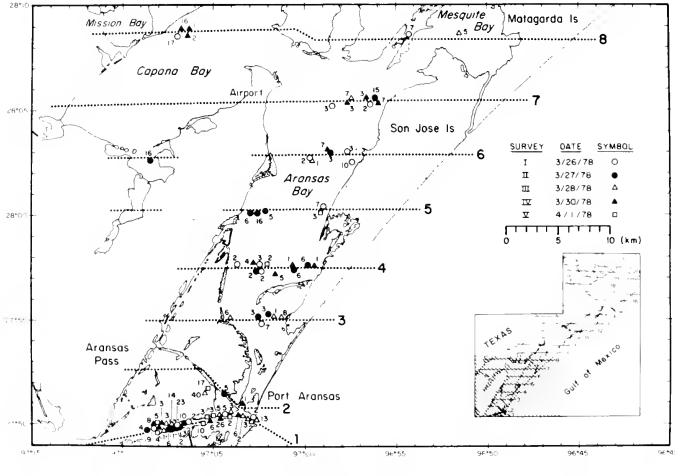


FIGURE 1.—Distribution of bottlenose dolphin herds and their estimated numbers from Aransas Pass to Mesquite Bay (transects 1-8) Texas

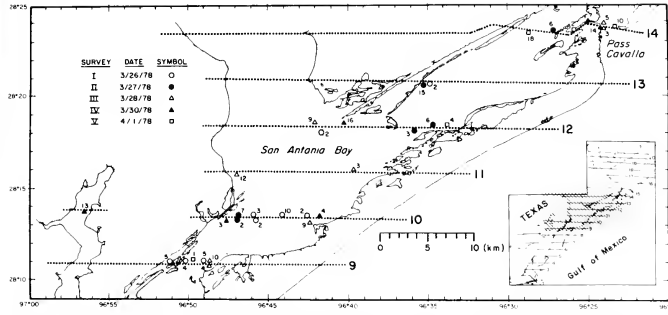


FIGURE 2.—Distribution of bottlenose dolphin herds and their estimated numbers from Ayres Bay to Pass Cavallo (transects 9-14), Texas.

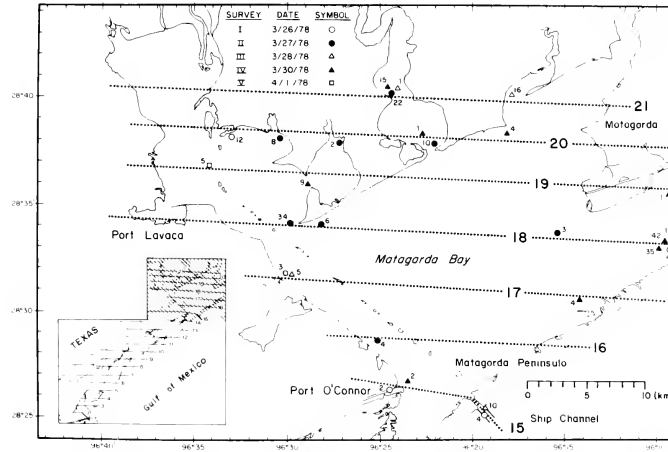


FIGURE 3.—Distribution of bottlenose dolphin herds and their estimated numbers from Port O'Connor ship channel to Tres Palacios Bay (transects 15-21), Texas.

cuts and channels run through the area. Five channels, two man-made, open to the Gulf of Mexico.

Operating from Aransas County Airport, a high-wing, four-seat airplane was flown along 21 transect lines spaced at approximately 4.63 km (2.5 n.mi.) intervels across the study area (Figures 1-3). With some exceptions the transect lines were oriented due east to west. To provide a reference point with a previous population study (Shane 1977) the first two lines were bent to conform to the narrow Corpus Christi and Aransas ship channels (Figure 1). Line 8 was jogged slightly to the north over the Lamar Peninsula so that its western extension would cross Mission Bay (Figure 1). Lines 14 and 15 were altered to overfly the Pass Cavallo and ship channel entrances into Matagorda Bay in the region of Port O'Connor, the location of a proposed *T. truncatus* study. In 12 cases the transects were interrupted by land that divided them into two or more parts, so that in all, 42 overwater crossings were flown. Eight of these crossings were 2 km or less in length while the longest was 42 km. Their average length was 10.2 km. Time of these crossings ranged from <1 to about 18 min.

Most transects were flown at 167 km/h and an altitude of approximately 152 m (500 ft). The first part of transect 1 was flown at 213 m (700 ft) to safely maneuver around large cranes and other structures. When not fully occupied with flying the plane, the pilot searched for bottlenose dolphins. An observer sat in the right front seat next to the pilot. This observer also functioned as the "navigator," talking the pilot onto transect landmarks, calling out the start and stop times for each transect, and charting the dolphin sightings. Two observers sat in the rear of the plane. The observer in the right seat mainly functioned as a recorder who kept a transect log noting the time of starting and ending of each transect and comments on visibility, weather, and other observations of interest. A sighting form was also kept in which was noted: the observer making the sighting, the nature of the observation which first alerted us to the presence of a dolphin herd, the sighting cue; the estimated numbers of adult animals and calves and their assumed behavior; and the estimated right angle, or perpendicular, distance of the sighted dolphin herds from the plane's track. While a strip transect design had been planned, the perpendicular distance estimations were essential for alternative dolphin density calculations utilizing line transect theory (Seber 1973). If time allowed, the herd configuration relative to the environment was also sketched.

Because of the low flying speed, the airplane was relatively quiet and voice communication between party members was feasible. The shortness of the transects and rest intervals between transect lines alleviated observer fatigue.

Observers searched outward to about 400 m (we estimated distances in yards). This distance was estimated with the aid of tape markings on the wing struts that had been calibrated against range marks on the landing strip. When a dolphin sighting was made, the pilot deviated from the transect line and usually orbited the herd twice while all observers counted the animals and noted the presence of calves. A consensus opinion was scored for these counts. Rarely only one circle was necessary, and on occasion three or more circuits were flown before the observers felt confident with the count. On occasion, individual animals or small herds could not be relocated and limited data based on the original sighting were logged.

Two observers worked all the flights, whereas one person was relieved as recorder-observer for the last three flights. The same pilot flew the plane on surveys 1-4. A different pilot took over on the last survey.

RESULTS

Operations

The survey design called for six replicate transect runs on successive days. The period of the operation (26 March-1 April 1978), however, was plagued by strong winds (33-46 km/h) that caused a 1-day postponement of survey 4, cancellation of survey 6, and affected the results of survey 5 to the extent that those data are of limited value (the specific effects of weather on the survey will be discussed later). Weather conditions were good to excellent on two runs, surveys 2 and 4, and marginal to fair on surveys 1 and 3. A malfunctioning airplane engine caused curtailment of the last three transects on survey 2. These were made up at the end of survey 4 under similar environmental conditions. A total of 436 track kilometers (235 n.mi.) was flown on each survey. Assuming a 402.25 m scan on each side of the aircraft, an area of 351 km^2 (102 $n.mi.^2$) was searched. With the 4.63 km transect line spacing, this would repre-

sent about 17% coverage of the survey area on any one replicate.

Dolphin Counts

During the first four survey flights 133 dolphin herds were sighted, containing an estimated 916 animals. A mean of 33.3 herd sightings per survey, composing 229 dolphins, was calculated for the four flights (Table 1). On survey 5, affected by adverse weather, only 19 herds estimated to contain 107 dolphins were sighted. Because these scores fell well below two standard deviations of the mean that was calculated for the first four replicates (Table 1), the results of survey 5 were excluded from our population calculations. Data from the last survey were used, however, for analyzing behavioral observations, sighting cues, and the perpendicular distances of dolphin herds from the trackline.

TABLE 1.—Bottlenose dolphin herd sightings, individuals, and calves estimated on surveys 1-4 Port Aransas to Matagorda, Texas.

Date (1978)	Survey number	Total no. of herds	Total no. of animals	Total no. of calves	Percent of calves
Mar. 26	1	36	175	17	9.7
Mar. 27[1]	2	36	260	17	6.5
Mar. 28	3	29	209	20	9.6
Mar. 30	4	32	272	31	11.4
Total		133	916	85	
Mean		33.3	229.0	21.3	9.3
SD		3.4	45.2	6.7	2.0

[1]The last four transects were run on March 30.

Calves

Among the animals sighted in surveys 1-4, some 85 were classified as calves, and they represented 9.3% of the total population observed (Table 1). Because the surveys were made just prior to the peak of the calving season, it was not always possible to differentiate between older calves of the year and young yearlings. Some 13 animals were in this questionable category.

Herd Size and Herd Density

While the estimated sizes of herds ranged from 1 to 42 animals, generally the aggregations were small. Groups of two and three *T. truncatus* represented the mode and composed 28.6% of all sightings, and 96 of the 133 sightings (72.2%) were composed of 7 or less animals (Figure 4).

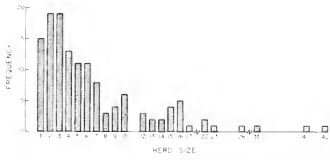


FIGURE 4.—Frequency distribution of bottlenose dolphin herd sizes on surveys 1-4, Port Aransas to Matagorda, Texas.

The mean herd size for each daily survey replicate was computed as:

$$\bar{h}_j = \sum_{i=1}^{n_j} \frac{h_{ij}}{n_j} \qquad (1)$$

where $\bar{h}_j$ = mean herd size,
h_{ij} = herd size of the ith sighted herd on replicate j,
n_j = the number of herds sighted during replicate j.

The estimated herd density for each replicate was obtained from:

$$\hat{D}_j = \frac{n_j}{a} \qquad (2)$$

where D_j = the estimated herd density on replicate j,
a = the surveyed area in km^2,
n_j = is defined as before.

These calculations produced a mean herd size of 6.95 and a mean herd density of 0.0947/km^2 (Table 2).

Estimated Population Size (Numbers of Dolphins)

In previous aerial assessments of bottlenose dolphin populations by Leatherwood and his coworkers, variance of the population size was calculated according to Goodman's (1960) equation for estimating the variance of a product of two independent variables. However, in these cases Goodman's equation was used to estimate variance of the mean population size over all the replicates

TABLE 2.—Basic terms and figures for population size and density estimates of bottlenose dolphin in the Texas bays resulting from replicate surveys 1-4.

Survey number (replicate)	Mean herd size ($\bar{h}_j$)	Variance mean herd size (Var $\bar{h}_j$)	Herd density (no. km^2) (D_j)	No. of dolphins (N_j)	Variance no. of dolphins[1] (Var N_j)	Dolphin density (no. km^2) (d_j)	Variance dolphin density[2] (Var d_j)
1	4 86	0 613	0 1026	1 008	58 828	0 575	0 0175
2	7 22	0 918	0 1026	1 498	100 613	0 854	0 0326
3	7 21	1 967	0 0826	1 204	103 000	0 685	0 0334
4	8 50	2 994	0 0912	1 567	175 232	0 893	0 0569
Mean	6 95		0 0947	1 319		0 752	
SD	1 52		0 0097	260 4		0 148	
SE	0 76		0 0049	130 2		0 074	
SE from theory					[3]189 43		[4]0 1080

[1]From Equation (9) [3]From Equation (10)
[2]From Equation (12) [4]From Equation (13)

and not the variances of each replicate. Quinn[9] has suggested a more refined treatment that is applicable if two conditions are met: the numbers of sightings for each replicate follows a Poisson distribution, and no real differences exist in the replicate herd densities. If these assumptions hold, a variance can then be legitimately computed for each replicate survey and these numbers pooled to produce a more precise estimate of mean population size variance. Accordingly, we proceeded as follows. The estimation of the population size for each replicate was calculated as:

$$N_j = AD_j\bar{h}_j \tag{3}$$

where N_j = estimated population size on replicate j,
A = total area assumed to be 5.76 × of the searched area (a),
D_j = estimated herd density on replicate j,
$\bar{h}_j$ = mean herd size on replicate j.

Results are shown as "number of dolphins" in Table 2.

The computed variance of the estimated population size for each replicate was:

$$\text{Var } N_j = A^2 \text{ Var}(D_j\bar{h}_j) \tag{4}$$

which simplifies to:

$$\text{Var } N_j = \left(\frac{A}{a}\right)^2 \text{Var } (n_j\bar{h}_j) \tag{5}$$

where a is assumed to be 17% of the total area (A).

The estimated variance of mean herd size within replicates was then estimated from:

$$\text{Var } \bar{h}_j = \sum_{i=1}^{n_j} \frac{(h_{ij} - \bar{h}_j)^2}{n_j\,(n_j - 1)} . \tag{6}$$

Following Elliott (1971), a chi-square value utilizing the index of dispersion was computed for the number of herd sightings on replicate surveys 1-4 to test agreement with a Poisson series. The index of dispersion was 0.35 with a resulting χ^2 value of 1.05. These values support the Poisson distribution assumption. This allows us to consider the variance of replicate herd sightings as equal to the numbers of herd sightings. Thus:

$$\text{Var } n_j = n_j. \tag{7}$$

Using the chi-square test again we also found that there was no difference at the 5% significance level in the herd densities of the replicate surveys. The mean herd size ($\bar{h}_j$) and the numbers of herds sighted (n_j), however, were obtained from the same set of observations, and as one reviewer has rightly pointed out, it is not known if in fact these estimates were independent. We therefore tested for interrelationship using Spearman's Rank Correlation Test (Zar 1974). Finding no demonstrable correlation at the 5% significance level, we proceeded to treat the results of the replicate surveys generated from Equation (5) in terms of Goodman's (1960) equation for estimating the variance of a product as suggested by Leatherwood et al. (1978). Thus:

$$\text{Var } N_j =$$

$$5^2(n_j^2\ \text{Var } \bar{h}_j + \bar{h}_j^2\ \text{Var } n_j - \text{Var } n_j\ \text{Var } \bar{h}_j)\ , \tag{8}$$

and substitution of n_j for Var n_j results in:

[9]Terrance J. Quinn II, Center for Quantitative Science, University of Washington, Seattle, WA 98195, pers. commun. to S. Leatherwood, March 1978.

$$\text{Var } N_j = 5^2(n_j^2 \text{ Var } \bar{h}_j + \bar{h}_j^2 n_j - n_j \text{ Var } \bar{h}_j) . \quad (9)$$

Before proceeding, a one-way analysis of variance with unequal sample sizes was performed on herd sizes with a $\log_{10}$ transformation for counts. No significant differences ($\alpha = 0.05$) between replicate herd sizes were found, thereby allowing the pooling of the four variances as:

$$\text{Var } \bar{N} = \text{Var}\left(\frac{\sum_{j=1}^{4} N_j}{4}\right) = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4} \text{Var } (N_j) . \quad (10)$$

These computations produced an estimated mean *T. truncatus* population size of 1,319 with a standard error (SE) of 189 (Table 2).

The susceptibility of the above analysis to possible nonindependence of the mean herd size and herd density parameters was recognized by Leatherwood et al. (1978), and they suggested that mean herd size be established in preliminary flights before the herd counting phase of the survey is initiated. In the case of our work, however, because of inclement weather and limited resources we decided to make as many replicate surveys as possible rather than dividing the flight functions.

Despite the assurance of ranking tests, if independence between $\bar{h}_j$ and n_j does not hold, use of Equation (9) will probably underestimate the variance of N_j. An alternative more robust approach suggested by one reviewer was to compute the SE of the replicate estimates of numbers of dolphin on the four surveys (Table 2). This procedure produces a SE of 130.0 which is reasonably close to the theoretical value of 189 obtained from Equation (9) and tempers to some extent doubts of the validity of this approach.

Estimated Dolphin Density

For comparative purposes we also estimated the density of dolphins in the study area from:

$$d_j = D_j \bar{h}_j = \frac{n_j}{a} \bar{h}_j . \quad (11)$$

The same rationale and procedures for calculating the replicate and overall variances of population estimates were used to calculate the variances for dolphin density. Thus:

$$\text{Var } d_j = \frac{1}{a^2}(n_j^2 \text{ Var } \bar{h}_j + \bar{h}_j^2 n_j - n_j \text{ Var } \bar{h}_j) \quad (12)$$

and

$$\text{Var } \bar{d} = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4} \text{Var } d_j . \quad (13)$$

This treatment gave an estimate of 0.752 dolphins km^2 with an SE of 0.074. The SE calculated from the variance of the mean of the replicates was 0.108 (Table 2).

Comparisons with Other Population Studies

We can roughly compare our counts from the Aransas Pass area with those of Shane's (1977) who counted *T. truncatus* in the same area from a skiff run on a meandering course through the ship channels and cuts almost on a daily basis over a 1-yr period. For March and April 1977, her mean was 95 dolphins. The mean of our scores for transects 1 and 2 that covered part of her study area was 53. Considering the differences in methods and area covered, the results do not seem unreasonably diverse.

Our mean density estimate for all transects is compared with the results of recent aerial surveys of *T. truncatus* populations in waters adjacent to Florida, Mississippi, and Louisiana in Table 3. While it is clearly tenuous to contrast densities from different environments, it is worth noting that the two semienclosed areas, Indian River, Fla., and the Texas bays, appear to support similar densities, 0.52 dolphins/km^2 and 0.75 dolphins/km^2, respectively. The mean percent of the calves

TABLE 3.—Density estimates of bottlenose dolphin populations in southeastern U.S. coastal waters, based on recent aerial surveys. There are considerable differences in the nature and extent of the areas covered in these studies, thus the results are not strictly comparable.

Location	Reference	Dolphins per km^2	Dolphins per n mi^2
Florida			
Indian River	Leatherwood 1979	0.52	1.79
Florida	Odell and Reynolds		
West coast	(text footnote 8)	0.27	0.93
Mississippi	Leatherwood et al.		
Gulf coast	(1978)	0.23	0.79
Louisiana	Leatherwood et al.		
Gulf coast	(1978)	0.44	1.51
Texas			
Gulf coast	This paper	0.75	2.57

[1] Derived from their table 10 by computing the product of mean herd size (5.43) and mean herd density (0.0497).

to the total number of animals counted (9.3±2.0%) is about the same as previously reported (Leatherwood 1979).

Distribution and Behavior

As can be seen from Figures 1-3 the distribution of dolphin herds in the area was hardly homogenous. Some 28 herds (21%) of the total were sighted in the narrow Aransas Pass ship channels (mainly transect 1) and 211 (23%) of the animals counted were in these herds. (This marked difference in densities is discussed below.) Transect 18 across Matagorda Bay was another area of high dolphin density. While we noted only eight herds on this line they were relatively large and accounted for 14% of the dolphins sighted. In general, aside from the ship channels, the shoreward side of the barrier islands and locations close to the beach appeared to be favorable situations for *T. truncatus*, whereas sightings were rare in the middle of large bays.

When possible, the apparent behavior of the herds was coded as either traveling, playing, feeding, or resting. Of the 97 herds classified, about half (48.5%) were considered to be feeding. Side or upside down swimming by dolphins actively pursuing prey as reported by Leatherwood (1975) was frequently observed. This was particularly true in the shallow regions inside the barrier islands where Gunter (1954) reported that bottlenose dolphins frequently chase mullet, *Mugil cephalus*. Feeding appeared to be associated with herd size, for of the 17 herds composed of 15 or more individuals, 13 (76.5%) were considered to be feeding. The next most common behavior was "traveling," and 36 herds (37.1%) were assigned to that behavioral mode.

Perpendicular Sighting Distances and Sighting Cues

As previously indicated, in most cases we estimated the perpendicular distance from the plane's track to the sighted herd. In addition we also logged the nature of the observation which first alerted us to the presence of a dolphin herd, the "sighting cue" (Figure 5). During the field work, 11 different codes were used but these could be reduced to four classes: 1) surface perturbations such as mud trails or boils, scars, and splashes; 2) an animal's body seen below the water (most easily noted when the dolphins are rolling or swimming upside down and their contrasting light ventral surfaces are showing); 3) an animal's body, or part of it, or its condensed respiratory exhalation "blow" noted above the water surface; and 4) "cue uncertain or unnoted."

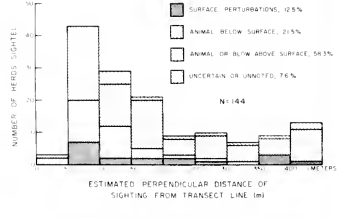


FIGURE 5.—Frequency distribution of estimated perpendicular distances of bottlenose dolphin herd sightings from transect lines on surveys 1-5, Port Aransas to Matagorda, Texas. Histograms are divided into the relative ratios of sighting cue classes

The "animal above surface" cue was effective at all ranges and was the predominant sighting cue, accounting for 58.3% of all sightings (Figure 5). The "animal below surface" instigated 21.5% of the sightings, but was more important at ranges under 200 m, contributing 28 of the 96 sightings (29.2%) at these ranges, whereas, at ranges >200 m, only 3 of 48 sightings (6.2%) were signaled by this cue. As will be discussed later, the effectiveness of both underwater sightings and surface perturbations appeared to be vulnerable to weather conditions. Most questionable or unrecorded sighting cues occurred on the initial survey.

DISCUSSION

Possible Biases to Population Estimates

Several factors, both operational and analytical, influenced the results, in some cases prejudicing the counts upward and in others to lowering them. We first discuss two factors, effects of weather and inability to sight all herds, that tended to cause underestimates.

Relatively strong southwest winds (22-41 km h) blew constantly for several days during the field operations. The wind's major effect on searching efficiency was not sea state, as is the case in the open ocean, for splashes were seldom the sighting cue, but rather the stirring of bottom materials into suspension creating large areas of highly tur-

bid water. On such days the only clear water was in the lee of barrier islands and headlands where the fetch was limited.

Increased turbidity limits the observer's chances of sighting underwater animals and noting mud boils and trails. For underwater animals, however, the overall effect on the number of sightings was tempered because submerged dolphins will frequently be spotted when they eventually surface. More important was the negative influence of high turbidity on the observer's ability to note surface signs. For example, on the two low-wind days 12 out of 68 (17.7%) sightings were cued by surface perturbations. In contrast, on the three medium to high-wind days only 8 of 83 (9.6%) of sightings were signaled by this cue. The effect was probably more important than those data indicate, for frequently the observer's attention was drawn to an area by subtle surface signs and then, if a dolphin's body showed at the surface, it was usually the second rather than the first cue that was logged. As stated earlier, we have reduced the effects of weather on the population estimates by excluding the results of survey 5, when the wind effects were extreme, from the density computations.

Regarding our inability to sight all herds, the supposition that all target animals will be seen is basic to the strip transect method (Eberhardt 1978). However, in terms of line transect theory (Seber 1973), which assumes that the herds will be randomly distributed, the frequency histogram of the estimated perpendicular sighting distances (Figure 5) gives strong evidence that one of these assumptions was incorrect, probably the former, as follows. First, only 3 of 144 sightings were made at under 50 m range. The aircraft's configuration which severly limits searching the water directly under and adjacent to the flight path was the major cause of this discrepancy. (A secondary factor was discomfort to the observer's neck caused by attempting to look down at a steep angle.) The only sightings made directly under or close to the track were when the aircraft was in a steep turn, and frequently herds were noted at moderate ranges when we were circling on a previous sighting. Secondly, the systematic decrease of the sighting frequencies from 50 to 200 m, suggesting a negative exponential curve, and the "tail" out to 400 m must at least in part reflect the inherent inefficiency of the observers to see beneath the water's surface at low angles or to detect relatively small, low-contrast objects at even moderate distances.

Three factors, dolphin movement, nature of the terrain, and observer experience, may have had mixed effects on the estimates, as follows.

Regarding effects of dolphin movement between the open Gulf of Mexico and the bay behind the barrier islands, it was originally planned that volunteer observers stationed adjacent to the passes would note the numbers and directional movements of bottlenose dolphins during the hours of the survey. However, a week's delay in starting the field work and the subsequent resumption of college classes following Easter vacation made it necessary to cancel that observational phase. At the termination of survey 4, however, we flew homeward just outside Matagorda Peninsula and Island. Outside Pass Cavallo at least 50 *T. truncatus* were seen lolling in small herds in and just outside the surf zone. These dolphins may have either been moving in from the Gulf or out of the bays, but their proximity to the beach and the pass indicates that there was frequent movement of dolphins between the two environments.

Factors of bathymetry of the bays and the nature of the terrain were not considered by the analysis. While *T. truncatus* were occasionally noted in shallow water just inside the barrier islands, extensive regions in the middle of the bays and in the shoreward areas were covered with a thin layer of water over sand and mud flats and there are numerous reefs and islands. Thus, within most of the 800 m swaths used to compute the density estimates there was territory that was not available to the dolphins that could legitimately be subtracted from the area searched. On the other hand, by multiplying the searched area by 5.76 (Equation (3)) to obtain an estimate of the total number of dolphins we were sometimes attributing dolphin habitat to dry land. This is particularly true for the Port Aransas ship channels that were limited to about 600 m width and were surrounded by large land areas.

We feel that observer experience possibly also biased the accounts. *Tursiops truncatus* herds appear to occupy a home range (Caldwell 1955; Shane 1977) and we frequently sighted herds that were of similar size and in the same approximate location of herds noted on previous surveys. The observers tended to concentrate their attention on these areas and thus searched them more efficiently in the latter surveys.

Despite the smallness of the herds, it was not easy to accurately count animals that were sometimes spread over a relatively large area, and in subgroups that only showed for brief periods at the surface. Obviously, accuracy of such counts will also improve with experience. However, by scoring a consensus opinion the judgment and bias of the most experienced observer probably carried more weight, and as a result we feel that in all cases the counts were conservative. Because of the experience factor we also think that, other influences being equal, the latter surveys were probably the more accurate.

Last, one factor, the "gerrymandered" lines of transects 1 and 2, clearly tended to influence the counts upward. Our rationale for altering the line of these transects was based on the desirability of obtaining data in an area for which baseline information already was available (Shane 1977). Unfortunately, the terrain was not ideal for transect sampling, and flying an east-west line over the ship channels would have resulted in gross underestimation of an area known to hold a relatively large number of dolphins.

Clearly, the results for transects 1 and 2 (23% of the animals sighted in only 6.6% of the total area) were strikingly different from those data for the rest of the transects. Estimated dolphin density for the ship channels was 2.633 km^2, some 4.25 times greater than the 0.619 km^2 estimated for transects 3-21 (Table 4). Based on these densities the total population estimate could be partitioned into 304 dolphins for the ship channels and 1,015 animals in the rest of the area. Shane's (1977) maximum estimate for the ship channel area for any month of the year was about 280, thus the two estimates are in reasonable agreement. We still feel, however, that there were some unresolvable problems with our survey methodology as it applied to the Aransas Pass ship channels, and that the soundest procedure was to lump the results from the minority area with those from the major region, as we have done.

Alternative Density Estimate

As previously discussed, the decrease in the number of dolphin sightings at increasing ranges of the herds from the flight path (Figure 5) indicated violation of strip transect theory assumption that all herds within the delineated area were sighted. Line transect theory (Seber 1973) provided an alternative method of analyzing the results. Because there were few observations in the 0-50 m increment, creating a marked gap in the frequency distribution, and the "tail" of the frequency distribution was truncated, in part because we limited observations to about 400 m range, our data were not strictly applicable to line transect theory, either. Despite these discrepancies, however, we obtained for comparative purposes a rough approximation of the level of bias by applying a simple modification of the so-called exponential estimator (Gates et al. 1968) which corrects for the gap in the 0-50 m frequency distribution interval as follows:

TABLE 4.—The basic terms and figures for comparing the estimated bottlenose dolphin density in two parts of the survey, the Port Aransas ship channels (transects 1 and 2) and rest of the area (transects 3 to 21).

Survey number (replicate)	Total no of herds	Total no of animals	Mean herd size (h_j)	Herd density no. km^2 (D_j)	Dolphin density (no. km^2) (d_j)	Variance dolphin density (Var d_j)
Transects 1 and 2						
1	5	41	8 20	0 2165	2 045	1 6005
2	8	35	4 38	0 3465	1 749	0 5162
3	8	84	10 50	0 3465	4 191	5 0629
4	7	51	7 29	0 3032	2 546	2 0490
Total	28	211				
Mean	7	52 6	7 59	0 3032	2 633	
SD	1 4	21 9	2 53	0 0613	1 090	
SE	0 7	10 9	1 27	0 0307	0 545	
SE[1]						0 8750
Transects 3 to 21						
1	31	134	4 32	0 0946	0 471	0 0121
2	28	225	8 04	0 0854	0 791	0 0350
3	21	125	5 95	0 0641	0 439	0 0133
4	25	221	8 84	0 0763	0 776	0 0552
Total	105	705				
Mean	26 3	176 3	6 79	0 0801	0 619	
SD	4 3	54 1	2 05	0 0130	0 190	
SE	2 1	27 0	1 03	0 0065	0 095	
SE[1]						0 0980

[1]From Equation (13)

$$\hat{d} = \frac{n}{2L(\bar{Y} - 0.05)} \quad (14)$$

where $\hat{d}$ = estimated dolphin density,
n = total number of dolphin sightings,
L = length of the track line in km,
$\bar{Y}$ = mean perpendicular sighting distance (minus the 50 m gap).

These calculations gave a density estimate for herds of 0.28 km^2 compared with 0.095 for the strip transect method (Table 2), evidence that the latter method may have underestimated the dolphin density by about a factor of 3.

In conclusion, the relatively few sightings in the 0-50 m perpendicular distance interval and the exponential decrease in sightings at ranges > 100 m, strongly indicate violation of the strip transect assumption that all herds within the delineated strip were noted. If this is true then the population has been underestimated to some degree, although the inclusion of transects 1 and 2 would tend to compensate for this. Conversely, one assumption of line transect theory is that the targets are randomly distributed. We found, however, that the distribution of the dolphin herds was strongly nonrandom. This factor may have caused an upward bias to those calculations, but the precise impact of this violation is presently unclear. These questions cannot be resolved until further surveys are done simultaneously with adequate "ground truth" counts.

ACKNOWLEDGMENTS

This study was a collaborative effort among organizations within the NOAA's National Marine Fisheries Service, the Marine Mammal Commission, Dinnes Memorial Veterinary Hospital, Sea Arama Marineland of Galveston, and the Naval Ocean Systems Center. We thank the administrators of these organizations for expediting the work. We are also indebted to James McGrew for his excellent piloting and Terrance Quinn II for his suggestions. Gary Stauffer advised on statistical matters; the art work was done by Kenneth Raymond and typing by Lorraine Prescott, all of the Southwest Fisheries Center. The originally submitted draft of this paper was read by William Fox, Joseph Powers, and Nancy Lo of the Southwest Fisheries Center and Pat Tomlinson of the Inter-American Tropical Tuna Commission. Following editorial review, Tim Smith of the Southwest Fisheries Center consulted with the senior author on additional statistical work in response to suggestions by the referees. We also thank Lee Eberhardt of Battelle Pacific Northwest Laboratories as well as an anonymous reviewer and the editor for their constructive comments and suggestions. Despite the many contributions from the junior authors, advisors, and reviewers, the senior author, of course, assumes full responsibility for the contents of this paper.

LITERATURE CITED

CALDWELL, D. K.
1955. Evidence of home range of an Atlantic bottlenose dolphin. J. Mammal. 36:304-305.

EBERHARDT, L. L.
1978. Transect methods for population studies. J. Wildl. Manage. 42:1-31.

ELLIOTT, J. M.
1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc., Sci. Publ. 25, 144 p.

GATES, C. E., W. H. MARSHALL, AND D. P. OLSON.
1968. Line transect method of estimating grouse population densities. Biometrics 24:135-145.

GOODMAN, L. A.
1960. On the exact variance of products. J. Am. Stat. Assoc. 55:708-713.

GUNTER, G.
1954. Mammals of the Gulf of Mexico. U.S. Fish Wildl. Serv., Fish. Bull. 55:543-551.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.
1979. Aerial survey of populations of the bottlenosed dolphin, *Tursiops truncatus*, and the West Indian manatee *Trichechus manatus*, in the Indian and Banana Rivers, Florida. Fish. Bull., U.S. 77:47-59.

LEATHERWOOD, S., J. R. GILBERT, AND D. G. CHAPMAN.
1978. An evaluation of some techniques for aerial censuses of bottlenosed dolphins. J. Wildl. Manage. 42:239-250.

ODELL, D. K.
1975. Status and aspects of the life history of the bottlenose dolphin, *Tursiops truncatus*, in Florida. J. Fish. Res. Board Can. 32:1055-1058.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Charles Griffin, Lond., 499 p.

SHANE, S. H.
1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. Thesis, Texas A&M Univ., 238 p.

TOWNSEND, C. H.
1914. The porpoise in captivity. Zoologica (N.Y.) 1:289-299.

ZAR, J. H.
1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J., 620 p.

ENERGETIC SIGNIFICANCE OF CHANGES IN SWIMMING MODES DURING GROWTH OF LARVAL ANCHOVY, *ENGRAULIS MORDAX*

DANIEL WEIHS[1]

ABSTRACT

The swimming behavior of larval northern anchovy, *Engraulis mordax*, in the first few days after hatching is different from the intermittent beat-and-glide mode used by older larvae and later stage fish. It is shown mathematically that the bursts of continuous swimming typical of these yolk-sac larvae is the more efficient form of locomotion at this stage, because of their small size. This advantage changes as the larva grows out of the size range in which water viscosity is the dominant factor (small Reynolds number). When the larva reaches a length of 5 mm, typical Reynolds numbers are such that intermittent swimming gradually becomes the more economical mode, and this mode is dominant when the larvae reach 15 mm. These analytical results compare well with observed behavioral changes.

Swimming behavior of the northern anchovy, *Engraulis mordax*, changes dramatically during growth in the larval stage (Hunter 1972). At hatching, the motion of yolk-sac larvae consists of bouts of continuous, very energetic swimming. This behavior persists for the first 3-4 days of growth, changing to beat-and-glide swimming at the close of the yolk-sac period. The beat-and-glide mode is then retained during the rest of the fish's life.

Intermittent swimming, or beat and glide, is an efficient mode of locomotion for adult fish, enabling increases by a factor of two or more in the range achieved for a given energy expenditure (Weihs 1974). The problem addressed in the present paper is whether the changes in swimming behavior mentioned above also have an energy-saving function. The energetic advantage of intermittent swimming may not exist during the early life stages of fishes because of the importance of viscous effects on small organisms. This study includes setting up a theoretical framework for the analysis of energetics of swimming during the various stages of the fish's life history. The forces and energy required for swimming in the continuous and intermittent modes are then calculated and compared at different stages of larval development. These stages are hydrodynamically distinguished by the nondimensional Reynolds number, Re, which is a function of both length and speed. The value of the Re defines the relative importance of viscous and inertial effects on the hydrodynamic resistance to motion.

THEORETICAL MODEL

Consider a fish swimming in a straight line at constant depth. We shall assume the fish to be neutrally buoyant so that the only forces acting are in the horizontal plane. Fish of negative buoyancy can be included in the following analysis by equating the excess weight of the fish in water (which is usually not more than 6% of its weight in air) and lift forces produced on the body and fins. However, this is not directly relevant to the present discussion as these forces are perpendicular to the plane of motion, and shall therefore be left out for simplicity.

Returning to the horizontal plane, the forces acting are the thrust applied by the fish, T, and the drag on the fish, D, acting in the opposite direction. The drag is a combination of viscous drag due to friction and form drag, which also is an indirect result of the friction caused by areas over which the flow is separated from the fish body. The drag force can be written (Hoerner 1965) as

$$D = \frac{1}{2}\rho A C_D u^2 \qquad (1)$$

where ρ is the water density; A the frontal area (seen in frontal projection); C_D a nondimensional drag coefficient dependent on shape, roughness, and other factors to be discussed below; and u the relative velocity between the fish and the water

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; present address: Department of Aeronautical Engineering, Technion, Haifa, Israel.

Manuscript accepted March 1979
FISHERY BULLETIN VOL. 77, NO. 3, 1980

some distance away, which is not disturbed by the fish's passage.

The drag coefficient C_D has been found experimentally to be a similar function of Re for various shapes. Thus, for all shapes tested (Hoerner 1965, chapter 3), the coefficient C_D is a decreasing function up to Re 200-300, being a constant for larger Re up to the turbulent regime which starts at about Re = 500,000, where a new, lower, constant value is obtained. Thus when Re >200, hydrodynamic drag becomes proportional to the velocity squared, as the other factors in Equation (1) do not change for a fixed body.

The Re >200 regime was examined by the author (Weihs 1974) previously and will therefore be mentioned here for comparisons only. When Re<200, two main regimes are observed, that of Re< 10 and 10< Re<200. The low Re range, in which velocity plays a much more important role than the inertial (acceleration) force effects, has $C_D \propto \mathrm{Re}^{-1}$. Strictly speaking, this regime ends when Re = 1, but experiments have shown that this relationship can be applied up to Re = 10 with good accuracy. Vlymen (1974) actually used this relationship at Re = 30, where C_D, estimated by the low Re formula, still is within 10% of the exact value, for his analysis of larval anchovy swimming. The remaining range is a transition regime where C_D gradually changes from the low Re form to the high Re ($C_D \propto \mathrm{Re}^0$) form.

As continuous swimming in anchovy larvae is observed mainly in the yolk-sac stage (2.8-5 mm long), the low Re regime is relevant. Thus, Re = 8 corresponds to a 3 mm long larva moving at 3 mm/s, and a 5 mm long larva, moving at 5 mm/s, experiences a Re< 30.

Applying the relationship for low Re ($C_D \propto \mathrm{Re}^{-1}$), Equation (1) can be written

$$D = \frac{1}{2}\,\rho\, ACu \qquad (2)$$

where C is a numerical constant depending on the shape.

When a fish is actively swimming by means of body and fin oscillations, the drag force is affected, both through the increase in frontal area A, and through the change in the numerical coefficient C. Thus, for example, $C = 20.37$ for a disc moving in a direction normal to its plane, and is equal to 13.6 when moving parallel to its plane. Experimental data collected by Webb (1975) show that the drag coefficient for fish swimming at high Re can be up to four times that of a rigidly gliding fish. For the low Re regime considered here, the increase in drag coefficient caused by swimming motions does not exceed a factor of 2, for a long slender body (Wu et al. 1975). This increase is written as

$$D_s = \frac{1}{2}\,\rho\, ACau \equiv \alpha Ku \qquad (3)$$

where α is the ratio of swimming to gliding drag and the subscript s stands for active swimming. The equation of motion for fish, while actively producing a thrust T is

$$T = m\frac{du}{dt} + \alpha Ku \qquad (4)$$

where m is the fish mass (slightly augmented by the added mass at higher Re), and K is defined in Equation (3).

The energy (E) required to traverse a distance L within time τ is

$$E = \int_0^{\tau} T\,u\,dt. \qquad (5)$$

There is no available information on the dependence of propulsive efficiency on swimming speed for larval anchovy, so that we have to perform the calculations on the energy required, and not the energy actually expended by the fish. However, for comparison of different swimming modes, these are equally applicable.

The purpose of the present study is to compare the effectiveness of continuous and intermittent swimming of larval fish so that we start by finding the energy, E_c, required for swimming at constant speed U_c over the same distance L. From Equation (5),

$$E_c = T_c U_c \tau = T_c L \qquad (6)$$

where the subscript c stands for continuous swimming. Defining the energy expenditure per unit distance as $\bar{E} = E/L$ we obtain, by applying also Equation (4),

$$\bar{E}_c = T_c = \alpha K U_c. \qquad (7)$$

Intermittent swimming, on the other hand, requires energy only during the beating part of the cycle so that the total energy for one beat-and-glide cycle is described by

$$E_i = \int_0^{t_b} T\,u\,dt = \int_0^{t_b} \left(mu\frac{du}{dt} + \alpha Ku^2\right) dt \qquad (8)$$

where t_1 is the time spent in active swimming during the cycle. In order to integrate Equation (8) we have to obtain the functional dependence of u on the time t. This is done with the aid of Equation (4). Taking the thrust applied to be constant (T_0), Equation (4) can be solved in closed and general form. It was previously shown (Weihs 1974) that constant thrust production is the most efficient procedure so that we can use this assumption here, recognizing that any other behavior will probably be more wasteful in terms of energy. After some rearrangement, Equation (4) is

$$\frac{du}{dt} + \frac{\alpha K}{m} u - \frac{T_0}{m} = 0 \qquad (9)$$

with boundary condition

$$u = U_i \text{ at } t = 0 \qquad (10)$$

where U_i is the initial velocity at the beginning of the beat phase, which is equal to the speed at the end of the gliding phase. The solution is

$$u = (U_i - U_0) \exp\left(-\frac{\alpha K}{m} t\right) + U_0 \qquad (11)$$

where $U_0 = T_0/K$ is the final velocity which the larva would attain if the beating phase were sustained for a long enough period. U_0 is higher than the final speed actually obtained during the beat phase U_f. Substituting Equation (11) into Equation (8) and integrating, recalling that the speed at t_1 is U_f, we have

$$E_v = mU_0 (U_0 - U_f) + \alpha K U_0^2 t_1. \qquad (12)$$

To find t_1, we substitute U_f in Equation (11) with $t = t_1$ and obtain, after algebraic reduction

$$t_1 = \frac{m}{\alpha K} \ln \frac{U_0 - U_i}{U_0 - U_f} \qquad (13)$$

so that the energy required during one beat-and-glide cycle is

$$E_v = mU_0^2 \left[\left(1 - \frac{U_f}{U_0}\right) + \ln \frac{1 - \frac{U_i}{U_0}}{1 - \frac{U_f}{U_0}} \right]. \qquad (14)$$

The energy per unit distance crossed during one cycle in intermittent swimming is

$$\bar{E}_v = \frac{E_v}{l_1 + l_2} = \frac{E_v}{U_i \bar{t}} = \frac{E_v}{U_i (t_1 + t_2)} \qquad (15)$$

where l_1, and l_2 are the distances crossed during beating and gliding phases, respectively. The sum of l_1 and l_2 is taken to be equal to the continuous swimming speed U_c multiplied by the total cycle time, as we compare energy required for crossing the same distance $l_1 + l_2$. Thus, U_c is also the average velocity during the whole intermittent swimming cycle

$$U_c = \frac{l_1 + l_2}{t_1 + t_2}. \qquad (16)$$

To compare energy expenditure in intermittent and continuous swimming, we define a ratio S

$$S = \frac{\bar{E}_v}{\bar{E}_c} = \frac{E_v}{\alpha K U_c^2 (t_1 + t_2)} = \frac{E_v (t_1 + t_2)}{\alpha K (l_1 + l_2)^2}. \qquad (17)$$

Intermittent swimming is more efficient only when the numerical value of S is less than unity. To calculate values of S we need explicit expressions for l_1, l_2, t_1, and t_2. The beat phase velocity has already been found, Equation (11), so that l_1 is easily obtained by integration, using t_1, Equation (13), as the upper bound

$$l_1 = \frac{m}{\alpha K} \left[U_0 \ln \frac{U_0 - U_i}{U_0 - U_f} - (U_f - U_i) \right]. \qquad (18)$$

The gliding phase of intermittent swimming is described by

$$m \frac{du}{dt} + Ku = 0 \qquad (19)$$

which is obtained from Equation (4) when no thrust is applied, and gliding drag is experienced by the fish. The relevant initial condition is

$$u = U_f \text{ when } t = 0 \qquad (20)$$

and the speed is

$$U = U_f \exp\left(-\frac{K}{m} t\right) \qquad (21)$$

with the time spent gliding t_2 obtained from the fact that at t_2 the speed is back to U_i. After some reshuffling

$$l_2 = \frac{m}{K} \ln \frac{U_f}{U_i} . \quad (22)$$

Integrating Equation 20 gives l_2

$$l_2 = \int_0^t U_f \exp\left(-\frac{K}{m} t\right) dt = \frac{m}{K}(U_f - U_i) . \quad (23)$$

To nondimensionalize, we now divide all velocities by U_0. Substituting Equations (13), (14), (18), (22), and (23) into S (Equation (17)) and simplifying results in

$$S = \frac{\left[(1-\bar{U}_f) + \ln\frac{1-U_i}{1-U_f}\right]\left[\ln\frac{1-\bar{U}_i}{1-U_f} + \alpha \ln\frac{\bar{U}_f}{U_i}\right]}{\left[(\alpha-1)(\bar{U}_f - \bar{U}_i) + \ln\frac{1-U_i}{1-U_f}\right]^2} \quad (24)$$

where the line over the speeds signifies values divided by U_0. The ratio S serves now as a quantitative criterion, showing which mode of swimming is more efficient. The advantages of the comparison approach are now clear, as the only parameter specific to the fish is α which, as mentioned before, can vary between 1 and 2 only. All other factors, such as fish mass, frontal area, and the numerical coefficient of drag, have cancelled out, dropping many of the uncertainties of such calculations.

Results and Discussion

Equation (24) is now studied for various values of the parameters involved. As mentioned before, the numerical value of S indicates the relative efficiency of intermittent and steady swimming. When $S < 1$ beat-and-glide swimming is more costly. The three variables appearing in S are bounded by well-defined limits, which makes the parametric study of Equation (24) easier. The nondimensional "final" velocity, at the end of the beat phase, is limited by $0 < \bar{U}_f < 1$ as U_0 is the highest velocity obtainable by the animal (see Equation (11)) under present conditions. By definition, $0 < U_i < \bar{U}_f$. The yolk-sac larvae and later stage larvae are combinations of elongated and round shapes so that the limits of α are $1 \leq \alpha \leq 2$. The range of values of α is obtained from the fact that for elongated (fish) bodies, the ratio of drag in normal motion to resistance to tangential relative motion does not exceed 2 in the viscous domain. Only some sections of the fish bodies are in pure normal motion (perpendicular to the local flow direction), consequently the average ratio is always <2.

It is also clear that the larger the numerical value of α, the larger the possible gains by means of intermittent swimming, because the drag when actively swimming is proportionally greater than while gliding so that breaks in the swimming phase will be more advantageous. Therefore, we first take $\alpha = 2$ as a reasonable upper limit. Figure 1 shows the results of such calculations. The coordinates are the energy ratio S versus the normalized average velocity U_c. The calculations were performed for different values of the final

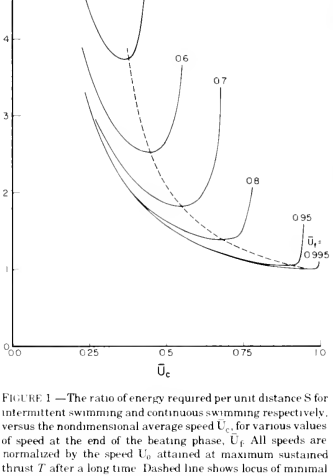


FIGURE 1.—The ratio of energy required per unit distance S for intermittent swimming and continuous swimming respectively, versus the nondimensional average speed $\bar{U}_c$, for various values of speed at the end of the beating phase, $\bar{U}_f$. All speeds are normalized by the speed U_0 attained at maximum sustained thrust T after a long time. Dashed line shows locus of minimal energy ratio at different $\bar{U}_f$. Ratio of swimming to gliding drag α 2

velocity U_f, varying the initial velocity U_i to obtain different average speeds.

The main result of this Figure is that S is always >1, i.e., for the speeds and sizes at which viscous effects dominate continuous swimming is always more efficient. This calculation is based on the relation $C_D \propto \mathrm{Re}^{-1}$ and is therefore valid for Re up to 10. Larval anchovy tend to swim at speeds of about 0.8 body length/s (Hunter 1972) when swimming intermittently. Thus the Re typical of 3-day-old larvae whose length (Zweifel and Hunter[2]) is about 4 mm at 18°C is also about 10. At age 3 days, larvae spent $<20\%$ of the time swimming intermittently, but 2 days later (Hunter 1972, fig. 1) about 90% of the time is spent in beat-and-glide motion. This level of intermittent swimming is retained thereafter. This sharp change coincides with the time the animal "grows out" of the viscous regime (the Re is essentially proportional to fish length squared), e.g., when the larvae is 5 mm long, the Re is 20.

Recalling that at high Re, beat-and-glide swimming is the more efficient motion (Weihs 1974), the energy saving obtained is probably one of the reasons for the observed change in swimming behavior.

The fact that the average continuous speeds are much higher also results in savings of energy. For a 3-4 mm long larva, swimming at over 1 cm/s brings it again to Re of over 20, so that the drag coefficient is smaller, and some coasting at the end of the bout of continuous swimming is possible. At lower Re, in the purely viscous regime, no coasting is possible as the inertial effects are negligible and motion ceases immediately when oscillations stop. It is therefore advantageous for the fish, for hydrodynamic reasons, to swim continuously during the first few days of the larval phase, changing to beat-and-glide swimming later on. It should be noted here that the present calculations and data are for a water temperature of 17°-18° C. Both viscosity of water and the growth rate of larvae (see footnote 2) depend on the temperature, so that data collected under different ambient conditions might lead to a later (or earlier, if the temperature is higher) change of swimming mode.

Further examination of Figure 1 shows that for each terminal velocity in the beating stage there is a value of $\bar{U}_c$ for which the ratio S attains a minimum (marked by the dashed line). The value of this minimum approaches unity and the curves become more shallow as $\bar{U}_f$ increases. Thus, if an anchovy larva swims intermittently at low Re, it should do so at high average speeds, so that the energy penalties incurred due to swimming in the beat-and-glide mode are minimal.

Figure 1 also shows that the lowest penalties for using intermittent swimming are obtained when $\bar{U}_f$ approaches unity, for the whole range of average speeds. Therefore, the value $\bar{U}_f = 0.995$ was chosen for calculations of the effect of varying α (the ratio of swimming to coasting drag). These appear in Figure 2, where the dependence of S on $\bar{U}_c$ is shown. The range of values of α to be expected in nature is described by the shaded area, showing as expected that the smaller the α the more advantageous is continuous swimming. When $\alpha > 2$, which can only happen at higher Re, a range of values of $\bar{U}_c$ and $\bar{U}_f$ exists where S is smaller than unity, i.e., intermittent swimming is more efficient. This is shown by the dashed curve on Figure 2 where for $\bar{U}_f = 0.995$ and $0.79 < \bar{U}_c < 1$, $S < 1$. This curve will be discussed later, in reference to the transition region between the low and high Re domains.

The results discussed above all dealt with the low Re range. For comparison, we now show the equivalent energy ratio for high Re, i.e., the domain relevant to larger larvae as well as adult anchovy (>15 mm long). The results presented

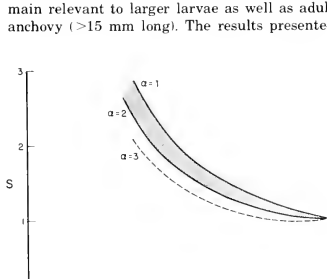


FIGURE 2.—Influence of changes in ratio of swimming drag to gliding drag α on the energy ratio S, versus nondimensional average speed $\bar{U}_c$. Shaded area is the range of possible α at low Reynolds numbers. $\bar{U}_f = 0.995$ (See Figure 1 for definitions).

[2]Zweifel, J. R., and J. R. Hunter 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 13 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

stem from calculations based on the analysis in Weihs (1974). The ratio of energy per unit distance traversed in intermittent swimming to that of continuous swimming at the same average speed R, can be shown to be, in present notation,

$$R = \frac{\tanh^{-1}\left(\frac{\tilde{U}_f - \tilde{U}_i}{1 - \tilde{U}_i\tilde{U}_f}\right)\left[\tanh^{-1}\left(\frac{\tilde{U}_f - \tilde{U}_i}{1 - \tilde{U}_i\tilde{U}_f}\right) + \alpha\left(\frac{1}{\tilde{U}_i} - \frac{1}{\tilde{U}_f}\right)\right]}{\left[\ln\left\{\cosh\left[\tanh^{-1}\left(\frac{\tilde{U}_f - \tilde{U}_i}{1 - \tilde{U}_i\tilde{U}_f}\right)\right] + \tilde{U}_i \sinh\left[\tanh^{-1}\left(\frac{\tilde{U}_f - \tilde{U}_i}{1 - \tilde{U}_i\tilde{U}_f}\right)\right] + \alpha \ln\frac{\tilde{U}_f}{\tilde{U}_i}\right\}\right]^2}. \quad (25)$$

The computed values of R, for $\alpha = 2$, appear in Figure 3. Each full line describes the values of R for a given $\tilde{U}_f$ as a function of the average velocity U_c. Each of these curves ends at $\tilde{U}_c = U_f$ and, in a similar manner to Figure 1, has a minimum for a lower value of U_c. Here, however, all curves have a large section in the range $R < 1$, i.e., intermittent swimming is more efficient. In fact, the slower the average velocity, the higher the possible gains, as shown by the dashed line which is the locus of lowest values of R as a function of $\tilde{U}_c$. As already mentioned in Weihs (1974), this curve goes monotonously from unity at $\tilde{U}_c = 1$ (continuous swimming by definition) to $1/\alpha$ at $U_c \to 0$. One can therefore predict that fish species using the anguilliform swimming mode (Breder 1926) will find intermittent swimming relatively more efficient than carangiform swimmers as α is greater for anguilliform swimming in which most of the body is oscillated. Another result is that for greatest gains, the average speed during the whole beat-and-glide should be as low as possible, with small differences between $\tilde{U}_i$ and $\tilde{U}_f$.

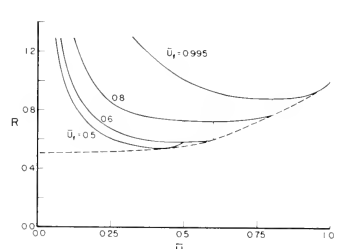


FIGURE 3.—The ratio of energy required per unit distance R, for intermittent and continuous swimming at high Reynolds numbers, respectively, versus nondimensional average speed U_c. Dashed lines shows locus of minimum values of R attainable as a function of U_c. See Figure 1 for definitions.

Anchovy, which swim in the anguilliform mode, fulfill both these predictions as adults and more mature larvae usually swim by means of a single beat followed by a long glide, so that 1) $\tilde{U}_i$ and $\tilde{U}_f$ are not too different and 2) $\tilde{U}_i$ is rather low.

Having examined the low and high Re domains, where the drag coefficient is porportional to the reciprocal of Re, and constant, respectively, we now look at the transition regime between them. Based on average swimming speeds of 0.8 body length/s, larvae will be in this regime when they are from 5 to 15 mm in length. Analysis of the forces and energy is much more complicated here because the hydrodynamic drag is

$$C_D \propto \mathrm{Re}^{-\beta} \quad (26)$$

where β is not constant, but itself is a function of both Re and body shape. This results in Equation (4) taking the form

$$T = m\frac{du}{dt} + \alpha K u^{2-\beta} \quad (27)$$

a differential equation that has to be solved numerically when β is not zero or one (the two cases discussed previously). While this in itself is a relatively straightforward task, the generality and accuracy of the previous solutions is immediately lost as numerical values for the mass and K have to be included. K especially is known very inaccurately as it includes the numerical drag coefficient and the frontal area (which varies at different speeds and times). The setting of β is even more problematical as it depends on the instantaneous swimming speed in an empirical manner (which

is, however, not known at the present time), thus changing during the beat-and-glide cycle. No single value may therefore be taken to describe a given beat-and-glide behavior and an average value has to be used. This adds greatly to the inaccuracy as β is an exponent. Bearing especially the latter factor in mind, no smooth curves of the type appearing in Figures 1-3 can be expected.

In order to try and make clear how the transition regime influences the energetics of swimming, in spite of the difficulties mentioned, curves such as those from Figures 1 and 3 are reproduced in Figure 4. The purpose of this Figure is to show that by using the correct nondimensional description, curves for the viscous and nonviscous regimes can be compared. Both the dashed and full curves have similar shape, going to infinity for $\bar{U}_c \to 0$ and having a minimum at the higher values of $\bar{U}_c$, the values increasing again for $\bar{U}_c \to \bar{U}_f$. One must recall that the absolute speeds and sizes are very much different for the two cases, this resulting from the difference in U_0, the maximum sustained speed. U_0 is much larger for the full curves. The dashed curves have $\beta = 1$ while the full lines are for $\beta = 0$. Therefore, calculations at any intermediate values of β are expected to fall between them.

Some calculated values appear in Figure 4, for two values of average β. While they show the expected behavior, their actual values are, as mentioned before, unreliable, because they are based on rough estimates of various coefficients which do not have to be made when $\beta = 0$ or 1. These computations are to be taken only as an indication that the expected gradual transition actually occurs and are not to be used for actual calculations.

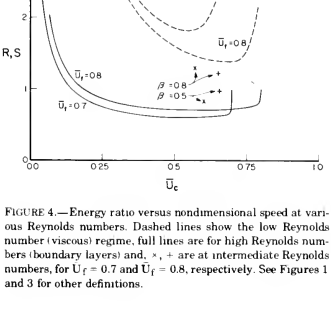


FIGURE 4.—Energy ratio versus nondimensional speed at various Reynolds numbers. Dashed lines show the low Reynolds number (viscous) regime, full lines are for high Reynolds numbers (boundary layers) and, ×, + are at intermediate Reynolds numbers, for $\bar{U}_f = 0.7$ and $\bar{U}_f = 0.8$, respectively. See Figures 1 and 3 for other definitions.

Keeping these limitations in mind, one can tentatively come to the conclusion that the intermediate Re regime is one of gradual transition. The advantage of beat-and-glide intermittent swimming becomes more and more significant as the larva grows, after the 4th day after hatching.

This conclusion can be strengthened, in a roundabout manner, by a different approach. The ratio of swimming to gliding drag for a given animal is 2 in the low Re regime, and up to 4 for high Re. Therefore taking a higher value of α for the viscous domain calculations can indicate, in a different manner, the trend of results when increasing Re. This appears in Figure 2, where the dashed line stands for $\alpha = 3$. It can be seen that this curve is intermediate between typical curves for the viscous (Figure 1) and inertial regimes (Figure 3).

CONCLUDING REMARKS

It was demonstrated in the previous section that the change in swimming style observed when anchovy larvae reach the age of 4-5 days is correlated with the passage of the animal from the highly viscous regime to the boundary layer regime. My calculations show that this behavioral change is an adaptive energy sparing mechanism. When the larva is <5 mm long, it can only progress by actively swimming as the enhanced effect of viscosity will bring it to a rapid halt when coasting. The yolk-sac, which still exists as a spherical protrusion, increases the drag even further at this stage. The drag coefficient here is inversely proportional to the velocity so that any low-speed motion is very costly in terms of energy. As a result, interspersing coasting and accelerating is not an efficient way of progressing. When the larva is larger (>5 mm) and moving faster, viscous effects are concentrated in a thin layer surrounding the fish and the influence of speed and shape on drag changes. At this stage, it is shown that intermittent motion is the more efficient for fish species such as anchovy which swim in the anguilliform mode. Intermittent motion is much less efficient for carangiform swimmers at all sizes (Weihs 1974) which may explain why species such as mackerel swim continuously at all phases of life.

ACKNOWLEDGMENTS

I would like to thank John Hunter and Reuben Lasker for their hospitality as well as for very helpful discussions and comments. This work was done while I was a NRC-NOAA Senior Resident Research Associate, on leave from Technion, Israel Institute of Technology, Haifa. I am grateful to the NRC, and especially R. C. Kinney, for making this visit possible.

LITERATURE CITED

BREDER, C. M., JR.
1926 The locomotion of fishes. Zoologica (N.Y.) 4:159-297.

HOERNER, S. D.
1965. Fluid dynamic drag. S. F. Hoerner, N.J., 420 p.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

VLYMEN, W. J. III.
1974 Swimming energetics of the larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 72:885-899.

WEBB, P. W.
1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can., Bull. 190, 158 p.

WEIHS, D.
1974 Energetic advantages of burst swimming of fish. J. Theor. Biol. 48:215-229.

WU, T. Y.-T., C. J. BROKAW, AND C. BRENNEN (editors).
1975. Swimming and flying in nature, Vol. 1, 421 p. Plenum Press, N.Y.

AN ANTIPREDATION MECHANISM OF THE POLYCHAETE *PHYLLODOCE MUCOSA* WITH NOTES ON SIMILAR MECHANISMS IN OTHER POTENTIAL PREY[1]

ROBERT S PREZANT[2]

ABSTRACT

The polychaete *Phyllodoce mucosa* exhibits an antipredation response via the extrusion of a repulsive mucoid secretion The mucus, secreted by large glandular regions of the dorsal and ventral parapodial cirri, prevents immediate ingestion of the worm by several species of small or juvenile fish A sipunculid, *Phascoleopsis gouldi*; a nemertean, *Lineus ruber*; and a large flatworm, *Stylochus zebra*, are also distasteful to some potential predators. Antipredation responses found in some organisms may play an important role in regulating benthic community dynamics by mediating the feeding habits of certain predators during at least some stage of their development

Feeding habits of many species of fish have been well established, but few studies have extended analyses beyond stomach contents. Results of such research frequently lead to labeling food found in the stomach as "preferred" (Onyia 1973; Smith and Daiber 1977). Reports of selective feeding behavior based mainly on stomach contents reveal the major types of food eaten by a fish but do not add substantially to our understanding of the interactions between predator and prey.

Ivlev (1961), discussing selective feeding by fishes, included the role of "constitutional defenses" of potential prey species as a mechanism which may contribute to predatory selectivity. Selectivity in food thus entails not only "preference" but avoidance of specific potential food items (Berg 1979). Bakus (1966) considered the possible role of antipredatory responses by some tropical reef inhabitants. He noted that several members of a reef community that are not readily able to retreat into the security of a coral crevice or not naturally protected by skeletal armor are either poisonous, venomous, or distasteful to predators. Acidic secretions from epidermal glands of some opisthobranch gastropods (Graham 1957; Thompson 1960, 1969) and some nemerteans (Gibson 1972) function as predatory deterrents. In view of the fact that predation is a well established cause of quantitative changes in a population of prey species, the ability of some members of a community to thwart extensive predatory cropping by using inherent protective devices may also affect community structure.

An accurate picture of community dynamics demands a closer examination of direct interactions between potential prey and predatory species. A start in this direction has been made on a limited number of fish. Hynes (1950), Tugendhat (1960), and Beukema (1968) examined some of the behavioral feeding patterns of the threespine stickleback, *Gasterosteus aculeatus*. They found that selective feeding of the stickleback is influenced by degree of satiation and palatability of food. This may have implications extending into the natural environment with regard to seasonal, predatory, or man-induced changes in community structure. In food-limited situations "selectivity" may decrease. The presence of a predatory deterrent in an organism may thus be functionally operative only in a nonstressed community with nonstarved predators.

Polychaetes often dominate marine benthic communities (Sanders et al. 1965) and many bottom feeding fish eat substantial quantities of these worms (Qasim 1957; Nikolsky 1963; Kislalioglu and Gibson 1977). Obscurance of taxonomic characters due to digestion often prevents identification of prey to species, so food items tend to be listed in terms of higher taxonomic levels (Hynes 1950; Kneib and Stiven 1978). This is especially true for soft bodied prey organisms and means that accurate feeding records are often nonspecific and possibly biased relative to the researcher's taxonomic expertise.

[1]University of Delaware, College of Marine Studies Contribution No 130

[2]University of Delaware, College of Marine Studies, Lewes, DE 19958.

Manuscript accepted April 1979
FISHERY BULLETIN VOL 77, NO 3, 1980

Phyllodocid polychaetes secrete copious amounts of mucus when irritated (Fauchald 1977). Pettibone (1963) briefly noted that the mucoid secretion of *Phyllodoce maculata* may be offensive to predators. Preliminary observations of *P. maculata* and *P. mucosa* (Prezant 1975, unpubl. data) have confirmed that an epithelial, mucoid secretion acts as an antipredatory mechanism against at least one species of fish, the rock gunnel, *Pholis gunnellus*.

The present study extends these observations by quantitative experiments on behavioral interactions of *Phyllodoce mucosa* with several species of small or juvenile fish, and examines the possible defensive mechanism of this polychaete. Initial observations concerning antipredatory mechanisms in the phyllodocids *Eumida sanguinea* and *P. maculata*, the large flatworm *Stylochus zebra*, the sipunculid *Phascoleopsis gouldi*, and the nemertean *Lineus ruber* are also reported.

METHODS

Phyllodoce mucosa (Phyllodocidae) was collected in late August 1978 in Nahant Bay, Mass., by epibenthic sled from a fine sand substratum at a depth of about 17 m. *Eumida sanguinea* and the orbiniid *Scoloplos fragilis* were collected intertidally from Henlopen Flat, Lewes, Del., in early September 1978. *Scoloplos fragilis* was used as a control in the behavioral experiments because, despite its overall gross similarity to phyllodocids (i.e., long, thin worms of similar proportions), *S. fragilis* produces considerably less external mucus than *P. mucosa*. Worms were maintained in separate finger bowls on a running seawater table at 17 C and 32‰ salinity.

Fish used in behavioral experiments (Table 1) were collected in July 1978 and allowed to acclimatize for 30-60 days in separate compartments on the seawater table. During acclimatization, the fish were fed a variety of foods from a widemouthed glass pipette. Foods included bits of fresh blue mussel, *Mytilus edulis*; and American oyster, *Crassostrea virginica*; live tubificid oligochaetes, *Tubifex* spp.; brine shrimp, *Artemia marina*; and, infrequently, frozen brine shrimp.

Phyllodoce mucosa, typically found on fine sand substrata from low water to depths over 500 m, ranges from Labrador to Mexico (Pettibone 1963) thus geographically overlapping with all fish species used in this study (Table 1).

Since this research dealt principally with the inability of certain predators to eat *P. mucosa*, it was important to insure that the fish used would actively feed throughout the experimental period. Accordingly, several other species of polychaetes

TABLE 1.—The range, habitat, food habits, and collection sites of the species of fish used in the feeding experiments. The last column lists the test organisms offered to fish. Quantitative results are available only for *Phyllodoce mucosa*. Range, habitat, and feeding habit data for the fish are from Hildebrand and Schroeder (1928), Bigelow and Schroeder (1953), Chao and Musick (1977), and Kneib and Stiven (1978).

Fish species	Range and habitat	Feeding habits	Fish collection site	Test organism
Atlantic silverside *Menidia menidia*	Nova Scotia to northern Florida; often over sandy or gravelly shores	Small crustaceans and molluscs, annelids, small fish, eggs, and plant material	Lewes Beach, Lewes, Del	*Phyllodoce mucosa* *Scoloplos fragilis*
Weakfish, *Cynoscion regalis*	Nova Scotia to Florida, shallow coastal waters in summer	Fish, crabs, amphipods, mysids, shrimp, molluscs, annelids	Lewes Beach	*P. mucosa* *Phascoleopsis gouldi* *S. fragilis*
Windowpane flounder, *Lophopsetta maculata*	Gulf of St. Lawrence to South Carolina; sand bottoms from low water to 50 m	Mobile prey such as mysids, fish, shrimp, errant polychaetes	Lewes Beach and near Delaware Bay mouth at 18 m	*Phyllodoce mucosa* *Eumida sanguinea* *S. fragilis*
Sheepshead minnow *Cyprinodon variegatus*	Cape Cod to Mexico; shallow waters of inlets and bays, salt marshes	Mobile epifauna including annelids	Lewes Beach	*P. mucosa* *S. fragilis*
Mummichog, *Fundulus heteroclitus*	Labrador to Mexico, shallow coastal waters especially salt marshes	Omnivorous (at least when ~30 mm) including small crustaceans, annelids, and carrion	Canary Creek, Lewes, Del	*P. mucosa* *Phascoleopsis gouldi* *S. fragilis*
Threespine stickleback, *Gasterosteus aculeatus*	Labrador to Virginia, salt and fresh waters	Small invertebrates, fish fry, eggs	East Point, Nahant, Mass., tide pool	*Phyllodoce mucosa* *S. fragilis*
Striped sea robin, *Prionotus evolans*	Gulf of Maine to South Carolina, coastal bottom dweller	Crustaceans, molluscs, annelids, small fish	Near Delaware Bay mouth at 18 m	*Stylochus zebra* *Phascoleopsis gouldi* *Lineus ruber*
Rock gunnel, *Pholis gunnelus*	Hudson Strait to Delaware, generally on rocky bottoms from low water to over 200 m	Molluscs, crustaceans, annelids	East Point, Nahant tide pool	*Phyllodoce mucosa* *P. maculata* *Nephtys incisa*

were fed to the fish before and following behavioral experiments. These worms, which were from various size classes, included: *Spio filicornis* (Spionidae) and *Nephtys incisa* (Nephtyidae) collected from Nahant Bay; and *Glycera americana* (Glyceridae), *Nereis virens* (Nereidae), *Scolecolepides viridis* (Orbinidae), and *Hydrodes dianthus* (Serpulidae) collected from Henlopen Flats.

The feeding behavior of each species of fish, excluding *Prionotus evolans* and *Pholis gunnellus*, was tested quantitatively with *Phyllodoce mucosa* and *Scoloplos fragilis*. Fish were starved for 24-48 h prior to testing. An individual fish was then placed in a separate 4 l glass aquarium or in a small compartment on the seawater table and allowed to acclimate for 60 min prior to experimentation. Each test session was composed of two sets of observations separated by a 5-min interval. A set consisted of five 1-min trials each separated by a 2-min interval. The trials entailed repeated exposure of randomly chosen worms to potential predation by each fish by dropping the worm from a widemouthed glass pipette in close proximity to the head of the fish. Since the fish were previously fed from a pipette, they showed no hesitation in accepting potential food items delivered in this manner. Following release from the pipette, several possible combinations of behavioral responses of the fish were noted: 1) ingestion of the worm, 2) rejection of the worm following an active attempt at ingestion, 3) presence or absence of investigations of the worm by the fish (investigation is defined here as an obvious "enticement" of the fish to the worm without an attempt at ingestion), and 4) avoidance of the fish to the worm. The behavior of *P. mucosa* was also noted following release from the pipette and after rejection or avoidance by the fish.

If the worm sank to the floor of the aquarium, either after rejection or without any contact with the fish, it was taken off the bottom and again dropped in front of the fish. This process was repeated as often as a 1-min trial would allow. Discounting delays due to behavioral interactions, this averaged one exposure every 6 s. Prior to the start of the first set of each test session and 1 min after each trial ended, the fish was fed a small portion of frozen brine shrimp to ensure active feeding. If at any time during a test the fish refused to eat the brine shrimp, the experiment was terminated. Because of terminations, the number of sessions per species of fish varied. Initial qualitative tests subjecting various other test organisms found on Henlopen Flats to potential predation are also noted on Table 1.

To test whether the mucoid secretion truly acts as the predatory inhibitor in *P. mucosa*, two further tests were carried out. First, mucus was removed from the surface of *P. mucosa* by repeatedly sucking the worm in and out of a narrow-mouthed glass pipette and then gently dabbing it with a clean, lintless cloth. The worm was then fed to a rock gunnel. Second, mucus from *P. mucosa* was collected by placing several of the worms in a small, dry stendor dish, allowing the worms to physically irritate each other and thus produce a copious supply of mucus. After the phyllodocids were removed from the dish, a small *Nephtys incisa*, which secretes very little external mucus, was placed in it and allowed to accumulate a thick mucoid coat. The nephtyd was then fed to the rock gunnel.

For histological study of the mucus-producing organs of *P. mucosa*, entire worms were fixed in Zenker's or Hollande's fixatives and embedded in polyester wax. Blocks were cut at 5 μm and sections stained with Mallory's "Azan" or toluidine blue in 1.0% borax.

To examine the ultrastructure of the parapodial cirri of *P. mucosa*, small worms were fixed for 1 h in cold Anderson's fixative, cut into 2 mm sections with a razor blade, thoroughly rinsed with phosphate buffer (pH 7.2), and postfixed for 1 h in 2.0% osmium tetroxide in a phosphate buffer. Following dehydration in a graded acetone series, the specimens were embedded in Spurr's low viscosity medium and polymerized at 60° C for 48 h. Thin sections, cut on a Porter-Blum[3] MT1 ultramicrotome using glass knives, were stained with uranyl acetate and Sato lead citrate. Sections were examined with a Philips EM201 transmission electron microscope at an accelerating voltage of 80 kV.

RESULTS

Response of Fish

Results of the feeding experiments for the various species of fish being fed *P. mucosa* along with the length of each are summarized in Tables 2 and

[3]Reference to trade names does not imply endorsement by the University of Delaware, College of Marine Studies or by the National Marine Fisheries Service, NOAA

TABLE 2.—Number of attempts to ingest *Phyllodoce mucosa* by several species of fish. An attempt is defined as a single intake and expulsion of the worm. The number following the abbreviated fish binomial stands for an individual fish and the small letter that follows stands for an individual worm. The two numbers in parenthesis in the first column are the standard lengths of the fish and maximum length of the worm, in millimeters, respectively. Fh = *Fundulus heteroclitus*, Ga = *Gasterosteus aculeatus*, Mm = *Menidia menidia*, Cv = *Cyprinodon variegatus*, Lm = *Lophopsetta maculata*, Cr = Cynoscion regalis, † =experiment terminated, * = worm eaten.

	Set A, trial					Set B, trial					
Session	1	2	3	4	5	1	2	3	4	5	Total
Fh1a (63,22)	3	5*									8
Fh1b (63,29)	9	4*									13
Fh2c (66,18)	4	2*									6
Fh3d (52,19)	13*										13
Fh4e (61,19)	10*										10
Ga1a (18,9)	4	7	3	1	0	6	5	0	0	0	26
Ga2a (18,15)	21	4	0	2	1	20	5*				53
Ga2b (18,12)	2	4	0	2	1	20	5*				34
Ga3c (18,13)	29	5*									34
Ga3d (18,24)	0	0	0	0	0	0	1	0	0	0	1
Ga4e (18,12)	14	5	0	0	0†						19
Ga5e (18,12)	8	0	0	0	0†						8
Mm1a (44,24)	5	2	1	3	1	0	0	0	0	0	12
Mm2b (37,22)	4	3	1	1	0	1	1	0	0	0	11
Mm3c (51,17)	10	4	4	0	0†						18
Mm4d (54,14)	3	2	2*								7
Mm5e (64,18)	1*										1
Mm5f (64,23)	2*										2
Mm6g (67,13)	4*										4
Cv1a (46,24)	2	2	1	1	1	1	1	3	1	2	15
Cv1b (46,24)	1	1	1	1	2	2	3	4	1	0	16
Cv2c (46,14)	3	1	1	1	0	1	1	0	0	0	8
Cv2d (46,12)	2	3	3	1	2	2	3	3	3	2	24
Lm1a (69,29)	3	1	1	2	1	2	0	0	1	0	11
Lm1b (69,21)	6	4	3	1	3	5	5	3	0	1	31
Lm2a (91,29)	2	1	2	2	2	2	0	0	1	1	13
Lm2c (91,17)	2	5	5	1	3	3	3	0	0	0	22
Lm2d (91,21)	7	3	3	4	3	3	3	0	0	1	27
Cr1a (42,24)	1	2	1	1	0	0	1	0	0	0	6
Cr1b (42,16)	2	2	4	2	2	2	2	3	2	2	23
Cr1c (42,26)	0†										0
Cr2d (46,14)	2	6	1	6	5	4	5	6	4	5	44
Cr2e (46,22)	0†										0
Cr2f (46,17)	2	4	5	5	3	4	5	3	5	4	40

3. The large number of ingestive attempts in a given trial (Table 2) resulted from the rapid, repetitive actions of a fish not allowing the worm to settle to the floor of the aquarium following initial attempts. Results of the control series using *S. fragilis* and sizes of fish and worms are given in Table 4.

Of the six species of fish quantitatively tested, only the mummichog, *Fundulus heteroclitus*, consistently ingested *P. mucosa* early in set A (Table 2). This species of fish showed no investigative behavior before taking the worm into its mouth. Nevertheless, *F. heteroclitus* did show some distaste for this polychaete; in two cases the mummichog sucked the worm in and out 13 times prior to ingestion. When *F. heteroclitus* did eat the worm, ingestion was immediately followed by a variable period (10-45 s) of choking or "coughing"

TABLE 3.—Number of investigations undertaken by four species of fish when exposed to *Phyllodoce mucosa*. This table excludes *Fundulus heteroclitus* and *Cyprinodon variegatus* because these species showed no or insignificant investigatory behavior without attempts at ingestion. Abbreviations and notations as in Table 2.

	Set A, trial					Set B, trial					
Session	1	2	3	4	5	1	2	3	4	5	Total
Ga1a (18,9)	0	0	0	0	4	0	0	4	3	3	14
Ga2a (18,15)	0	0	0	0	2	0	*				2
Ga2b (18,12)	0	0	0	0	3	2	*				5
Ga3c (18,13)	0	*									0
Ga3d (18,24)	3	0	2	1	1	0	0	1	0	1	9
Ga4e (18,12)	0	0	5	1	†						6
Ga5e (18,12)	0	2	2	1	†						5
Mm1a (44,24)	0	0	0	2	0	2	0	1	0	1	6
Mm2b (37,22)	4	0	0	1	0	0	0	0	0	0	5
Mm3c (51,14)	0	1	3	1	†						5
Mm4d (54,14)	0	0	*								0
Mm5e (64,18)	*										0
Mm5f (64,23)	*										0
Mm6g (67,13)	*										0
Lm1a (69,29)	0	0	0	0	0	0	0	0	0	1	1
Lm1b (69,21)	0	2	0	3	3	2	2	1	2	3	18
Lm2a (91,29)	0	0	0	0	2	0	0	0	1	0	3
Lm2c (91,17)	0	0	0	0	0	0	0	0	0	0	0
Lm2d (91,21)	0	0	0	3	2	1	2	2	0	2	12
Cr1a (42,24)	3	0	1	6	2	3	4	0	3	1	23
Cr1b (42,16)	2	1	1	3	1	3	2	4	2	4	23
Cr1c (42,26)	†										0
Cr2d (46,14)	2	0	3	2	3	2	3	1	4	3	23
Cr2e (46,22)	†										0
Cr2f (46,17)	1	2	2	2	2	1	1	3	1	4	19

TABLE 4.—Number of attempts to ingest the control polychaete *Scoloplos fragilis* and size of fish and worm used. Abbreviations and notations as in Table 2

	Trial			Trial	
Session	1	2	Session	1	2
Fh1x (48,15)	1		Lm1w (69,16)	4	
Fh1y (48,20)	1		Lm1x (69,25)	1	
Ga1x (18,11)	1		Lm2y (91,17)	12	9
Ga2y (18, 9)	1		Lm2z (91,23)	11†	
Mm1x (37,14)	1		Cr1x (42,14)	1	
Mm2y (64,13)	1		Cr1y (42,17)	5	
Cv1x (46,13)	1				
Cv2y (46,26)	1				

(rapid protraction and retraction of jaws and intake and expulsion of water). In session Fh1a, the worm was held in the mouth and only partially ejected many times prior to ingestion. During trial 2 of set A in session Fh1b, the fish, on the fourth attempt, took in the worm and exhibited a choking response which lasted 15 s before spitting out the posterior portion of the worm. The remaining portion of the polychaete was eaten after two further attempts. The maximal number of attempts prior to ingestion by *F. heteroclitus* was demonstrated by the smallest mummichog (Fh3d) and in trials involving the largest phyllodocid (Fh1b) (Table 2). *Scoloplos fragilis* was consumed on the first attempt by *F. heteroclitus* in each control test (Table 4).

While only one size class of *Gasterosteus aculeatus* was used, there was no trend between size of the worm and ingestion by the fish (Table 2). The largest as well as some of the smaller worms were not consumed. Sessions Ga1a, 2b, and 3a all resulted in ultimate ingestion of *P. mucosa* but involved 34-53 prior ingestive attempts. Of the seven sessions observed with *G. aculeatus*, these three sessions showed the highest number of attempted ingestions prior to consumption. In session Ga2a, there was a renewed expression of the antipredation mechanism at the start of set B (Table 2). Thus, sets A and B start with 21 and 20 attempts, respectively, followed by a decrease in the number of attempts in set A and consumption in trial 2 of set B.

In most of the sessions between *G. aculeatus* and *P. mucosa*, lack of ingestive attempts seemed to correspond with the presence of investigative responses (Tables 2, 3). These investigations involved a close approach to the worm as it sank through the water column, and in some cases a recoil from the worm without evidence of direct contact. In cases where the worm was consumed, the fish exhibited a coughing response which lasted several seconds. *Gasterosteus aculeatus* readily consumed *S. fragilis* (Table 4).

A correlation between the size of the Atlantic silverside, *Menidia menidia*, and its ability to consume *P. mucosa* is suggested (Table 2). Smaller fish showed little interest in the worms following initial experiences in set A, while the larger fish often consumed the worm very early in the first set. During set A, fish 50 mm initiated several attacks on the phyllodocids, and the worm was easily taken into the buccal cavity before rejection. A rejected worm was often so densely covered with mucus that it would cling to the lower lip of the fish by a mucus thread for several seconds. *Menidia menidia* also exhibited coughing reactions following attempted and successful ingestions. Larger silversides were quick to respond to potential food items released into the aquarium and swiftly sucked them in. In set Mm5f, a 64 mm fish was fed a 23 mm worm. On the first attempt at ingestion by the fish, the worm was quickly taken, whereupon the fish reacted with a coughing response lasting 45 s. The fish also exhibited a violent lateral head shaking during this time. Following this, the worm was totally ejected but the fish continued reacting as described for several seconds. This was the only case where an entire worm was injured prior to ejection. The worm, though alive, lost several parapodia and cirri and appeared sluggish. This same worm was again placed in the aquarium with the fish and was again set upon, producing a coughing response lasting 30 s but was not rejected. This fish did postfeed on *A. marina* and *M. mendia* showed no hesitation in consuming *S. fragilis*.

Only a single size class of sheepshead minnow, *Cyprinodon variegatus*, was available. This species was exposed to *P. mucosa* ranging in size from 12 to 24 mm and showed a consistent rejection of each size class (Table 2). In no case was a coughing reaction noted. *Cyprinodon variegatus* appeared able to distinguish between *P. mucosa* and *A. marina* from short distances (up to 15 cm). The fish showed almost no investigatory behavior after initial ingestive attempts in a given trial but did quickly swim over to feed on *A. marina* in every case of exposure. *Scoloplos fragilis* was eaten on the first attempt in each control test with *C. variegatus* (Table 4).

The windowpane flounder, *Lophopsetta maculata*, was the largest fish used in this study. This species rejected the phyllodocids without fail, showing 11-31 attempts at ingestion (Table 2) and also exhibited coughing responses following ingestive attempts. The two sessions with *L. maculata*, making the greatest number of attempts to ingest (Lm1b and 2d) (Table 2), also registered the greatest degree of inquisitiveness (Table 3). There was no relation between size of fish and size of worm in these interactions. As Table 4 shows, there was some hesitation by the larger *L. maculata* in the control series when offered *S. fragilis*. In all of these control tests but one (Lm2z was terminated), the fish eventually ate the worm, but in Lm2y the fish made 21 attempts and ran into the second trial of set A prior to ingestion. Less than 1 h later, this same fish actively and quickly fed on 12 mm *Scolecolepides viridis* and 31 mm *Nereis virens*.

Juvenile weakfish, *Cynoscion regalis*, also refused to eat *P. mucosa* (Table 2). There may be a relationship between the number of attempts to ingest and the size of the worm in these cases (Table 2). In Cr1c and 2e, the worms used were among the three largest (26 and 22 mm, respectively), and in both cases the fish showed a violent headshaking response to void its buccal chamber. It thereafter became "nervous" and would not feed on *A. marina*. In Cr1a a 24 mm worm was used, and in the entire session only six attempts at ingestion were made. All the remaining *P. mucosa*

tested with *C. regalis* were ~20 mm long, and ingestive attempts ranged from 23 to 44/session. *Cynoscion regalis* exhibited frequent investigative responses (Table 3) which, unlike those of most of the other fish, usually involved direct contact with the worm by bumping it with its snout. In some cases following this contact, the fish would show a headshaking reaction similar to that produced by attempted ingestion. *Cynoscion regalis* consumed *Scoloplos fragilis* during the first trials of the control series (Table 4).

During the course of these experiments, individuals of each species of fish were given the opportunity to feed on several other species of polychaetes. These included *Spio filicornis, Nephtys incisa, Nereis virens, Glycera americana, Scolecolepides viridis,* and *Hydroides dianthus*. Each fish readily consumed each of these species from several size classes, in almost every case on the first attempt.

Preliminary data has also been collected on *Eumida sanguinea* tested with *L. maculata*. Test worms ranged from 9 to 13 mm long and were consistently rejected. A 69 mm *L. maculata* rejected a 13 mm long *E. sanguinea* 20 times over a single session, while a 91 mm flounder rejected a 12 mm long worm 38 times in a session. Investigations ranged from 6 to 10/session and showed no obvious relationship with ingestive attempts. In qualitative observations, it was also noted that the rock gunnel rejected both *P. mucosa* and *P maculata*.

Removal of the mucus coat from *P. mucosa* resulted in quick consumption by *Pholis gunnellus*. Emplacement of the phyllodocid mucus on a small *Nephtys incisa*, which were previously a quick meal for *P. gunnellus*, resulted in rejection of the nephtyd polychaete by the rock gunnel many times prior to ingestion.

Initial observations were also made on the sea robin, *Prionotus evolans*, fed *Stylochus zebra, Lineus ruber*, and *Phascolcopsis gouldi*. *Fundulus heteroclitus* and *C. regalis* were also tested with *P. gouldi*. In each case the fish showed adverse reactions (coughing, headshaking, and rejection) after ingestive attempts. The sea robin rejected *S. zebra* 75 times over eight trials before consuming the flatworm. In many cases, the turbellarian was held in the buccal chamber for as long as 21 s before ejection. Both the nemertean and the flatworm produced copius quantities of mucus when irritated, whereas the sipunculid did not.

Behavior of *Phyllodoce mucosa*

Phyllodoce mucosa showed relatively consistent reactions upon release into the aquarium and following rejection. When first released, the worm fell slowly through the water in a semicurl position, or curled in a tight ball and fell at a slightly faster rate. After a worm was taken and rejected by a fish, it was covered with a thick layer of viscous mucus. Immediately after rejection, the worm coiled into the tight, spheroid position. In this position, it was either retaken by the fish and the process repeated until the worm was eaten, or the worm was dropped, after initial attempts, to the floor of the tank. If the worm drifted unharmed to the floor of the aquarium, it usually started what appeared to be an exploratory phase which consisted of several short excursions in various directions before setting out on a single, straight path toward one of the corners of the aquarium. During this exploratory period, the worm held its dorsal parapodial cirri folded against its dorsum.

Histology and Ultrastructure of *Phyllodoce mucosa* Parapodial Cirri

The glandular and sensitive dorsal and ventral parapodial cirri of *P. mucosa* are the primary sources of externally released mucoid secretion.

The dorsal cirrus possesses a large nerve which runs along the cirral axis and then radiates centrally into several smaller nerves which wind between the large cirral mucocytes (Figure 1). Numerous free neural extensions penetrate the cirral epithelium. Large, ovoid mucocytes, which stain beta-metachromatically with toluidine blue (Figure 1, lower), fill most of the cirrus. These broad and elongated cells have small basal nuclei. In worms that have been irritated prior to fixation, the previously metachromatic mucocytes appear as large, empty vacuoles surrounded by many immature mucus cells (Figure 1, upper). The latter are usually small, irregularly shaped cells which are densely packed with basophilic but orthochromatic secretory granules. The outer, central portion of the dorsal cirrus has a narrow bank of melanic pigment cells. There are also thin muscle bands which enter the cirrus along the dorsal region of the cirral peduncle.

Electron microscopy reveals a dense microvillar and ciliary border lining the short, columnar epithelium of the dorsal cirrus (Figure 2). The epithelial cells have large, irregular nuclei with

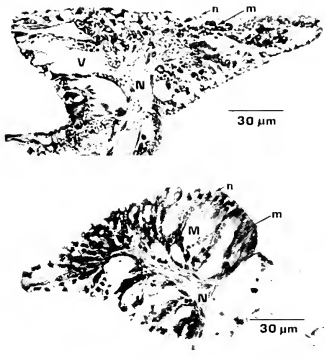


FIGURE 1.—Upper: An oblique-frontal section of the dorsal parapodial cirrus of the polychaete *Phyllodoce mucosa*. This specimen was irritated prior to fixation resulting in the loss of the mucoid secretion produced by mature cirral mucocytes. The vacuolated regions mark the remnants of the mature mucocytes. The large cirral nerve is also evident. Zenker's fixative, "Azan" stain. m = immature mucocyte; n = neural extension; N = cirral nerve; V = vacuolated mucocyte. Lower: The dorsal parapodial cirrus of a relaxed specimen of *P. mucosa* in transverse section, fixed without excessive mucus loss. The cirral mucocytes show a beta-metachromatic reaction with toluidine blue. Hollande's fixative, toluidine blue stain. M = metachromatic mucocyte.

abundant heterochromatin material. Many immature secretory inclusions are present near the epithelial surface as well as subepithelially. The immature secretory droplets occur in a loose formation and are surrounded by a dense array of smooth endoplasmic reticulum. The larger, less electron dense, mature secretory droplets occur in tighter, membrane bound accumulations. Figure 2 shows a portion of a vacuolated mucous cell bounding a central nucleus. Both the mature and vacuolated secretory cells have numerous, small mitochondria associated with them.

The smaller, ventral cirrus is histologically and cytologically similar to the dorsal cirrus, and is equipped with oblong mucocytes in both mature and immature stages. Also present is a large cirral nerve and thin longitudinal muscle bands. Melanic pigmentation is not obvious in sections of the ventral cirri.

DISCUSSION AND CONCLUSIONS

Many factors influence successful predation. Griffiths (1975) believed that prey abundance and prey size are two of the prime variables affecting predation success but that situations do occur in which predators react to prey characteristics other than body size. These characteristics include physical avoidance by potential prey (Fagade and Olaniyan 1973) which may be chemically mediated by a secretion released by the predator (Mackie et al. 1968; Doering 1976; Mayo and Mackie 1976), physical deterrents of the potential prey species such as spines (Hoogland et al. 1956; Bakus 1966), or innate defense mechanisms of the potential prey such as toxicity or unpalatability (Thompson 1960; Bakus 1966, 1968; Gibson 1972; Rahemtulla and Løvtrup 1974). An epidermal, mucoid secretion is responsible for the protection of at least some phyllodocid polychaetes from active predation by some small or juvenile fish. Since phyllodocids are relatively small benthic worms, it is unlikely that many large fish would expend the energy needed to use them as a primary food source; thus only smaller fish would potentially make any notable impact on the phyllodocid populations.

Russell (1966) tested the palatability of tissues from 48 species of marine organisms with two marine (*Pelatus quadrilineatus* and *Torquigener hamiltoni*) and two freshwater (*Gambusia affinis* and *Carassius auratus*) species of fish ranging from 25 to 90 mm. This involved choice experiments with the fish simultaneously offered a known palatable organism and a test organism of unknown palatability. The results revealed many unpalatable species which were rejected by the fish. The majority of these tests involved only three or fewer trials and there is little note concerning specific reaction of fish to potential prey items. Among the palatable items found by Russell was *Phyllodoce malgremi*. Phyllodocids, as all other test organisms, were cut to acceptable sizes based on preliminary trials which noted size limits of prey for each fish. *Phyllodoce malgremi* might indeed be consumed by these particular fish but the limited number of trials (two per fish) and lack of corresponding worm size data plus the previous treatment of the worms (i.e., sectioned into fragments) may have led to misleading data concerning palatability.

Few reports list phyllodocids as a major portion of a fish's diet; however, Wigley (1956) did list four

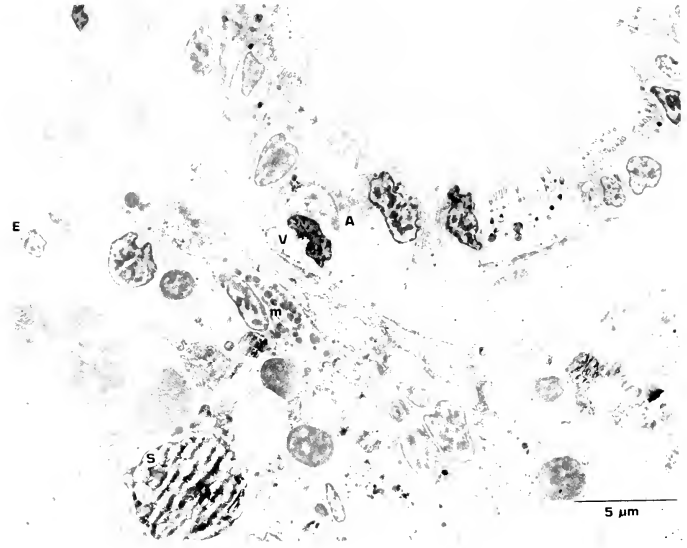


FIGURE 2.—The ultrastructure of the dorsal parapodial cirrus of the polychaete *Phyllodoce mucosa*. The micrograph shows the dense array of cilia and microvilli which line the cirral epithelium as well as mature and immature secretory droplets and associated organelles. Anderson's and osmium tetroxide fixation, uranyl acetate, and Sato lead stain. S = mature secretory droplets, A = mitochondria, E = smooth endoplasmic reticulum. Other abbreviations as in Figure 1.

species of phyllodocids in the food of the haddock, *Melanogrammus aeglefinus*. No phyllodocids were among the 11 dominant prey species of the larger fish examined. Wigley noted, however, that because of the small, subterminal mouth, most of the haddocks' prey were small and thin. Small invertebrates, including phyllodocids, were listed as dominant foods of the few smaller (14-30 cm) haddock examined. Annelids composed only 1.9% of the prey items found in the haddock study and no note was made of the diet of fish < 14 cm. Data for small juveniles is found in only a few studies involving bulk analysis of fish stomach contents (Stickney et al. 1975; Chao and Musick 1977).

In nature, initial rejection and adverse reaction of a fish to *P. mucosa* may give the potential prey sufficient time to retreat from harm. Chiszar and Windell (1973) found that satiated bluegill, *Lepomis macrochirus*, have more selective feeding habits than starved fish. This may imply that in natural conditions a normally feeding fish may not persist in an attack on an unpalatable prey organism.

Murdoch et al. (1975) suggested that predators distribute attacks among prey species in response to the prey's relative densities. These authors broke down events leading to final ingestion of prey into a series of predatory behaviors, including "choosing" to attack the prey species. Once a potential prey is perceived and located, the "choice" is up to the predator whether to attack or not. If the organism is attacked and successfully

consumed, the predator may set up a "specific searching image" (Tinbergen 1960), which would increase its chance of locating additional specimens provided more of the same prey species can be found while reinforcement is still fresh. Thus, this pattern is only relevant when prey species occur in relatively high densities. *Phyllodoce mucosa* is found in moderately high densities in Nahant Bay with many other polychaetes such as *Prionospio malmgreni*, *Scoloplos armiger*, and *Nephtys* spp. If a small fish encounters and attempts to eat a *Phyllodoce mucosa* but is repulsed by the worm's defenses several times, the fish may eventually set up a negative searching image and thus avoid further "discomfort" caused by attempted ingestion. While simultaneous choices of food may be a rare event in nature (Beukema 1968), when it does occur between a phyllodocid and another type of prey of similar size, a fish with a negative image may "select" the nonphyllodocid prey. This is indicated in the present data by the relationship between ingestive attempts and investigations of *Gasterosteus aculeatus* and the "loss of interest" shown by the smaller *Menidia menidia*.

Kneib and Stiven (1978) recently found that the diet of *F. heteroclitus* in a North Carolina salt marsh varied with the size of the fish (smaller fish were carnivorous while larger individuals were omnivorous). In this case, alteration in diet seemed to reflect a physiological and morphological change in the fish with growth. This conversion of food habits may be based upon the ability of the fish to eat different food items because of its proportionally larger size or it might indicate a change in the "ability" of the fish to consume less appealing food items if the "need" arises. Data presented here indicate that larger *M. menidia* might be more effective in consuming phyllodocids than smaller *M. menidia*. Smaller fish may not be able to "handle" a phyllodocid of a size that a larger fish might readily consume. This is based solely upon the reaction of the fish to the mucoid secretion since smaller fish were able to consume comparatively large nonphyllodocid polychaetes.

The largest fish used in the present study, a juvenile *Lophopsetta maculata*, about 9 cm long, consistently rejected *P. mucosa*. *Lophopsetta maculata* is an active predator of mobile prey (Table 1). The large buccal chamber and distensibility of the esophagus of this flounder preclude the possibility that the phyllodocid mucus acts as a physical barrier to ingestion (i.e., an occlusive plug) but instead indicate that the mucus contains some irritating or obnoxious substance which repels the fish.

The high sensitivity and secretory nature of the parapodial cirri is reflected in the complex ultrastructure shown in Figure 2, however, *P. mucosa* does not seem able to continually produce an adequate supply of protective mucus. This is indicated by ingestion of the worm by *G. aculeatus* following numerous rejections from this fish's small, sharply toothed buccal cavity which may have removed the protective cover. Similar results are obtainable with a smallmouthed pipette, which simulates this. The large, empty vacuoles in the dorsal cirri surrounded by immature mucocytes indicate a lag between total loss of available secretion and maturation of additional, functional mucocytes.

Beukema (1968) suggested that *G. aculeatus* hunts by sight only and its sense of smell plays little if any role in finding food. This is supported in the data presented here by the correlation between investigations and ingestive attempts. Investigations involved no direct contact but only close observation of the worm by the fish.

Ejectory behavior by *G. aculeatus* feeding on clumps of *Tubifex* spp. oligochaetes was discussed by Tugendhat (1960) who found that this action caused a breakdown of the clumps into individual worms which were easily ingested. Hynes (1950) noted that young *G. aculeatus* feed on proportionally smaller prey items and that the diet changed to larger prey as the fish grew. The largest phyllodocid fed to a *G. aculeatus* in the present study was 24 mm long, and it was investigated but only one attempt at ingestion was made. In this case, the worm probably was too large for the fish to deal with.

The only species of fish tested which consistently ate *P. mucosa* was *F. heteroclitus*. *Fundulus heteroclitus*, a well-known inhabitant of salt marshes, is only rarely found in strictly saline environments (Hildebrand and Schroeder 1928). Vince et al. (1976) showed that *F. heteroclitus* may cause an impact on the abundance and distribution of some prey species, and Fraser (1973) found that *Fundulus* spp. would consume prey items in proportion to prey densities. Since *P. mucosa* is not a normal resident of salt marshes the question must be asked: does the fact that these two organisms occur in different environments influence the predator-prey interactions between these species when brought together? According to Tin-

bergen (1960), there may be an obvious delay in the attack on a potential prey if it is new to the predator. No such delay was seen in these experiments using semistarved fish. It is unlikely that *P. mucosa* has developed a defense mechanism which is specific in its action only to marine fish. The ability of *F. heteroclitus* to consistently consume *P. mucosa* probably reflects the predaceous mummichog's lack of sensitivity or its ability to overcome the irritation or unpalatability of this worm.

Cyprinodon variegatus always rejected the phyllodocids and rarely investigated the worm without attempted ingestion. The small, terminal mouth of this fish, with its large tricuspid teeth and protractile premaxillaries, was quite efficient at quickly devouring all nonphyllodocid polychaetes offered to the fish during these experiments.

Cynoscion regalis is primarily an active pelagic predator (Table 1). There has been some research concerning the feeding habits of juvenile sciaenids (Thomas 1977; Chao and Musick 1977) which found that small *C. regalis* feed mainly on mysids, copepods, and small fish. Annelids do form, however, a portion of the weakfish's diet (Table 1). Bigelow and Schroeder (1953) noted that the diet of *C. regalis* varies with locality and availability of prey. Small weakfish reject *P. mucosa* as a food item. *Cynoscion regalis* showed active investigatory behavior which usually consisted of tapping or bumping the sinking worm with its snout. Direct contact often resulted in a rapid shunning of the worm by the fish. This may indicate the presence of sensitive nares chemoreceptors. The juvenile fish would not be a major threat to these worms even were they readily available.

Preliminary work indicates that antipredation responses are active in *P. maculata, E. sanguinea, Phascolopsis gouldi, Stylochus zebra*, and *Lineus ruber*. All these organisms, except the sipunculid, secrete large quantities of mucus. The epidermis of many sipunculids is densely packed with gland cells (Tetry 1959) and some secretion from these glands may serve to protect the animal from predation. *Stylochus zebra*, is a commensal of pagurid crabs; abundant production of mucus by this worm may tend to keep this relationship commensal.

The role of secretory defense mechanisms is well established in many species of marine animals (Graham 1957; Thompson 1960, 1969; Bakus 1968), but many questions concerning the broader aspects of antipredational responses remain unanswered. Are antipredation responses reflected in the composition of marine benthic communities? How does effectiveness of antipredation mechanisms vary with size of predators or degree of predator satiation? In similar-sized predators, what differences allow one species to prey on a given organism and not on the other? What changes in diet would be found if feeding studies involving analyses of stomach contents typically were extended to include all size classes of fish? Does previous exposure to an antipredation mechanism produce "learning" in potential marine predators?

In responding to slow-moving predators many potential prey species have evolved escape reactions (Doering 1976). In dealing with highly mobile fish predators, many species of potential prey have developed such defense mechanisms as protective secretions. Lagler et al. (1977:142) stated, "In general the esophagus [of fish] is so distensible that it can accommodate anything that the fish can get into its mouth . . . ." With the discovery of the repulsive characteristics of certain phyllodocids, the indications of antipredation mechanisms in a sipunculid and turbellarian reported here, added to what is known of nemerteans and opisthobranchs, it is clear that a closer examination must be made of interspecific molecular interactions which occur within marine communities.

ACKNOWLEDGMENTS

I gratefully acknowledge the many helpful suggestions concerning this manuscript which were received from M. R. Carriker, F. C. Daiber, B. Brown, R. Palmer, and L. Williams. I also thank L. Watling and G. Entrot for constructive criticisms of an earlier draft of this paper. Harlan Dean, G. Entrot, S. Howe, P. Nimeskern, F. Prezant, J. Vargas, and W. Wehling helped in the collection of animals used in this study, and I thank them for their efforts. The use of the RV *Clione* and facilities at the Marine Science Institute, Nahant, Mass., were kindly supplied by N. W. Riser. Thanks also to P. Savage for typing the manuscript.

LITERATURE CITED

BAKUS, G. J.
1966 Some relationships of fishes to benthic organisms on coral reefs. Nature (Lond.) 210:280-284.
1968 Defensive mechanisms and ecology of some tropical holothurians. Mar. Biol. (Berl.) 2:23-32.

BERG, J.
1979 Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. (Berl.) 50:263-273.

BEUKEMA, J. J.
1968 Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. Behaviour 31:1-126.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953 Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

CHAO, L. N., AND J. A. MUSICK.
1977 Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

CHISZAR, D., AND J. T. WINDELL.
1973 Predation by bluegill sunfish (*Leopomis macrochirus* Rafinesque) upon mealworm larvae (*Tenebrio molitor*). Anim. Behav. 21:536-543.

DOERING, P. H.
1976 A burrowing response of *Mercenaria mercenaria* (Linnaeus, 1758) elicited by *Asterias forbesi* (Desor 1848). Veliger 19:167-175.

FAGADE, S. O., AND C. I. O. OLANIYAN.
1973 The food and feeding interrelationship of the fishes in the Lagos Lagoon. J. Fish. Biol. 5:205-225.

FAUCHALD, K.
1977 The polychaete worms. Definitions and keys to the orders, families and genera. Nat. Hist. Mus. Los Ang. Cty., Sci. Ser. 28:1-190.

FRASER, A.
1973 Foraging strategies in three species of *Eudulus*. M.S. Thesis, Univ. Maryland, College Park. 54 p.

GIBSON, R.
1972 Nemerteans. Hutchinson Univ. Library, Lond. 224 p.

GRAHAM, A.
1957 The molluscan skin with special reference to Prosobranchs. Proc. Malac. Soc. Lond. 32:135-144.

GRIFFITHS, D.
1975. Prey availability and the food of predators. Ecology 56:1209-1214.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, 366 p.

HOOGLAND, R., D. MORRIS, AND N. TINBERGEN.
1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*). Behaviour 10:205-236.

HYNES, H. B. N.
1950 The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

IVLEV, V. S.
1961 Experimental ecology of the feeding of fishes. (Translated from Russ. by D. Scott). Yale Univ. Press, New Haven, 302 p.

KISLALIOGLU, M., AND R. N. GIBSON.
1977. The feeding relationship of shallow water fishes in a Scottish sea loch. J. Fish. Biol. 11:257-266.

KNEIB, R. T., AND A. E. STUVEN.
1978 Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31:121-140.

LAGLER, K. F., J. E. BARDACH, R. R. MILLER, AND D. R. M. PASSINO.
1977 Ichthyology. Wiley, N.Y., 506 p.

MACKIE, A. M., R. LASKER, AND P. T. GRANT.
1968 Avoidance reactions of a mollusc *Buccinum undatum* to saponin-like surface-active substances in extracts of the starfish *Asterias rubens* and *Marthasterias glacialis*. Comp. Biochem. Physiol. 26:415-428.

MAYO, F., AND A. M. MACKIE.
1976 Studies of avoidance reactions in several species of predatory British seastars (Echinodermata: Asteroidea). Mar. Biol. (Berl.) 38:41-49.

MURDOCH, W. W., S. AVERY, AND M. E. B. SMYTH.
1975 Switching in predatory fish. Ecology 56:1094-1105.

NIKOLSKY, G. V.
1963 The ecology of fishes. (Translated from Russ. by L. Birkett). Acad. Press, London and N.Y., 352 p.

ONYIA, A. D.
1973. A contribution to the food and feeding habit of the threadfin, *Galeoides decadactylus*. Mar. Biol. (Berl.) 22:371-378.

PETTIBONE, M. H.
1963 Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae. U.S. Natl. Mus. Bull. 227, 356 p.

QASIM, S. Z.
1957 The biology of *Centronotus gunnellus* (L.) (Teleostei). J. Anim. Ecol. 26:389-401.

RAHEMTULLA, F., AND S. LOVTRUP.
1974 The comparative biochemistry of invertebrate mucopolysaccharides. II. Nematoda, Annelida. Comp. Biochem. Physiol. 49B:639-646.

RUSSELL, E.
1966 An investigation of the palatability of some marine invertebrates to four species of fish. Pac. Sci. 20:452-460.

SANDERS, H. L., R. R. HESSLER, AND G. R. HAMPSON.
1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-Sea Res. 12:845-867.

SMITH, R. W., AND F. C. DAIBER.
1977 Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull., U.S. 75:823-830.

STICKNEY, R. R., G. L. TAYLOR, AND D. B. WHITE.
1975 Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesapeake Sci. 16:104-114.

TETRY, A.
1959 Classe des sipunculiens. *In* P.-P. Grasse (editor) Traite de zoologie, Tome V, p. 785-854. Libraires de l'academie de medecine, Paris.

THOMAS, D. L.
1977 The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3, 247 p.

THOMPSON, T. E.
1960 Defensive acid secretion in marine gastropods. J. Mar. Biol. Assoc. U.K. 39:115-122.
1969 Acid secretion in Pacific ocean gastropods. Aust. J. Zool. 17:755-764.

TINBERGEN, L.
1960. The natural control of insects in pine wood I. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13:265-343.

TUGENDHAT, B.
1960. The normal feeding behavior of the three-spined stickleback (*Gasterosteus aculeatus* L.) Behaviour 15:284-318.

VINCE, S., I. VALIELA, N. BAKUS, AND J. M. TEAL.
1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23:255-266.

WIGLEY, R. L.
1956. Food habits of Georges Bank haddock. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 165, 26 p.

CONTRIBUTION OF WILD AND HATCHERY-REARED COHO SALMON, *ONCORHYNCHUS KISUTCH*, TO THE OREGON OCEAN SPORT FISHERY

DENNIS L. SCARNECCHIA[1] AND HARRY H. WAGNER[2]

ABSTRACT

Eight scale characters of known hatchery and wild coho salmon, *Oncorhynchus kisutch*, were compared, and a linear discriminant function was used to determine whether hatchery and wild adult coho salmon could be reliably separated on the basis of scale characteristics. Attempted separation was based upon known differences in rearing environments of hatchery and wild juvenile coho salmon and upon hatchery smolts being larger than wild smolts. Identifications were correct for 82% of the hatchery fish and 89% of the wild fish. Based on analysis of scales from adult coho salmon of unknown origin (hatchery or wild) and the estimated catch of marked, hatchery-reared coho salmon taken by the Oregon sport fishery, we concluded that 75% of the fish caught in the ocean along the Oregon coast from mid-June to mid-September 1977 had been released as smolts from hatcheries. Percentages of hatchery fish in the catch ranged from 85 near the mouth of the Columbia River to 61 at Winchester Bay on the central Oregon coast. Fisheries along the south and central Oregon coast may have had access to higher percentages of wild coho salmon after mid-August than prior to this time, probably because wild fish from coastal streams remained near these ports, whereas most fish destined for Columbia River hatcheries had already migrated northward.

The coho salmon, *Oncorhynchus kisutch*, is the most abundant species of salmon contributing to Oregon's commercial troll and ocean recreational fisheries (Oregon Department of Fish and Wildlife[3]). Numbers of this species caught commercially in Oregon have historically fluctuated widely. Catches from 1952 to 1962 averaged 292,000 fish and ranged from 551,000 in 1957 to 112,000 in 1960. Numbers of coho salmon caught increased generally in 1963-77 and averaged 860,000 fish/yr while ranging from 1,827,000 in 1976 to 450,000 in 1977. Catches by the Washington and California troll fisheries have also increased in recent years (Wright 1976; Pacific Fishery Management Council 1978). This rise in catch has been attributed to increased production by Federal and state hatcheries of larger and healthier smolts (Pacific Fishery Management Council 1978; Reed[4]).

This increased abundance of coho salmon has coincided with, and partly led to, the development of a substantial sport fishery in the ocean off Oregon, Washington, and California. The number of coho salmon caught in the ocean by sport fishermen has been fairly stable in Oregon since 1964 but has increased rapidly in Washington since the early 1960's (Phinney and Miller 1977; Pacific Fishery Management Council 1978).

Although both total releases of coho salmon smolts from public hatcheries and catch have increased, indices of escapement of wild fish indicate that the numbers of wild coho salmon spawning have decreased (Cummings[5]). In an analysis of counts of spawning salmon from selected areas of eight Oregon coastal streams from 1964 to 1974, we found that counts of adult salmon have declined significantly in the Nestucca ($P < 0.01$), Alsea ($P < 0.01$), Yaquina ($P < 0.05$), and Coquille ($P < 0.005$) Rivers and Beaver Creek ($P < 0.05$), but no significant trends were observed in the Nehalem, Wilson, and Coos Rivers. For all spawning areas combined, the conclusion is that overall escapements are declining ($P < 0.01$) on coastal

[1]Oregon Cooperative Fishery Research Unit (cooperators are the Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and Oregon State University), Oregon State University, Corvallis, Oreg.; present address: Colorado Cooperative Fishery Research Unit, Colorado State University, Fort Collins, CO 80523.

[2]Oregon Department of Fish and Wildlife, Corvallis, OR 97331.

[3]Oregon Department of Fish and Wildlife. 1977 unpubl. stat. of troll salmon investigations group. Marine Science Drive, Bldg. #3, Newport, OR 97365.

[4]Reed, P. H. 1976. A history and current status of Oregon ocean salmon fisheries-troll salmon investigations. Oregon Department of Fish and Wildlife, Marine Science Drive, Bldg. #3, Newport, OR 97365.

[5]Cummings, E. 1977. Spawning coho and chinook salmon surveys in coastal watersheds of Oregon, 1976. Oregon Department of Fish and Wildlife, 17330 SE Evelyn Street, Clackamas, OR 97015.

Manuscript accepted March 1979
FISHERY BULLETIN: VOL. 77, NO. 3, 1980

rivers (Berry[6]; Cummings see footnote 5). The escapement of wild fish is also declining in the lower Columbia River (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1976).

Management agencies do not know how many wild fish are caught in Oregon's troll and sport fisheries, even though they strongly suspect that the number of wild fish in the catch is smaller now than it was 10 yr ago. If they knew the numbers of hatchery and wild fish contributing to Oregon's fisheries, they could recommend management strategies according to the needs of the respective stocks. Also, if they could distinguish hatchery and wild fish caught in the fisheries at various times and localities, they could determine the potential for differentially harvesting the stocks. Consequently, we elected to attempt separating hatchery and wild coho salmon caught in the Oregon ocean sport fishery by measuring and counting characters of scales taken from adult fish. Our objective was to determine the percentages of hatchery and wild fish contributing to the Oregon ocean sport fishery at different times and locations.

METHODS

Scales are a logical choice for separating hatchery and wild coho salmon, since they have been used to differentiate stocks of salmon in rivers (Henry 1961), and for classifying mixed stocks of salmon caught on the high seas to continent of origin (Mosher 1963; Tanaka et al. 1969; Anas and Murai 1969). A review of the use of scales for identification of stocks of salmon was given in Major et al. (1972). Peck (1970) successfully differentiated between hatchery and wild juvenile coho salmon by using several scale characters.

Scales from coho salmon of known hatchery origin (identified by missing adipose fins), and scales of unmarked salmon of unknown origin were collected by personnel of the Oregon Department of Fish and Wildlife from adult fish captured in the ocean by sport fishermen from mid-June to mid-September 1977. Samples were collected weekly from eight coastal ports, listed from north to south Hammond, Garibaldi, Depoe Bay, Newport, Winchester Bay, Coos Bay, Gold Beach, and Brookings. We obtained scales from 178 adipose clipped salmon and from 2,054 unmarked salmon (Table 1).

Because few wild fish were available, we had to use wild fish of several different brood years to increase our sample. Geographic location, brood year, and number of scale samples used in the subsequent analysis are shown in Table 2.

Two nonregenerated scales obtained from the left side of each fish, one to four rows above the lateral line between the dorsal and adipose fins, were mounted on gummed cards, and acetate impressions were made by methods similar to those described by Clutter and Whitesel (1956). A conscious effort was made to select the largest nonregenerated scales within each sample. Scale impressions were read with the aid of a projector at a magnification of 80×.

Based on Peck's (1970) analysis of scale characters of hatchery and wild smolts of coho salmon and on our analysis and observations of scale characters from known wild adult fish and those from three Oregon hatcheries, we selected eight characters that we believed were potentially useful in separating hatchery from wild fish (Table 3). Characters were selected based on the assumption that the freshwater rearing environments for hatchery and wild coho salmon are distinctly different and differences in scales between the two groups would be manifest during this period.

We selected for analysis preocean radius and preocean circulus counts on the basis of results of Peck (1970) and on data on weights of smolts being

TABLE 1.—Number of adipose clipped and unmarked coho salmon sampled for scales at Oregon ports in 1977. Ports are arranged from north to south.

Port	Marked	Unmarked	Port	Marked	Unmarked
Hammond	5	356	Coos Bay	9	165
Garibaldi	43	188	Gold Beach	0	30
Depoe Bay	64	516	Brookings	0	56
Newport	33	412			
Winchester Bay	24	331	Total	178	2,054

TABLE 2.—Origin of scales of wild coho salmon, brood year, and number of scale samples from each geographic location.

River system	County of collection	Brood year	Number of samples
Necanicum	Clatsop	1974	3
Salmon	Lincoln	1973	45
Salmon	Lincoln	1974	15
Alsea (Flynn Creek)	Lincoln	1962	7
Alsea (Flynn Creek)	Lincoln	1963	32
Alsea (Needle Branch)	Lincoln	1963	27
Alsea (Deer Creek)	Lincoln	1963	28
Coos and Coquille	Coos	1974	4
Total			162

[6]Berry, R. L. 1975. Spawning surveys in coastal watersheds, 1974. Oreg. Dep. Fish Wildl. Coastal Rivers Inf. Rep. 75-4. P.O. Box 529, Tillamook, OR 97141.

TABLE 3.—Description of scale characters measured or counted in this study from known hatchery and wild coho salmon. All measurements are made at angles ventral to the longest axis.

Character	Description
1	Radius of preocean zone at 20°
2	Number of circuli in the preocean zone at 20°
3	Distance between circuli 1 and 5 of the preocean zone at 90°
4	Distance between circuli 1 and 10 of the preocean zone at 90°
5	Distance between circuli 1 and 15 of the preocean zone at 90°
6	Radius of preocean zone at 90°
7	Number of circuli in preocean zone at 90°
8	Number of broken or branched circuli within precisely defined zone (see Methods)

released by hatcheries of the Oregon Department of Fish and Wildlife. Most hatchery-reared smolts currently being released by Oregon's hatcheries are larger than wild smolts (Oregon Department of Fish and Wildlife[7]). Because radii of scales and number of circuli appear to be well correlated to length of Pacific salmon smolts (Clutter and Whitesel 1956), they are logical selections for scale characters to use in separating hatchery and wild fish.

Some scales had no "plus" (Anas and Murai 1969) or estuarine growth whereas others had substantial amounts. We chose to measure total freshwater growth plus any spring and estuarine growth and to call that distance the "preocean" zone.

We chose three spacing characters, 3 through 5 (Table 3), to determine whether the plentiful food supply of hatchery coho salmon would yield different spacing of circuli than that observed for wild fish. We measured these characters at 90° to the longest axis of the scale because breaking and branching of circuli is less at that angle than at lower angles to the longest axis.

The number of broken or branched circuli (character 8, Table 3) was used to determine if circuli of hatchery fish were more or less branched than circuli of wild fish. It was postulated that regular feeding by hatchery fish would result in less breaking and branching of circuli. For this character an acetate sheet with thin parallel lines 1 cm apart and a dotted line parallel to and midway between these lines was used as a guide. A small point at the end of the dotted line was placed at the center of the focus of the scale and a dotted line extended outward at 90° ventral to the longest axis. The two solid outer lines then enclosed a rectangular area. Within this area, we counted circuli 5 through 12 inclusive in the preocean zone of the scale and recorded the number of these circuli that were broken or branched.

The eight characters in Table 3 were measured and counted from scales of known hatchery fish (Table 1) and known wild fish (Table 2). These measurements were subjected to discriminant function analysis, which reduced all characters for each scale to a single value and then, through a linear model, classified the scales as hatchery or wild (Nie et al. 1975). Assumptions in this analysis were that data were multivariate normal and had common variance-covariance matrices. Plotting the data for each of the eight characters individually showed that only character 8 deviated somewhat from normal. Although normality of individual characters does not imply joint normality, it indicates that the data conform fairly well with the assumption of multivariate normality.

From the discriminant function analyses, it was concluded that preocean radius at 20° (character 1) was the most efficient individual character for separating hatchery and wild fish. Preocean radius at 20° is generally larger in hatchery fish than in wild fish. By using the character, we reliably separated 82% of the hatchery fish and 89% of the wild fish.

While characters 1, 3, and 8 in combination would do as well, there would be no benefit to their use except that a slightly higher percentage (1.1) of hatchery fish would be correctly classified at the expense of a lower percentage (1.2) of wild fish correctly classified (Table 4).

Since preocean radius at 20° was the most useful character for discriminating between adult hatchery and wild coho salmon, this character was mea-

TABLE 4.—Combinations of scale characters to which discriminant function analysis was applied and effectiveness at classifying coho salmon as to wild or hatchery origin.

Character	Percentage correctly classified		
	Hatchery	Wild	Total
1	81.5	88.9	85.0
2	69.7	82.1	75.6
3	74.7	72.8	73.8
4	69.1	81.5	75.0
5	75.3	75.3	75.3
6	78.7	85.8	82.1
7	70.2	69.1	69.7
8	68.0	65.4	66.8
1, 8, and 3	82.6	87.7	85.0
1 and 2	79.8	88.9	84.1
1 through 8	82.6	87.0	84.7
1, 8, 3, 2, and 5	81.5	87.0	84.1

[7]Oregon Department of Fish and Wildlife. Unpubl. stat. of the Fish Culture Division, 17330 SE Evelyn Street, Clackamas, OR 97015.

sured from scales from 2,054 unmarked coho salmon (Table 1). In all scale readings only scales that had one or more ocean annuli were read. Fewer than 0.5% of the fish were age 2.1, and the scales indicated that the fish grew slowly in their first year of life.[8] These scales were assumed to be from wild fish.

Wild and hatchery fish were assumed to have similar numbers of regenerated scales, most of which were regrown because of scale loss during freshwater rearing. If wild fish tend to lose more scales because of their more rigorous rearing environment in freshwater, the numbers of wild fish are slightly underestimated, since those samples taken from unmarked salmon that were discarded for lack of useable scales would have been biased toward being wild fish.

Once we had classified scales from unmarked fish as hatchery or wild we weighted the number of unmarked fish that were landed at each port during 2-wk periods (sampling strata) for the season by our estimated percentages of hatchery and wild fish for that stratum. The estimated catch of known marked fish was then added to the unmarked hatchery fish to find the total number of hatchery fish caught in that stratum (Table 5).

Because of the small number of scales available from unmarked fish for several strata, we combined 2-wk periods for a given port where necessary to obtain a sample of at least 50 fish. Small sample sizes necessitated combining samples for Brookings and Gold Beach.

The observed percentage of hatchery coho salmon in the unmarked sample was corrected for wild fish incorrectly classified as hatchery fish, and hatchery fish incorrectly classified as wild fish. Confidence levels were also computed. Both procedures are described by Worlund and Fredin (1962).

RESULTS

The percentages of hatchery fish contributing to Oregon's sport fishery were highest near the Columbia River and decreased steadily southward (Table 6). The percentages of wild fish in the catch were highest late in the season at Garibaldi, Depoe Bay, Newport, and Winchester Bay and near midseason at Hammond. Total estimated percentages of hatchery fish landed at each port from mid-June to mid-September 1977 were 85 at Hammond, 83 at Garibaldi, 79 at Depoe Bay, 77 at Newport, 61 at Winchester Bay, 65 at Coos Bay,

[8]Most adult coho salmon caught off Oregon are age 1.1, where numbers left and right of the decimal indicate number of freshwater and marine annuli on the scales, respectively. Age 1.1 fish are in their third year of life.

TABLE 5.—Estimated number of coho salmon landed and the catch per angler day (in parentheses) by Oregon sport fishery by port in 1977. Data are for 2-wk periods from 16 June to 15 September.

Port	16-30 June	1-15 July	16-31 July	1-15 Aug	16-31 Aug	1-15 Sept
Hammond	5,548	10,058	12,701	11,810	5,056	1,845
	(1 34)	(1 33)	(1 35)	(0 88)	(0 45)	(0 36)
Garibaldi	217	859	2,285	1,438	1,625	279
	(0 06)	(0 28)	(0 45)	(0 24)	(0 28)	(0 09)
Depoe Bay	1,090	2,624	7,909	2,927	5,032	616
	(0 24)	(0 32)	(0 70)	(0 28)	(0 46)	(0 13)
Newport	568	2,447	4,349	4,492	3,283	516
	(0 11)	(0 27)	(0 41)	(0 59)	(0 43)	(0 16)
Winchester Bay	2,602	5,328	10,175	9 217	1,639	1,287
	(0 65)	(0 57)	(0 99)	(0 65)	(0 24)	(0 27)
Coos Bay	641	1,923	3,522	1,553	638	244
	(0 23)	(0 33)	(0 60)	(0 35)	(0 13)	(0 14)
Gold Beach	9	2	812	337	68	17
	(0 05)	(0 00)	(0 29)	(0 08)	(0 02)	(0 01)
Brookings	33	19	8,603	2,141	96	180
	(0 01)	(0 00)	(0 49)	(0 16)	(0 03)	(0 04)

TABLE 6.—Estimated percentages and 95% confidence intervals of hatchery-reared coho salmon in the total catch landed in 1977 by the Oregon sport fishery.

	Period					
Port	16-30 June	1-15 July	16-31 July	1-15 Aug	16-31 Aug	1-15 Sept
Hammond	(91 8 ± 5 6)		69 2 ± 11 7	90 9 ± 6 2	(90 6 ± 5 3)	
Garibaldi	(84 8 ± 7 3)		( )	(80 8 ± 8 0)		
Depoe Bay	79 7 ± 6 7	95 7 ± 4 4	88 3 ± 6 4	68 6 ± 12 0	(64 1 ± 7 8)	
Newport	100 0 ± 0 2	92 3 ± 5 5	(74 1 ± 6 1)		(72 0 ± 10 9)	
Winchester Bay	(64 5 ± 11 7)		70 7 ± 7 3	(49 7 ± 8 9)		
Coos Bay	(58 9 ± 10 3)		(67 3 ± 10 3)			
Gold Beach-Brookings	(62 8 ± 10 1)					

and 63 at Brookings-Gold Beach. An estimated 75% of all coho salmon landed by the entire sport fishery from mid-June to mid-September 1977 originated from hatchery releases. Percentages of hatchery coho salmon by port and period, along with confidence intervals, are shown in Table 6.

Since the sport fishery is mainly composed of private and charter boats on day-long trips, our estimated percentages of hatchery and wild fish by port probably reflect fairly well the actual percentages occurring near each port, assuming similar catchability of hatchery and wild fish.

DISCUSSION

Of the estimated 140,660 coho salmon caught in the ocean in 1977 by Oregon sport fishermen from mid-June to mid-September, 35,300 were wild fish. Although scales from fish caught by the commercial troll fishery were not analyzed in 1977, it is likely that the overall percentages of wild and hatchery fish were similar to those of sport fishery. To evaluate this likelihood, we compared observed percentage of marked fish in the monthly catch of the sport fishery for six Oregon ports with the percentage of marked fish in the corresponding commercial catch. In only 7 of the 18 comparisons for which sample sizes were adequate did percentages of marked fish caught in a given strata by the sport fishery differ from those of the commercial fishery ($P > 0.05$), which indicates that overall percentages of hatchery and wild fish are similar for the two fisheries.

We can explain the north to south trend toward increasing percentage of wild fish in the catch (Table 6) by assuming a northward movement of hatchery and wild coho salmon as the season progresses, as Van Hyning (1951) concluded, with wild fish from south and north coastal streams ceasing their northward movement near their natal streams. Since over 80% of the coho salmon produced by hatcheries in California, Oregon, and Washington (excluding Puget Sound) are released in the Columbia River and its tributaries (Oregon Department of Fish and Wildlife see footnote 7), many of the hatchery fish off the Oregon coast are probably headed for the Columbia River. These hatchery fish continue northward and concentrate near the mouth of the Columbia River. The argument for south to north movement of coho salmon is supported by the occurrence of lower percentages of hatchery fish late in the fishing season in catches off of Garibaldi, Depoe Bay, Newport, and Winchester Bay (Table 6). Late in the season, hatchery fish may be proportionately less abundant along the south and central coast, since most Columbia River fish would have moved northward by this time, leaving mostly coastal hatchery and wild fish contributing to the south and central coast fisheries. The lowest percentage of hatchery fish noted was 49.7 at Winchester Bay, from 1 August to 15 September.

Another possible factor contributing to lower percentage of hatchery coho salmon in the fishery to the south is that a substantial portion of adult hatchery fish released as smolts from Columbia River hatcheries do not migrate far southward along the Oregon coast. The argument is supported by the large number of coho salmon caught per angler day at Hammond early in the fishing season (Table 5), perhaps indicating that coho salmon returning to the Columbia River are concentrated near the river in early summer. The high percentage of hatchery fish caught at Hammond from 16 June to 15 July further supports this hypothesis (Table 6).

The total catch of coho salmon and catch per angler day were low after mid-August 1977 from Winchester Bay southward, and were low for all ports after August (Table 5), so that while the percentage of wild coho salmon caught rose late in the season, the numbers caught were low, especially along the southern coast. Closing the season for salmon fishing after mid-August would not have protected many wild coho salmon, and would have made only a small sacrifice in catch of hatchery fish. Almost twice as many chinook salmon, *O. tshawytscha*, would have been lost to the sport fishery.

Combined data obtained from the Oregon Department of Fish and Wildlife from Winchester Bay to Brookings from mid-August to mid-September showed that an estimated 1.8 chinook salmon were caught for every coho salmon landed by sport fishermen. During years of higher abundance of coho salmon, fishermen may tend to fish more for coho and less for chinook salmon than they did in 1977, which would increase fishing pressure on wild stocks of coho salmon late in the season.

If wild and hatchery fish are distributed differently in oceanic areas, fishing pressure could be adjusted to meet management goals. If, however, there is substantial variability in the localities of capture of wild fish, either because of the fishery or because of environmental factors, and if hatchery

fish intermingle extensively with wild fish, it will be difficult to protect wild stocks while maintaining high rates of harvest of hatchery fish in the ocean.

Total Oregon troll and sport catch of coho salmon in the ocean plus the Columbia River commercial catch was only 645,000 fish in 1977. Assuming that 75% are hatchery fish, only 162,000 of the fish originated from natural production. Average annual catch of coho salmon by the Oregon troll fishery alone from 1952 to 1956 was 312,000 fish, probably almost all wild fish. The lowest catch over the 5-yr period was 227,000 fish in 1954. This figure excludes fish caught in the ocean by sportsmen and also excludes the Columbia River catch. The average catch from 1952 to 1956 was 1.9 times higher than the catch of wild coho salmon from the combined ocean troll and Columbia River net fisheries in 1977. Yet, the catch of wild fish in the 1950's was considered low enough to warrant closure of commercial gill net fisheries in all Oregon coastal streams to increase the escapement of wild stocks. The efficient net fisheries of the 1950's were considered a primary threat to the production of wild salmon by some biologists. Recent analyses of marking experiments with coho salmon show some Oregon coastal stocks of hatchery fish with a catch to escapement ratio of 6 (Pacific Fishery Management Council 1978). Assuming wild fish are as readily catchable as hatchery fish, the effectiveness of the troll and offshore sport fisheries in harvesting coho salmon now rivals that of many terminal fisheries. Despite elimination of coastal Oregon net fisheries, abundance of wild coho salmon, from all indications of catch and escapement, is at an all-time low.

The catch of wild fish might be considerably less if it were not for the natural spawning of some hatchery fish and later rearing of their progeny in streams. The number of wild coho salmon that results from natural spawning of hatchery fish that fail to return to hatcheries is unknown. Considering the large numbers of smolts being released, even a small percentage of straying by returning adults could lead to significant production in the wild, assuming that the progeny do not differ significantly in fitness from the progeny of wild parents.

ACKNOWLEDGMENTS

We thank John D. McIntyre, Carl B. Schreck, James A. Lichatowich, and James D. Hall for offering valuable comments; Robert Mullin, Robert McQueen, and District Biologists of the Oregon Department of Fish and Wildlife for providing the scales; Stephen Lewis, Malcolm Zirges, and David Loomis for providing unpublished data on the sport and troll fisheries; Norbert Hartmann, David Niess, Allyson Macdonald, and Tumi Tomasson for assistance with the statistics; and Jan Ehmke for typing the manuscript.

LITERATURE CITED

ANAS, R. E., AND S. MURAI
1969. Use of scale characters and a discriminant function for classifying sockeye salmon (*Oncorhynchus nerka*) by continent of origin. Int. North Pac. Fish. Comm. Bull. 26:157-192.

CUTLER, R. L., AND L. E. WILLESEN
1956. Collection and interpretation of sockeye salmon scales. Int. Pac. Salmon Fish. Comm. Bull. 9, 159 p.

HENRY, K. A.
1961. Racial identification of Fraser River sockeye salmon by means of scales and its applications to salmon management. Int. Pac. Salmon Fish. Comm. Bull. 12, 97 p.

MAJOR, R. L., K. H. MOSHER, AND J. E. MASON
1972. Identification of stocks of Pacific salmon by means of their scale features. *In* R. C. Simon and P. A. Larkin (editors), The stock concept in Pacific salmon, p. 209-231. H. R. MacMillan Lect. Fish., Univ. B.C., Vancouver.

MOSHER, K. H.
1963. Racial analysis of red salmon by means of scales. Int. North Pac. Fish. Comm. Bull. 11:31-56.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT
1975. Statistical package for the social sciences. 2d ed. McGraw-Hill, 675 p.

OREGON DEPARTMENT OF FISH AND WILDLIFE AND WASHINGTON DEPARTMENT OF FISHERIES
1976. Status report: Columbia River fish runs and fisheries 1957-75. 2 v., 74 p.

PACIFIC FISHERY MANAGEMENT COUNCIL
1978. Final environmental impact statement and fishery management plan for commercial and recreational salmon fisheries off the coast of Washington, Oregon, and California commencing in 1978. Pac. Fish. Manage. Counc., Portland, Oreg., [229] p.

PLUNK, T. H.
1970. Differentiation of hatchery and stream juvenile coho salmon (*Oncorhynchus kisutch*) from Washington and Oregon by the use of scales and otoliths. M.S. Thesis, Univ. Washington, Seattle, 67 p.

PRINNEY, L. A., AND M. C. MILLER
1977. Status of Washington's ocean sport salmon fishery in the mid 1970's. Wash. Dep. Fish. Tech. Rep. 24: 72 p.

PANCAKE, M. P. SHEPARD, AND H. T. BILTON
1969. Origin of chum salmon (*Oncorhynchus keta*) in offshore waters of the North Pacific in 1956-1958 as determined from scale studies. Int. North Pac. Fish. Comm. Bull. 26:57-155.

VAN HYNING, J. M.
1951. The ocean salmon troll fishery of Oregon. Pac. Mar. Fish. Comm. Bull. 2:43-76.

NEEDHAM, P. D., AND R. A. FREDIN
1962. Differentiation of stocks. In N. J. Wilimovsky (editor), Symposium on pink salmon, p. 144-153. H. R. MacMillan Lect. Fish., Univ. B.C., Vancouver.

WRIGHT, S. G.
1976. Status of Washington's commercial troll salmon fishery in mid 1970's. Wash. Dep. Fish. Tech. Rep. 21, 50 p.

LARVAL MORPHOLOGY OF *PANDALUS TRIDENS* AND A SUMMARY OF THE PRINCIPAL MORPHOLOGICAL CHARACTERISTICS OF NORTH PACIFIC PANDALID SHRIMP LARVAE

EVAN HAYNES[1]

ABSTRACT

Larval stages I-VII of *Pandalus tridens* from plankton of lower Cook Inlet, Alaska, are most similar morphologically to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis* from the North Pacific Ocean. Larvae of *P. tridens* are distinguished from larvae of *P. borealis*, *P. goniurus*, and *P. jordani* by the shape of the rostrum and antennal scale, and spination of the abdominal somites. Larvae of *P. tridens* differ from larvae of *P. stenolepis* by shape of the carapace, abdominal somites, and telson; length of the antennal flagellum and rostrum; and setation of the antennal scale. Differences in larval morphology support classification of *P. tridens* as a species rather than a subspecies of *P. montagui*. A summary of the principal morphological characteristics of the described larvae of pandalid shrimp found in the North Pacific Ocean is provided.

In 1976, the Northwest and Alaska Fisheries Center Auke Bay Laboratory of the National Marine Fisheries Service and the Alaska Department of Fish and Game conducted a survey to determine the seasonal distribution of larvae of king crab and pandalid shrimp in the Kachemak Bay-lower Cook Inlet area (Haynes[2]). During the survey, Stages I-VII zoeae of *Pandalus tridens* (= *P. montagui tridens* Rathbun 1902) were captured in plankton tows in lower Cook Inlet. Except for Stage I, zoeae of *P. tridens* have not been described in the literature. In this report I describe and illustrate each of the seven zoeal stages captured and compare my descriptions with those of pandalid shrimp zoeae given by other authors. I also discuss the evidence from larval morphology that supports raising the subspecies, *P. montagui tridens*, to full species status, *P. tridens* Rathbun 1902. A summary of the principal morphological characteristics of described pandalid shrimp larvae of the North Pacific Ocean is also given.

METHODS

During the 1976 survey, plankton was collected by hauling 61 cm bongo samplers vertically from about 1 m above the ocean bottom to the surface at a velocity of slightly < 1 m s. Nets with 0.333 mm mesh and cod end jars with 0.571 mm mesh were used. Zoeae of *P. tridens* were collected in water 120-160 m deep about 16 km west of the Kenai Peninsula in lower Cook Inlet.

The terminology, methods of measurement, techniques of illustration, and nomenclature of gills and appendages are those used by Haynes (1979). Identification of the zoeae is based on description of Stage I zoeae hatched from known parentage by Ivanov (1971) and undescribed Stage I specimens hatched from known parentage by Ethelwyn Hoffman of the Auke Bay Laboratory's staff. Only those morphological characteristics useful for readily identifying each stage are given. For clarity, setules on setae are usually omitted from the figures, but spinulose setae are shown.

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 3.2 mm (range 3.1-3.5 mm; 6 specimens). Rostrum slender, somewhat sinuate, without teeth, about two-thirds length of carapace, and projects horizontally. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

[2]Haynes, E. 1977. IV. Summary status on the distribution of king crab and pandalid shrimp larvae in Kachemak Bay-lower Cook Inlet, Alaska, 1976. *In* L. L. Trasky, L. B. Flagg, and D. C. Burbank (editors), Environmental studies of Kachemak Bay and lower Cook Inlet, vol. 4, 52 p. Alaska Dep. Fish Game, Anchorage.

Manuscript accepted March 1979.
FISHERY BULLETIN: VOL. 77, NO. 3, 1980

rounded prominence near posterior edge. These two prominences occur in all seven zoeal stages. Pterygostomian spines present, but minute and usually hidden by sessile eyes. Three to four minute denticles on ventral margin of carapace immediately posterior to pterygostomian spine, and about 12 somewhat larger denticles along posteroventral margin of carapace. Denticles in Stages I-III, but rarely in Stage IV. Denticles vary in number among stages and among individuals in

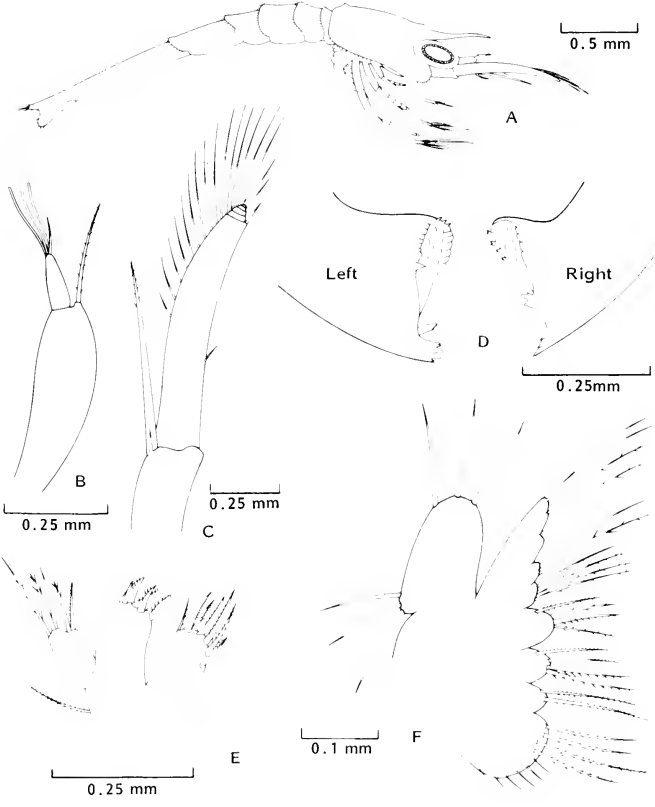


FIGURE 1.—Stage I zoea of *Pandalus tridens*. A, whole animal, right side. B, antennule, dorsal. C, antenna, ventral. D, mandibles, left and right, posterior. E, maxillule, dorsal. F, maxilla, dorsal. G, first maxilliped, lateral. H, second maxilliped, lateral. I, third maxilliped, lateral. J, second pereopod, lateral. K, telson, dorsal.

each stage. Posterior margins of abdominal somites fringed with spines.

ANTENNULE (Figure 1B).—First antenna, or antennule, has a simple, unsegmented, tubular basal portion; plumose seta terminally; and terminal conical projection bearing four aesthetases: one long, one short, and two of intermediate length.

ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum spiniform, unsegmented, about three-fourths length of scale, and spinulose distally. Protopodite bears spinous seta at base of flagellum, but no spine at base of scale. Antennal scale distally divided into four joints, fringed with 17 heavily plumose setae along terminal and inner margins. Distinct seta on outer margin at base of terminal segments; another seta on outer margin, near the protopodite.

MANDIBLES (Figure 1D).—Without palps in this stage and all later zoeal stages examined. Incisor process of left mandible has six teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) and subterminal tooth only on left mandible in all zoeal stages examined.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) has seven spinulose spines terminally. Median lobe (basipodite) bears five spinulose spines and a large setose seta proximally. Endopodite originates from lateral margin of basipodite and has three terminal and two subterminal spines; two of the spines have especially long spinules.

MAXILLA (Figure 1F).—Bears platelike exopodite (scaphognathite) with six long plumose setae: three on distal margin and three on proximal margin. Endopodite has 10 nonplumose setae: 7 bear distinct setules. Basipodite and coxopodite bilobed. Basipodite bears four setae on each lobe; each seta has distinct pattern of setules. Coxopodite bears 12 setae: 2 on distal lobe and 10 on proximal lobe, 6 distal setae of coxopodite somewhat plumose, remaining 6 setae have few, if any, setules.

FIRST MAXILLIPED (Figure 1G).—Most setose of natatory appendages. Protopodite not segmented, bears 11 setae (7 of them spinulose). Endopodite distinctly four-segmented; setation formula 3, 4, 1, 1. Exopodite is long slender ramus, segmented at base; exopodite bears two terminal and four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite not segmented; bears seven sparsely plumose setae. Endopodite distinctly five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 2, 1, 1, 3. Exopodite with two terminal, eight lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite unsegmented, bears two setae. Endopodite distinctly five-segmented, about the same length as exopodite; setation formula 5, 3, 1, 1, 3. Exopodite has 2 terminal and 10 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, not segmented, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3. All pereopods without setae.

PLEOPODS.—Absent until Stage IV.

TELSON (Figure 1K).—Continuous with sixth abdominal somite; slightly emarginate distally; bears seven pairs of densely plumose setae. Fourth pair of setae longest; length about one-half maximum width of telson. Minute spinules at base of each seta except lateral pair. A few larger spinules on distal margin between bases of four inner pairs. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 4.2 mm (range 3.9-4.6 mm; 5 specimens). Rostrum without teeth, sinuate, projects somewhat dorsally. Carapace bears two prominent, supraorbital spines, one on each side of carapace; antennal and pterygostomian spines clearly visible. All zoeal stages examined except Stage I bear supraorbital, antennal, and pterygostomian spines. Epipodite slightly larger than in Stage I, but not bilobed. No

pleurobranchiae. Spines on posterior margins of abdominal somites similar in size and number to spines in Stage I.

ANTENNULE (Figure 2B).—Three-segmented; bears large lateral flagellum and smaller inner flagellum on terminal margin. Inner flagellum unsegmented, conical, and has one long spine terminally. Outer flagellum has five aesthetases of various lengths and one plumose seta. Proximal segment bears four setae laterally near base, single seta subdistally, and two setae distally. Second segment has two setae distally. Distal segment has four plumose setae laterally near inner flagellum and has small seta laterally and subdistally.

ANTENNA (Figure 2C).—Flagellum styliform, about one-third length of scale. Antennal scale about 5½ times as long as wide and fringed along distal and inner margins with 22 long, thin plumose setae. Antennal scale still divided distally into four joints; bears two setae on lateral margin; one at base of proximal joint, one proximally. Protopodite bears spine at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 2D).—Incisor processes of both mandibles more pronounced and have more teeth than in Stage I. Molar processes somewhat more developed than in Stage I, especially forward lip of truncated end.

MAXILLULE.—Similar in shape to maxillule of Stage I, except coxopodite and basipodite each bear additional spine

MAXILLA.—Shape similar to Stage I maxilla, except scaphognathite is slightly longer proximally, bears 9-11 marginal plumose setae, and large plumose seta at proximal end. Endopodite same as endopodite of Stage I. Lobes of basipodite bear either 6 + 6 or 7 + 5 setae; lobes of coxopodite bear 3 + 11 or 3 + 12 setae.

FIRST MAXILLIPED (Figure 2E).—Epipodite of first maxilliped longer than in Stage I. Setation formula of endopodite 3, 2, 1, 3. Protopodite unsegmented, bears about 20 setae.

SECOND MAXILLIPED.—Same as Stage I, except each segment of endopodite may have an additional seta.

THIRD MAXILLIPED.—Dactylopodite (Figure 2F) narrower, longer than in Stage I

FIRST AND SECOND PEREOPODS (second pereopod shown in Figure 2G).—Endopodites of first and second pereopods functionally developed, five-segmented and terminating in simple conical dactylopodite. Exopodite of first pereopod is longest exopodite of pereopods. Exopodites of first and second pereopods have two terminal and eight lateral natatory setae.

THIRD PEREOPOD (Figure 2H).—Exopodite and endopodite nonfunctional but segmented at base. Endopodite tipped by four simple setae.

FOURTH AND FIFTH PEREOPODS (Figure 2I).—Poorly developed, unsegmented, and without exopodites.

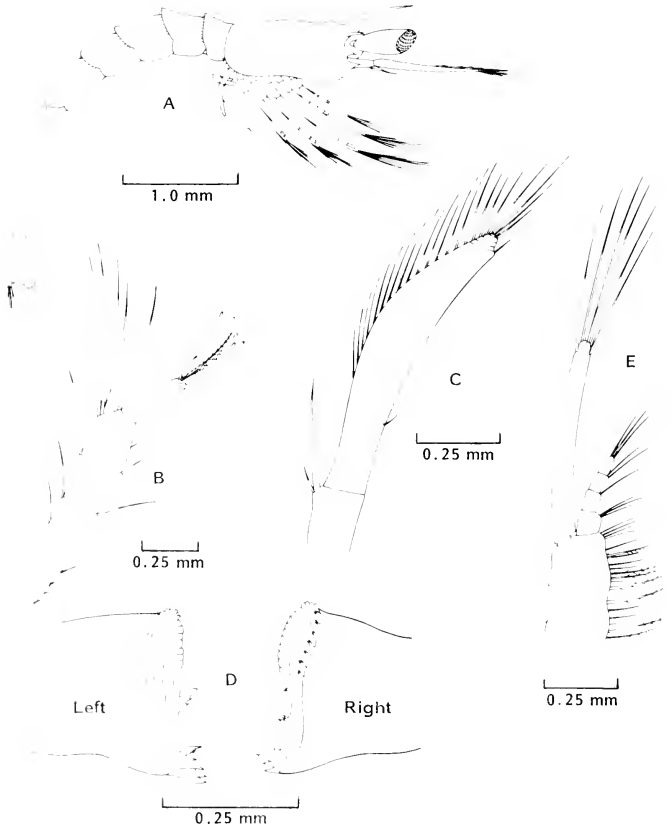
TELSON (Figure 2J).—Telson similar in shape to Stage I, but distinctly segmented from sixth abdominal somite. Telson has eight pairs of densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

Total length of Stage III zoea 5.9 mm (range 5.6-6.3 mm; 7 specimens). No change in shape of rostrum from Stage II. Spines along anteroventral and posteroventral margin of carapace still present, but minute and fewer than in Stage II. Epipodite on first maxilliped still only gill structure present. Spines on posterior margins of abdominal somites smaller than in Stage II.

ANTENNULE.—Similar in shape to antennule of Stage II but bears several additional setae; a spine projects downward from ventral surface of proximal segment. From this stage on, change in antennule slight; inner flagellum lengthens, more setae on antennule.

ANTENNA.—Flagellum styliform, two-segmented, still only about one-third length of scale. Antennal scale about six times as long as wide; two complete joints at tip (Figure 3A). Terminal spine on lateral margin of scale does not quite reach tip of scale. Protopodite bears small spine at base of flagellum and minute projection at base of scale.


A
1.0 mm
B
0.25 mm
C
0.25 mm
E
0.25 mm
D
Left
Right
0.25 mm

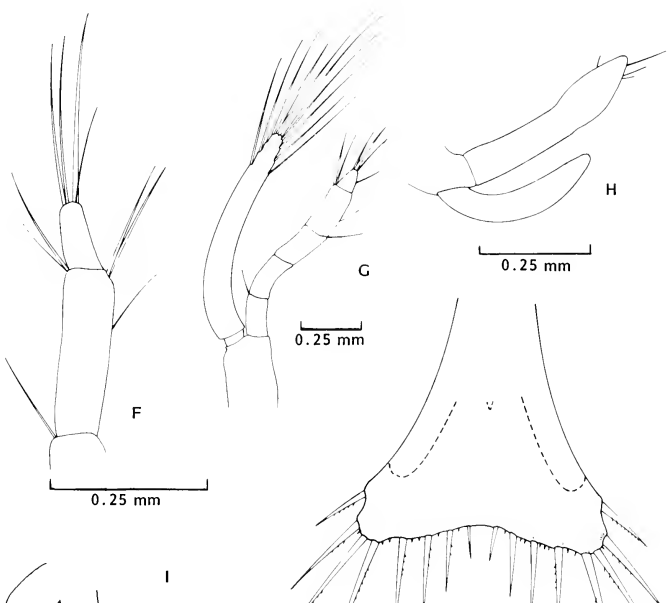


FIGURE 2.—Stage II zoea of *Pandalus tridens*. A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, first maxilliped, lateral; F, third maxilliped (distal segments), lateral; G, second pereopod, lateral; H, third pereopod, lateral; I, fourth and fifth pereopods, lateral; J, telson, dorsal.

FIRST AND SECOND PEREOPODS.—Essentially same as Stage II, except exopodite of second pereopod bears additional pair of setae.

THIRD PEREOPOD (Figure 3B).—Functional, five-segmented. Exopodite bears two terminal and eight lateral natatory setae.

FOURTH PEREOPOD (Figure 3C).—Functional. Dactylopodite tipped by spine and simple seta.

FIFTH PEREOPOD.—Similar to fourth pereopod except terminal spine not as fully developed.

TELSON (Figure 3D).—Uropods free. Endopodite

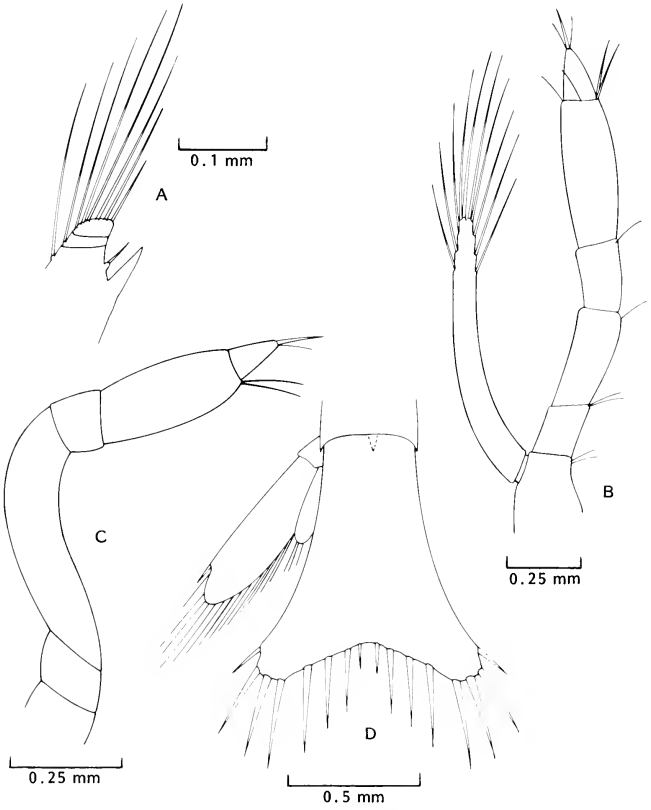


FIGURE 3.—Stage III zoea of *Pandalus tridens*. A, antennal scale (distal portion), ventral; B, third pereopod, lateral; C, fourth pereopod, lateral; D, telson, dorsal

undeveloped, less than one-half length of exopodite, bears three setae distally. Anal spine clearly visible.

STAGE IV ZOEA

Total length of Stage IV zoea 7.8 mm (range 7.0-8.4 mm; 9 specimens). Rostrum (Figure 4A) projects horizontally but curves slightly downward at tip, bears two teeth at base. A few minute spines still on anteroventral and posteroventral margins of carapace. Epipodite of first maxilliped bilobed. Posterior margins of abdominal somites fringed as in Stage III.

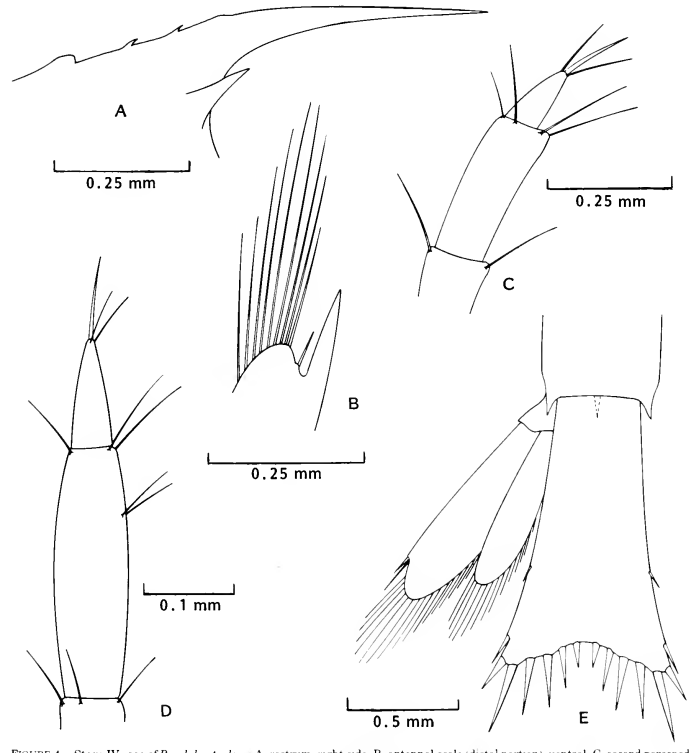


FIGURE 4.—Stage IV zoea of *Pandalus tridens*. A, rostrum, right side; B, antennal scale (distal portion), ventral; C, second pereopod (terminal segments), lateral; D, third pereopod (distal segments), lateral; E, telson, dorsal

ANTENNA.—Flagellum still styliform, only about one-third length of scale. Antennal scale about seven times as long as wide, no joints at tip; terminal spine projects considerably beyond tip of scale (Figure 4B). Protopodite bears small spine at base of flagellum and antennal scale.

SECOND PEREOPOD.—Distal joint of propodite (Figure 4C) widened, projects distally in later stages.

THIRD PEREOPOD.—Dactylopodite lengthened (Figure 4D); exopodite has an additional pair of setae.

PLEOPODS.—Minute buds.

TELSON (Figure 4E).—Endopodite of uropod about three-fourths length of exopodite and fringed with about 15 setae. Lateral margins of telson widen posteriorly, have two spines each. Distal margin emarginated, bears 6 + 6 spines.

STAGE V ZOEA

One specimen with rostrum broken and exopodites of third pereopods missing. Posterior margins of abdominal somites minutely fringed.

ANTENNA.—Flagellum slightly rounded at tip, two-thirds length of antennal scale, five-segmented.

SECOND PEREOPOD.—Chela partially formed; distal joint of propodite projected somewhat distally, tipped by spine (Figure 5A).

SECOND PLEOPODS.—About one-fourth height of second abdominal somite.

TELSON (Figure 5B).—Uropods fully developed, no evidence of transverse hinge. Lateral margins somewhat parallel but widen slightly posteriorly.

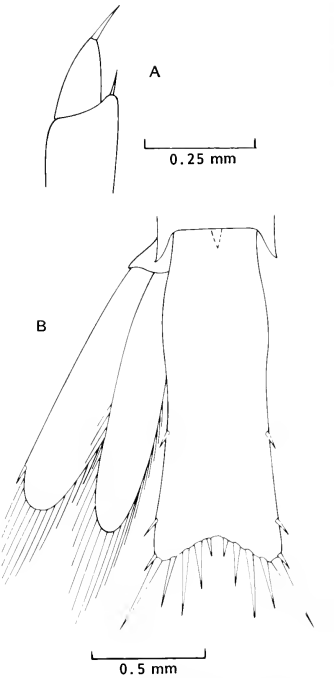


FIGURE 5.—Stage V zoea of *Pandalus tridens*. A, second pereopod (distal segments), lateral; B, telson, dorsal.

STAGE VI ZOEA

Total length of Stage VI zoeae 10.7 mm (range 10.2–11.2 mm; 2 specimens). Rostrum (Figure 6A) about one-third length of carapace, projects horizontally, bears six teeth dorsally, tip bears hump indicating future location of distal tooth. A few minute spines on posterior margin of fifth somite. Bud of epipodite on second maxilliped. Pleurobranchiae at base of all five pereopods.

ANTENNA.—Inner flagellum nearly as long as antennal scale, about 25-segmented.

SECOND PEREOPOD.—Chela well formed (Figure 6B). Terminal spines of propodite and dactylopodite each bear single spine at base.

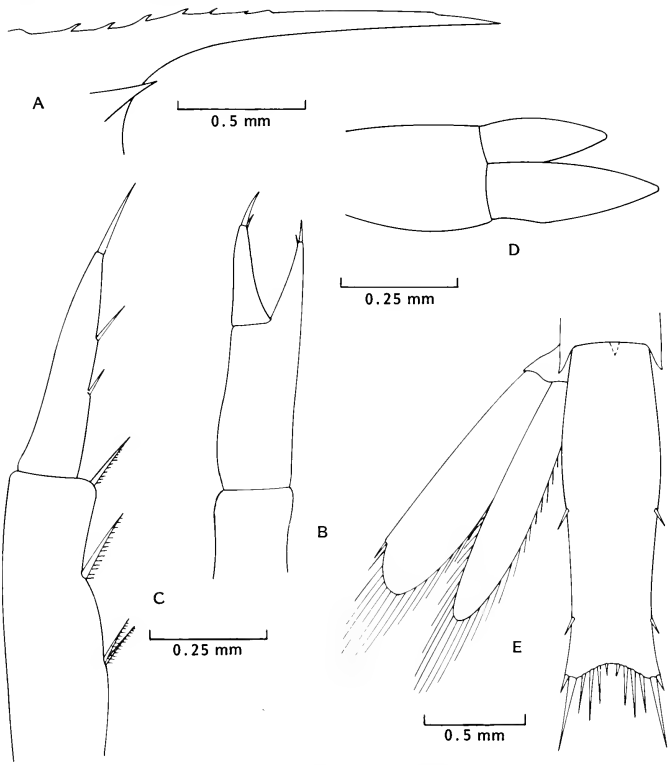


FIGURE 6.—Stage VI zoea of *Pandalus tridens*. A, rostrum, right side; B, second pereopod (distal segments), lateral; C, third pereopod (distal segments), lateral; D, second pleopod, lateral; E, telson, dorsal.

THIRD PEREOPOD.—Dactylopodite well developed; has two distinct spines along inner margin (Figure 6C).

PLEOPODS.—Pleopods segmented at base; no setae or appendices internae. Second pleopod about one-half height of second abdominal somite (Figure 6D).

TELSON (Figure 6E).—Lateral margins somewhat parallel, but not as much as in Stage VII; each margin bears two spines. Posterior margin

slightly emarginated and bears 6 + 6 spines distally. Transverse hinge of exopodite of uropod not evident.

STAGE VII ZOEA

Total length of Stage VII zoea 13.0 mm (1 specimen). Rostrum (Figure 7A) curved slightly upward, slightly less than one-half length of carapace; bears seven teeth dorsally, tooth near tip not developed. No change in number of gill structures from Stage VI.

SECOND PEREOPOD.—Terminal spine of dactylopodite may bear two spines at base instead of one spine, as in Stage VI; carpopodites unsegmented.

PLEOPODS.—Exopodite and endopodite of pleopods tipped by a few setae; no appendices internae. Second pleopod (Figure 7B) about two-thirds height of second abdominal somite.

TELSON (Figure 7C).—Lateral margins essentially parallel, each bears two spines. Transverse hinge of exopodite of uropod partially complete.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The only previously published description of larvae of *Pandalus tridens* is that of Ivanov (1971) who described and figured Stage I zoeae reared from known parentage. My description of the

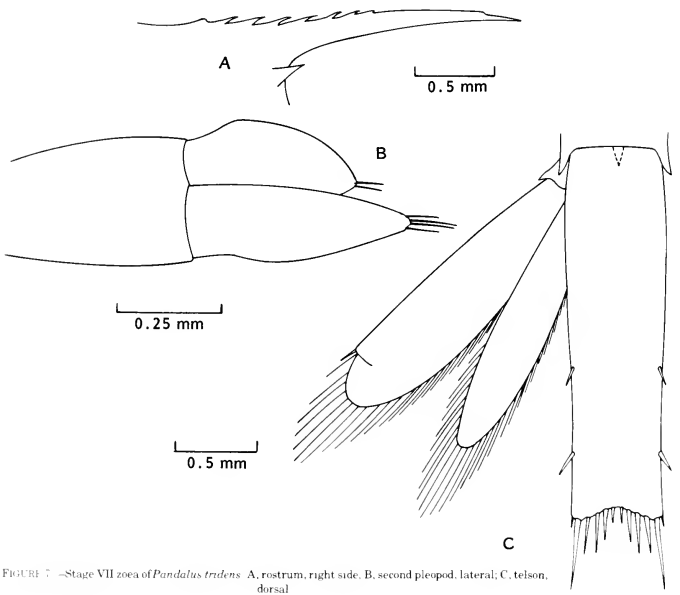


FIGURE 7.—Stage VII zoea of *Pandalus tridens*. A, rostrum, right side. B, second pleopod, lateral; C, telson, dorsal

Stage I zoeae agrees in all essential aspects with Ivanov's description.

Larvae of *P. tridens* are similar to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis*: all have poorly developed pereopods and exopodites on pereopods 1-3 in Stage I. Larvae of *P. borealis* (described by Haynes [1979]), and *P. goniurus* (described by Haynes [1978]), and *P. jordani* (described by Modin and Cox [1967]) are readily distinguishable from larvae of *P. tridens* by the lack of spines on the posterior margins of the abdominal somites and by the rostrum, which in early stages is spiniform and projects downward rather than being sinuate and projecting upwards as in *P. tridens*. In addition, the antennal scales of larvae of *P. borealis*, *P. goniurus*, and *P. jordani* are markedly shorter and wider than in larvae of *P. tridens*.

Zoeae of *P. tridens* described in this report are most similar to zoeae of *P. stenolepis* described by Needler (1938), especially in Stage I. In Stage I zoeae of both species the carapace bears denticles, the abdominal somites are fringed with spines, and the antennal scale is relatively long and narrow. The Stage I zoeae of these species differ: the carapace and abdominal somites of Stage I zoeae of *P. stenolepis* are flared laterally, and the antennal scale bears 9-12 plumose setae; the carapace and abdominal somites of Stage I zoeae of *P. tridens* are not flared, and the antennal scale bears 17 plumose setae. Also, the telson of Stage I zoeae of *P. stenolepis* is considerably wider and the posterior margin more emarginate than the telson of Stage I zoeae of *P. tridens*. Other morphological differences between zoeae of the two species are the antennal flagellum and rostrum. The antennal flagellum in all zoeal stages of *P. stenolepis* is longer than the antennal scale; the antennal flagellum of zoeae of *P. tridens* remains shorter than the antennal scale through at least Stage V. The rostrum of *P. stenolepis* zoeae is as long as, or longer than, the carapace and bears teeth as early as Stage II; the rostrum of *P. tridens* zoeae remains shorter than the carapace as late as Stage VII and does not bear teeth until Stage IV.

The morphology of Stages I-VII zoeae of *P. tridens* from lower Cook Inlet confirms the opinion (Ivanov 1971; Squires[3]) that *P. montagui tridens*, the Pacific subspecies of *P. montagui* Leach, should be given the full specific rank of *P. tridens* Rathbun 1902. Rathbun's (1902, 1904) separation of the Pacific subspecies, *P. montagui tridens*, from the Atlantic species, *P. montagui*, was based on slight differences in adult morphology. For instance, the rostrum of the Pacific subspecies was $1^1/_2$-$1^2/_3$ times the length of the carapace compared with $1^2/_3$-$1^1/_2$ times the length of the carapace for the Atlantic species. Also, termination of the dorsal rostral spines of the Pacific subspecies was behind the middle of the carapace rather than in the middle or in front of the middle of the carapace as in the Atlantic form. Squires' (see footnote 3) conclusion that the Pacific subspecies should be given specific status was based on coloration of adults. Ivanov's (1971) conclusion was based on morphological differences between Stage I larvae of *P. tridens* from the Gulf of Alaska and Pike and Williamson's (1964) description of Stage I larvae of *P. montagui* from the North Atlantic. In Stage I *P. montagui* the margins of the carapace and abdominal somites are smooth; in Stage I *P. tridens* the carapace bears pterygostomian spines, the antero- and posterolateral margins of the carapace bear denticles, and the posterior margins of the abdominal somites bear minute spines. In *P. tridens*, the rostrum is longer and the number of setae and spines on the antennal scale is greater than in *P. montagui*. Also, *P. tridens* larvae are larger than larvae of *P. montagui*. My comparison of the seven zoeal stages of *P. tridens* from Cook Inlet with the zoeae of *P. montagui* raised in the laboratory and collected from North Atlantic plankton by Pike and Williamson (1964) confirms the morphological differences found by Ivanov (1971) for Stage I and shows that these differences persist through later stages.

SUMMARY OF PRINCIPAL MORPHOLOGICAL CHARACTERISTICS

Certain characteristics of larvae of pandalid shrimp from the North Pacific Ocean change form as the larvae develop. I discuss changes of these characteristics and categorize the larvae by number of stages. I also discuss the probable morphology of larvae of *Pandalopsis ampla* Bate, *P. alcutica* Rathbun, and *P. longirostis* Rathbun and larvae tentatively identified as *Dichelopandalus leptocerus* (Smith).

Although the number of pereopods bearing exopodites does not change during larval development, the exopodites themselves degenerate

[3]Squires, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian Eastern Arctic. Fish. Res. Board Can., MS Rep. Ser. Biol. 810: 1-212. Biological Station, Nanaimo, B.C. V9R-5K6.

during later stages, usually at the molt to the megalopa. In Table 1, poorly developed pereopods in Stage I are unsegmented pereopods that are directed anteriorly under the cephalothorax. Usually pereopods become functional by Stage III.

Denticles on the carapace and spines on the abdominal somites are most prevalent in Stage I and tend to disappear during larval development. Thus, in *Pandalus platyceros* most of the denticles and spines have disappeared by Stage III; in *P. stenolepis* and *P. tridens* most have disappeared by Stage VI.

For most pandalid shrimp larvae, the typical number of telsonic spines is 7 + 7 in Stage I and 8 + 8 in later stages. In the latest stage another pair may be added. The total number of telsonic spines of *P. kessleri* varies from 30-34 (Stage I) to 14-15 (Stage V); *Pandalopsis coccinata* has 55-56 telsonic spines in Stage I (Kurata 1955, 1964). Stage I *Pandalus kessleri* and *Pandalopsis coccinata* usually have 16 + 16 and 28 + 28 telsonic spines, respectively (Table 1).

The number of larval stages of *Pandalopsis dispar*, *P. coccinata*, *Pandalus tridens*, and *P. jordani* has not been verified. Seven zoeal stages are known for *Pandalopsis dispar* and *Pandalus tridens*. Based on morphological development, Stage VII of *Pandalopsis dispar* is probably the last larval stage. *Pandalus tridens* probably has an additional stage before the larvae molt to the first juvenile stage. Only the first zoeal stage of *Pandalopsis coccinata* is known, but development of this stage is so far advanced that only one or, at the most, two more stages probably appear before the larvae molt to the first juvenile stage. For *Pandalus jordani*, I have estimated six larval stages based on development of larvae of morphologically similar species, *P. borealis*, *P. gonurus*, and *P. tridens*, rather than the 11-13 stages obtained by Modin and Cox (1967) or the 8+ stages obtained by Lee (1969) in the laboratory. Modin and Cox (1967) noted that the 11-13 larval stages of *P. jordani* obtained by them in the laboratory were nearly twice the number of larval stages of the closely related *P. borealis*. Artificial laboratory conditions may have caused a greater number of larval stages than natural conditions.

The numbers of larval stages cited in Table 1 include the megalopa stage because the transition from zoea to megalopa is not always abrupt and may extend over several molts. For example, *P. hypsinotus* has functional pleopods in Stage VII, but other morphological characteristics normally associated with postzoea occur earlier (Haynes 1976). Also, the number of larval stages of some species vary slightly depending on geographical origin. Larvae of *P. hypsinotus*, *P. gonurus*, and *P. borealis* from the western North Pacific Ocean and *P. borealis* from British Columbia waters have one or two more stages than larvae of these species from Alaskan waters (Haynes 1976, 1978, 1979). Geographical variation in larval morphology has not been verified for other species of pandalids from the North Pacific.

The number of larval stages given in Table 1 refers to development in the sea rather than in the laboratory. Development in the laboratory often results in molt retardation and extra stages. Although the number of molts required to reach a specific point in development may vary in wild pandalid shrimp (Haynes 1978), the stages are, for the most part, remarkably constant and limited in number (Gurney 1942).

For identification purposes, pandalid shrimp larvae of the North Pacific Ocean can be categorized into two groups on the basis of morphological

TABLE 1.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the North Pacific Ocean. + = yes, − = no. (Only the most complete references on larval morphology are given.)

Species	Pereopods bearing exopodites	Pereopods poorly developed in Stage I	Spines on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages	References[1]
Pandalopsis coccinata	1-2				28 + 28	3	4
P. dispar	1-2				12 + 12	7	1
Pandalus kessleri	1-2				16 + 16	4	3 4
P. danae	1-2				7 + 7	6	1
P. hypsinotus	1-2				7 + 7	7	1 10
P. platyceros	1-3				8 + 8	5	1 9
P. tridens	1-3	+	+	+	7 + 7	8	8, 13
P. stenolepis	1-3	+	+	+	7 + 7	6	2
P. borealis	1-3				7 + 7	6	1 4 12
P. gonurus	1-3				7 + 7	6	5 11
P. jordani	1-3				7 + 7	6	6 7

[1]References: 1) Berkeley (1930), 2) Needler (1938), 3) Kurata (1955), 4) Kurata (1964), 5) Ivanov (1965), 6) Modin and Cox (1967), 7) Lee (1969), 8) Ivanov (1971), 9) Price and Chiew (1972), 10) Haynes (1976), 11) Haynes (1978), 12) Haynes (1979), 13) this report.

characteristics: species with exopodites on pereopods 1-3 and species with exopodites only on pereopods 1 and 2. Species with exopodites on pereopods 1 and 2 are characterized by well-developed pereopods in Stage I, and no spines on the abdominal somites or denticles on the carapace margin. For three of the species with exopodites on pereopods 1 and 2 (*Pandalopsis coccinata*, *P. dispar*, and *Pandalus kessleri*), the numbers of telsonic spines in Stage I are considerably greater than for species with exopodites on pereopods 1-3.

Fewer thoracic exopodites usually indicate fewer stages before the megalopa (Pike and Williamson 1964). This is not always true for pandalid shrimp larvae of the North Pacific Ocean. For instance, larvae of *P. danae*, *P. hypsinotus*, and *Pandalopsis dispar* also bear exopodites on first and second pereopods; but, the number of their larval stages is 6, 7, and 7, respectively. Also, Stage I larvae of *P. dispar* have dorsal and ventral teeth on the rostrum, 12 + 12 spines on the telson, and a long, jointed antennal flagellum that is about six times the length of the antennal scale; but the pleopods are not tipped with setae until Stage V, and Stage VII zoeae still bear a supraorbital spine.

A greater number of telsonic spines in Stage I is associated with fewer larval stages in development of the Caridea (Gurney 1942; Pike and Williamson 1964). This is true for *Pandalus platyceros*, *P. kessleri*, and *Pandalopsis coccinata*, which have 8 + 8, 16 + 16, and 28 + 28 telsonic spines in Stage I and 5, 4, and 3 larval stages, respectively. An exception is *P. dispar*, which has 12 + 12 telsonic spines in Stage I, but may have as many as seven larval stages.

Four species of pandalid shrimp in the North Pacific Ocean are not listed in Table 1: *Pandalopsis ampla*, *P. aleutica*, *P. longirostris*, and *Dichelopandalus leptocerus*. Larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* have not been described. If larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* undergo typical development of larvae of the genus *Pandalopsis* (Kurata 1964; Berkeley 1930), they will be characterized by advanced development, especially their large size and long antennal flagellum. Stage I *Pandalopsis* spp. larvae are at least 10.0 mm long and the antennal flagellum is longer than the body and segmented throughout its length. For comparison, Stage I larvae of *Pandalus* are 8.0 mm or less in length and the antennal flagellum is usually unsegmented and shorter than the length of the carapace. Stage I and II larvae of *D. leptocerus* have been tentatively identified from western Greenland waters (Pike and Williamson 1964). The larvae identified as *D. leptocerus* are most similar to larvae of *P. stenolepis* and *P. platyceros*: in Stage I and II, *D. leptocerus*, *P. stenolepis*, and *P. platyceros* bear prominent denticles on the anteroventral margin of the carapace, the anteroventral margin of the carapace and posterior margin of the third abdominal somite are flared, the rostrum is about as long as the carapace, and exopodites are present on pereopods 1-3. Larvae of *D. leptocerus* can be distinguished, however, from the identified pandalid shrimp larvae of the North Pacific Ocean, including larvae of *P. stenolepis* and *P. platyceros*, by the presence of posterolateral spines on the fifth abdominal somite.

LITERATURE CITED

BERKELEY, A. A.
1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. 6: 79-163.

GURNEY, R.
1942. Larvae of decapod Crustacea. Ray. Soc. (Lond.) Publ. 129, 306 p.

HAYNES, E.
1976. Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory. Fish. Bull., U.S. 74: 323-342.
1978. Description of zoeae of the humpy shrimp, *Pandalus goniurus*, reared in situ in Kachemak Bay, Alaska. Fish. Bull., U.S. 76: 235-248.
1979. Description of larvae of the northern shrimp, *Pandalus borealis*, reared in situ in Kachemak Bay, Alaska. Fish. Bull., U.S. 77: 157-173.

IVANOV, B. G.
1965. A description of the first larva of the far-eastern shrimp *Pandalus goniurus* [In Russ., Engl. summ.]. Zool. Zh. 44: 1255-1257. (Transl. by U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Off. Int. Fish. Affairs, Code No. F44.)
1971. The larvae of some eastern shrimp in relation to their taxonomic status. [In Russ., Engl. summ.] Zool. Zh. 50: 657-665. (Transl. by U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Off. Int. Fish. Affairs, Code No. F44.)

KURATA, H.
1955. The post-embryonic development of the prawn, *Pandalus kessleri*. [In Jpn., Engl. synop.] Bull. Hokkaido Reg. Fish. Res. Lab. 12: 1-15.
1964. Larvae of decapod Crustacea of Hokkaido. 3. Pandalidae. [In Jpn., Engl. synop.] Bull. Hokkaido Reg. Fish. Res. Lab. 28: 23-34.

LEE, Y. J.
1969. Larval development of pink shrimp, *Pandalus jordani* Rathbun reared in laboratory. M.S. Thesis, Univ. Washington, Seattle, 62 p.

MODIN, J C, AND K W COX
1967 Post-embryonic development of laboratory-reared ocean shrimp, *Pandalus jordani* Rathbun Crustaceana 13 197-219

NEEDLER, A B
1938 The larval development of *Pandalus stenolepis* J Fish Res Board Can 4 88-95

PIKE, R B, AND D I WILLIAMSON
1964 The larvae of some species of Pandalidae (Decapoda) Crustaceana 6 265-284

PROFF, V A, AND K K CHEW
1972 Laboratory rearing of spot shrimp larvae (*Pandalus platyceros*) and description of stages J Fish Res Board Can 29 413-422

RATHBUN, M J
1902 Descriptions of new decapod crustaceans from the west coast of North America Proc U S Natl Mus 24 885-905

1904 Decapod crustaceans of the Northwest coast of North America *In* C H Merriam (editor), Alaska the Harriman Expedition, Vol 10, Crustaceans, p 1-210 Doubleday, N Y (Also published in 1910 as Smithson Inst, Harriman Alaska Ser 10 (Publ 1997))

SPAWNING INCIDENCE AND BATCH FECUNDITY IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*[1]

J. ROE HUNTER[2] AND STEPHEN R. GOLDBERG[3]

ABSTRACT

Histological criteria were developed to age postovulatory follicles from examination of laboratory-spawned northern anchovy and used to estimate the frequency of spawning of natural populations. One-day-old, postovulatory follicles were the preferred estimator of spawning frequency, 48 hours after spawning postovulatory follicles could not be consistently identified because of their rapid degeneration; and the occurrence of postovulatory follicles less than 24 hours old was affected by hour of sampling and sexual composition of the school. The nightly spawning incidence was estimated to be 16±4% of the northern anchovy population in February and 12% in March. Thus, females spawned about every 6-8 days during the peak of the breeding season. The rate of oocyte development corresponded with this reproductive rate, indicating that a new mode of yolked oocytes matured about once a week. Nearly all eggs in the most advanced mode in the ovary were spawned in one night and the number of eggs spawned was estimated to be 389±59 eggs/g of female (ovary-free wet weight). The high spawning frequency and the prolonged breeding season of the northern anchovy indicate that total fecundity may be limited by food availability and energy reserves.

Ichthyoplankton surveys have become one of the standard methods for estimating biomass of marine fish populations. At high latitudes many fishes produce a single spawning batch per year (Qasim 1956) and spawning biomass may be directly estimated from total fecundity and production of eggs and larvae. Multiple (fractional) spawning fishes are characteristic of subtropical and tropical seas (Nikolsky 1963) and estimation of spawning biomass from egg and larval production is dependent upon the number of spawnings per year and the number of eggs per spawning. At present, no adequate method exists for estimating these two parameters for pelagic, multiple spawning fishes.

Past methods have employed measurements of size-frequency distribution of yolked oocytes (usually eggs >0.2 mm in diameter). Eggs are often distributed in one to three modes and the number of eggs in the most advanced mode has been assumed to be equal to the number of eggs produced per spawning (Clark 1934; MacGregor 1968). Another approach has been to count all yolked oocytes in reproductively active females and to assume that these are equal to the number of eggs spawned in a season (Macer 1974). Neither approach provides conclusive evidence for the number of spawnings nor total egg production. All eggs in the most advanced mode may not ovulate (Clark 1934; Yamamoto and Yamazaki 1961) and atresia may reduce the number of eggs per spawning (Macer 1974; Ivankov 1976). Further, the total number of yolked oocytes may not provide an estimate of total fecundity because some of the small unyolked oocytes, not included in such counts, could mature later during the same breeding season.

It has long been known in teleost fishes (Cunningham 1898) that at ovulation a remnant of the ovulated follicle (empty or postovulatory follicle) remains in the ovary. Postovulatory follicles are believed to be transitory because of their rarity in field-collected material (Wheeler 1924; Yamamoto 1956; Gokhale 1957; DeVlaming 1972; Goldberg 1977; Andrews[4]), but actual measurements of their longevity are rare because the time of spawning must be known. Yamamoto and Yoshioka (1964), using *Oryzias latipes* which spawns every 3 days, reported postovulatory follicles were barely distinguishable on the third day after spawning. They suggested that the frequency of spawning

[1]Supported in part by the Marine Research Committee of the State of California.

[2]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3]Department of Biology, Whittier College, Whittier, CA 90608.

[4]Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford University, Stanford, CA 94305.

Manuscript accepted March 1979.
FISHERY BULLETIN: VOL. 77, NO. 3, 1980

could be determined by the presence of postovulatory follicles but the estimate would have to be made soon after spawning. Through techniques of Leong (1971) it was possible to induce spawning in the northern anchovy, *Engraulis mordax*, in the laboratory, making it possible to characterize the histological degeneration of postovulatory follicles on a time basis. Thus, it seemed feasible that spawning frequency of natural populations of *E. mordax* could be estimated from incidence of postovulatory follicles in females once the period in which they could be detected was established. Moreover, once recently spawned fish were identified, the rate of maturation of subsequent egg batches as well as the number of eggs produced per batch could be estimated.

The objectives of this study were to establish the detection period for postovulatory follicles in northern anchovy and to estimate the incidence of natural spawning through histological examination of these structures. In addition, by using this information to guide our selection of specimens, we provide a new estimate of the number of eggs released per spawning or batch fecundity, and the time required for subsequent spawnings. Previous estimates for anchovy based on frequency distributions of yolked oocytes include those of MacGregor (1968) and Norberg.[5]

[5]Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel and Pacific mackerel. Unpubl manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

METHODS

The period over which postovulatory follicles can be detected in the ovary was determined from anchovy held in the laboratory. Groups of anchovy reared to sexual maturity were induced to spawn using the method of Leong (1971). A total of 119 females were sampled; fish were killed at the time of spawning and thereafter at 24-h intervals up to 9 days after spawning. Ovaries were fixed in Bouin's fixative or 10% neutral buffered Formalin[6] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris' hematoxylin followed by eosin counterstain, Masson's trichrome, periodic acid-Schiff reagent, or Heidenhain's iron hematoxylin. A classification system for postovulatory follicles was established and laboratory specimens were classified without prior knowledge of their age to estimate the accuracy of the technique. Field samples were then classified using the same criteria. Three field collections of anchovy females from the Southern California Bight were examined to determine the frequency of spawning in natural populations: 3 commercial purse seine samples of 38-65 females each from March 1977; 4 research trawl samples of 1-11 females from September 1977; and 29 research trawl samples of 10 or 11 females from February 1978 (Figure 1).

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

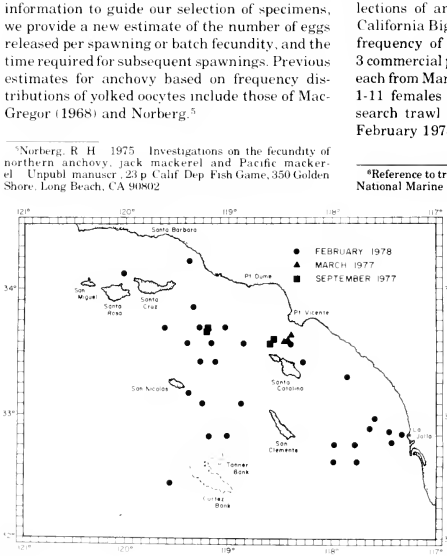


FIGURE 1.—Location of samples of female northern anchovy taken off southern California in March and September 1977 and February 1978.

The number of eggs per mode was estimated for 117 of the field-caught specimens by fixing a weighed sample in Gilson's fluid and determining the size-frequency distribution of yolked oocytes (MacGregor 1968; Macer 1974). One-hundred and fifty of the oocytes >0.20 mm on the major axis were measured to the nearest 0.05 mm from each sample and all the remaining oocytes (>0.20 mm) were counted. We shall use "diameter" to refer to these measurements but since anchovy eggs are longer than wide, it is not a diameter in a strict sense but the major axis of an oblate spheroid.

The form of the distribution of egg diameters within an ovary was similar to those illustrated for other multiple spawning fishes (Macer 1974). Distributions varied from ones composed of two to three distinct modal groups of eggs to ones with only a single mode. Even in those with very distinct modal groups the tails of adjacent modes often overlapped. We used the program NORMSEP (Abramson 1971) to separate modal groups, estimate the mean egg diameter within a mode, and estimate iteratively the number of eggs within a mode. Although one must arbitrarily assume egg diameters within a mode are normally distributed, the program does eliminate some of the subjectivity in judging the range of diameters to include within a mode and how the tails of adjacent modes should be proportioned.

Just prior to ovulation and spawning the modal group of eggs about to be spawned takes up fluid and swells to three or four times its former volume (Fulton 1898). These hydrated eggs greatly increase the ovary weight and increase the total weight of the female. To avoid this bias in female weight we used female weight less ovary weight (ovary-free wet weight) to express fecundity-weight relations. We also provide fecundity estimates based on total weight in tabular form so that conversions can be made if desired.

CLASSIFICATION OF OVARIES

Ovaries of laboratory matured females that had spawned within 24 h in all cases contained postovulatory follicles. They were similar in appearance to those described for a variety of teleosts (Cunningham 1898; Wheeler 1924; Bowers and Holliday 1961; Yamamoto and Yoshioka 1964; Moser 1967; Scott 1974). In specimens killed 0-6 h after spawning, postovulatory follicles consisted of irregularly shaped structures composed of columnar follicle cells and an underlying connective tissue theca (Figure 2A, B). In some cases the columnar cells had hypertrophied slightly. The lumen characteristically contained eosinophilic granules of uncertain origin.

Degeneration was pronounced in material examined 24 h after spawning. The postovulatory follicle (Figure 2C) had greatly shrunken or collapsed on itself, vacuoles had become common, and walls of the follicle cells were no longer distinguishable (Figure 2D). The granular material that was observed in postovulatory follicles taken at the time of spawning was still present but not as abundant. The prominent underlying connective tissue theca seen in new postovulatory follicles was no longer distinct. Degeneration had progressed further, 48 h after spawning. The follicle was one-half to one-fourth smaller than at 24 h, the lumen was very small or indistinguishable, eosinophilic granules were absent, and nuclear sizes were greatly reduced.

Owing to their rapid degeneration, postovulatory follicles were difficult to age in laboratory specimens sampled 48 h after spawning. At this time they may be confused with intermediate stages of atretic oocytes (Lambert 1970). On the other hand, classification of postovulatory follicles into age 0 day and age 1 day was done with an accuracy of 76 to 84% (Table 1). In view of this, the following system was established for classification of ovaries from field-caught specimens:

Hydrated: ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no postovulatory follicles. (Spawning considered to be imminent.)

Age 0 day: new postovulatory follicles, showing no sign of degeneration as described above (Figure 2A, B). Hydrated eggs may occasionally be present. Elapsed time from spawning <24 h.

Age 1 day: regressing postovulatory follicles, showing degeneration as described for specimens (Figure 2C, D) sampled 24 h after spawning. Elapsed time from spawning ≥24 h but <48 h.

Nonspawning (mature): ovaries with many yolked oocytes; may contain postovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from other atretic structures. Elapsed time from spawning 48 or more hours.

Immature: few or no yolked oocytes.

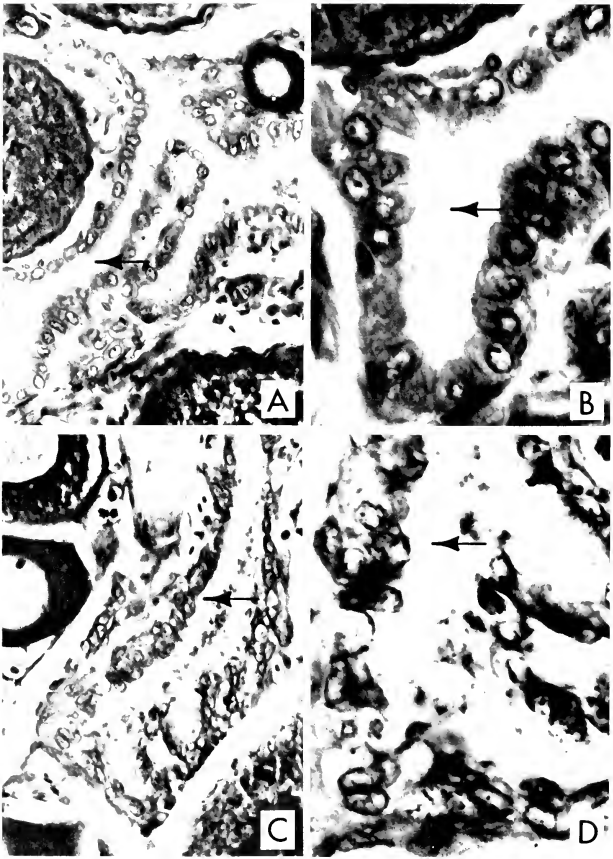


FIGURE 2.—Photomicrographs of northern anchovy ovaries from laboratory specimens: A (400×) and B (1,000×), postovulatory follicles (elapsed time from spawning 0.6 h); C (400×) and D (1,000×), postovulatory follicles (elapsed time from spawning 24 h). Arrow indicates lumen of postovulatory follicle.

TABLE 1.—Results of blind classification[1] (number of females) of postovulatory follicles of female northern anchovy spawned in the laboratory.

Elapsed time from spawning (days)	n	Classification: Postovulatory follicles, 0 day	Postovulatory follicles, 1 day	Postovulatory follicles older than 2 days or no evidence of spawning	Percent correctly classified
0	21	16	5	0	76
1	19	0	16	3	84
2	23	0	0	23	100
3	20	0	0	20	100
4-9	38	0	0	38	100

[1]Elapsed time from spawning was unknown to classifier

All sea samples were classed into the above categories. The mean incidence for each category was calculated without regard to the classification uncertainties reported in Table 1. Confidence intervals for mean incidence for each reproductive state were calculated for the February set of samples but not for those taken in March or September because these sets contained only three or four samples. The normal approximation of the binomial distribution was used to estimate the confidence interval (C.I.) for the mean incidence of day 1 postovulatory follicles (95% C.I., Table 2). A normal-log negative binomial distribution (Johnson and Kotz 1970; Zweifel[2]) was used to estimate confidence intervals for the mean incidence of hydrated eggs and new postovulatory follicles because it gave a better fit to the data distribution than did the binomial distribution (Figure 3).

RESULTS

Sexual Maturity

All females taken in February and March were mature, but only 67% of those taken in September were mature. No relation existed between reproductive activity and length in the females examined. Twelve females taken in February in southern inshore stations (Figure 1) were < 90 mm standard length (SL), which is smaller than any of

[2]Zweifel, J. R. 1978. Confidence intervals for the mean when sampling from natural environments. Unpubl. manuscr., 10 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038

TABLE 2.—Reproductive state[1] of female northern anchovy collected off southern California in February 1978.

Station number	Day of month	Time of day	Mean length (mm)	Number of females in various reproductive states: Hydrated eggs	Postovulatory follicles: 0 day	Postovulatory follicles: 1 day	Mature, no evidence of spawning	Total females
2	15	1822	124	0	0	2	9	11
3	15	2053	122	1	2	2	5	10
4	15	2121	116	1	1	1	7	10
5	15	2308	117	2	2	2	4	10
7	16	1908	116	4	0	0	6	10
8	16	2147	106	2	6	0	3	11
9	16	2215	114	0	2	0	8	10
10	16	2326	114	0	1	0	9	10
11	17	0044	112	0	1	1	8	10
13	17	1835	138	0	0	1	10	11
15	17	2132	134	6	0	1	3	10
21	18	2002	137	1	0	0	9	10
27	19	2100	141	0	2	4	4	10
28	19	2230	135	0	1	2	7	10
34	20	2254	138	3	0	3	4	10
37	21	2002	139	0	0	5	5	10
38	21	2117	132	0	0	3	7	10
42	22	1934	103	4	0	3	4	11
45	22	2332	80	0	2	0	8	10
48	23	1838	136	0	0	3	7	10
49	23	2005	122	1	0	1	8	10
50	23	2202	120	0	0	1	9	10
52	24	0125	117	0	0	1	9	10
55	24	1915	126	0	1	3	6	10
57	24	2224	125	2	0	0	9	11
58	25	0009	120	1	2	4	3	10
62	25	1915	116	2	1	1	6	10
72	27	0045	111	0	0	2	8	10
75	27	2112	112	2	0	1	7	10
Σx				32	24	47	192	295
%				11	8	16	65	100
95% C.I.				6-19	5-14	12-20	—	—

[1]Immature state not included in table because all females were mature.
[2]95% confidence intervals for mean percent of females in each reproductive class

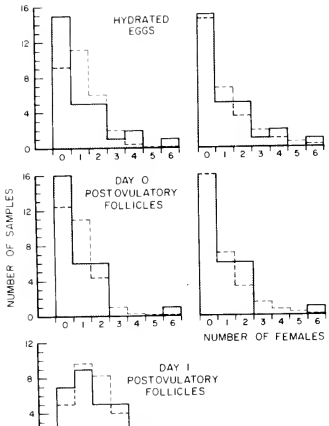


FIGURE 3.—Frequency distribution of the numbers of samples from February 1978 containing 0-6 females in each of three reproductive classes (solid bars). On left sides of the upper two panels are distributions for hydrated eggs and for day 0 postovulatory follicles, compared with that expected (dashed line) from the binomial distribution. On the right sides they are compared with that expected from the negative binomial; the negative binomial gave the better fit in both cases. Bottom panel: the frequency distribution for day 1 postovulatory follicles is compared with that expected (dashed line) from the binomial distribution, which gave an adequate fit to the data.

the reproductively active females found by Clark and Phillips (1952). They reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-120 mm, and 50% at 130 mm, whereas all females we collected in February and March, regardless of size, were sexually mature. Similar to our observations, Brewer (1978) reported anchovy as small as 81 mm SL with well-developed ova from San Pedro Bay. The size of anchovy at first reproduction may have changed since 1946-52 when Clark and Phillips made their observations. On the other hand, all of our collections and those of Brewer (1978) were from southern California whereas those of Clark and Phillips (1952) included collections from the north (Monterey). It is possible that specimens living at the northern end of the range of the central subpopulation could be larger at first maturity.

Incidence of Spawning

Variation existed in the percentage of females occurring in the three reproductive states that were indicative of imminent or recent spawning. Of the females taken in February, 11% had only hydrated eggs, 8% had new postovulatory follicles, and 16% had 1-day-old postovulatory follicles (Table 2). It is critical to our objective of estimating spawning frequency to consider which of these states provided the better estimates. The distribution of the number of samples containing females with hydrated eggs and that for females with 0 day postovulatory follicles gave a poor fit to the binomial distribution indicating possible bias from contagion within samples, whereas no such problem existed for 1-day-old postovulatory follicles (Figure 3). Furthermore, evidence existed for a bias in sampling females with hydrated eggs and those with new postovulatory follicles that was related to time of day (discussed below) and with sexual composition of the school (to be discussed in a separate section). For these reasons, we believe the 1-day-old postovulatory follicles are the preferred estimator of spawning frequency.

Anchovy spawn only at night, and estimates made by Smith[8] from staged eggs indicated that most spawning occurs between 2000 and 0400 h. Since hydration precedes ovulation and spawning, one would expect the females with hydrated eggs to be the most common before 2000. In February, females with new postovulatory follicles were probably undersampled and females with hydrated eggs possibly oversampled, because most samples were taken before midnight. No females with hydrated eggs occurred in the February collections at night before 1900 h; six March females taken in the morning showed the first signs of hydration but the eggs were not sufficiently developed to be classified as hydrated. In February the number of females with hydrated eggs increased sharply after 1900 and generally remained high until 2400 (Table 3). Females with new postovulatory follicles occurred for the first

[8]Smith, P. E. 1978. A field study of anchovy spawning time. Southwest Fish. Cent. Admin. Rep. No. LJ-78-8, 1 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 3.—Percent of female northern anchovy sampled off southern California in February 1978 with hydrated eggs, and postovulatory follicles (age 0 day and age 1 day) by time of day

Time	Percent of females			Total no. of females
	Hydrated eggs[1]	Postovulatory follicles		
		0 day[2]	1 day	
1801-1900	0	0	19	32
1901-2000	24	5	17	41
2001-2100	6	8	24	50
2101-2200	22	14	12	51
2201-2300	10	6	12	51
2301-2400	7	17	7	30
0001-0100	3	10	23	30
0101-0200	0	0	10	10
Total				295

[1]Only hydrated eggs, no postovulatory follicles
[2]Includes some females with hydrated eggs and new postovulatory follicles

time between 1900 and 2000, but were more common later in the night. As expected, the occurrence of females with 1-day-old postovulatory follicles showed no pattern with time of sampling.

Despite our failure to obtain fish over the entire night of spawning, the proportion of females in February with hydrated eggs, combined with those with new postovulatory follicles, was 19% and within the confidence interval for the estimate based on 1-day-old postovulatory follicles (Table 2).

February data indicate that spawning over a 2-wk period occurred at a rate of about 16±4% of the population per night. This means that mature females spawned every 6-7 days. The three purse seine samples taken in March 1977 also indicated a high frequency of spawning; 14% of the females had 1-day-old postovulatory follicles and 9% had new postovulatory follicles (Table 4). The March collections were taken in the early morning after spawning had ended, hence the new and 1-day-old postovulatory follicles can be considered as separate estimates of spawning frequency for different days. This line of reasoning leads to the conclusion that the proportion of females spawning in March may have been about 12%, equivalent to spawning every 8 days.

Of the 24 females taken in September, only 1 had hydrated eggs, 2 had new postovulatory follicles, and none had 1-day-old postovulatory follicles. Lower spawning activity would be expected in September because egg and larval survey data indicate peak spawning usually occurs in February and March and has declined greatly by September although some spawning occurs throughout the year (Lasker and Smith 1977).

Sex Ratio and Incidence of Spawning

The sex ratio of northern anchovy schools is known to vary markedly from schools composed of nearly all females to ones composed of nearly all males (Collins 1969; Klingbeil 1978). It seemed useful to determine if spawning activity varied with sex ratio because the greatest variability in sex ratio occurs during the peak months of spawning (Klingbeil 1978). Twenty-five fish from each trawl sample taken in February 1978 were sexed. We grouped these samples into three classes on the basis of sex ratio (number of females/(males + females)) and calculated the proportion of females in each of the three sex ratio classes that fell within the following reproductive classes: spawning on the night of capture (females with hydrated eggs or new postovulatory follicles); spawning on the night before capture (females with 1-day-old postovulatory follicles); and no evidence of spawning (none of the above categories).

TABLE 4.—Reproductive state of female northern anchovy collected in March 1977 and September 1977 off southern California

Station number	Day of month	Time of day	Mean SL (mm)	Number of females in various reproductive states					Total females
				Hydrated eggs	Postovulatory follicles		Mature, no evidence of spawning	Immature	
					0 day	1 day			
				March 1977					
1	20	0400	120	0	2	11	32	0	45
2	21	0330	119	0	7	6	54	0	67
3	21	0630	113	0	5	4	29	0	38
Σx				0	14	21	115	0	150
%				0	9	14	78	0	
				September 1977					
1	9	2108	124	1	0	0	4	0	5
2	9	2300	129	0	2	0	9	0	11
3	10	2043	113	0	0	0	0	1	1
4	10	2236	112	0	0	0	1	6	7
Σx				1	2	0	14	7	24
%				4	8	0	58	29	

In samples containing mostly males (mean sex ratio = 0.25), nearly 40% of the females spawned on the night of capture, whereas in samples containing mostly females (mean sex ratio = 0.84), only 10% of the females spawned on the night of capture (Table 5). A chi-square test indicated that the proportion of females spawning on the night of capture differed among the three classes of sex ratios ($P<0.001$) but no difference existed for females with 1-day-old postovulatory follicles. Therefore, most spawning occurred in male dominated schools but females that spawned on the previous night occurred in about equal proportions in all schools.

That groups of pelagic spawners could be male dominated is indicated by the reproductive behavior of another pelagic spawner, the Pacific bonito, *Sarda chiliensis*, described by Magnuson and Prescott (1966). They reported that during courtship, groups of males closely follow a single female. If male anchovy show similar behavior, then trawl collections taken at the time of spawning might be male dominated. To explain the dominance of females in commercial catches, Klingbeil (1978) suggested that male-dominated groups may not form the large dense schools necessary for effective purse seining. It seems reasonable that actively spawning (male-dominated) groups, would not be as likely to preserve the density or the integrity of the school as well as nonspawning groups. Thus, the variability in sex ratio of anchovy schools may be attributable in part to reproductive behavior, that is, the formation of male-dominated spawning groups which may be smaller and less dense than commercial schools. The female component of such groups would be expected to change from day to day because after 24 h, spawned out females occurred with equal frequency in all samples regardless of sex ratio.

Growth of Oocytes

Incidence of postovulatory follicles indicated that in February 16% of the females spawned daily or an individual female spawned on the average once every 6.25 days. In the fecundity section that follows, we show that nearly all of the eggs in the most advanced mode are spawned in one night. Thus, a new mode of eggs must mature every 6-7 days to maintain a spawning frequency of 16%. In the laboratory, spawning begins when the average diameter of the eggs in the most advanced mode is between 0.6 and 0.7 mm. Thus the eggs remaining in the ovary after spawning must attain this size in 6-7 days.

To determine if such rapid oocyte growth seemed reasonable, we estimated the mean diameter of eggs in the most advanced mode and in the second mode for some of the females taken in February and March. Females with hydrated eggs were placed in the same class as those with new postovulatory follicles because hydrated eggs were not included in this analysis. The number of females analyzed and the elapsed time from spawning were: elapsed time 0 day (hydrated eggs and new postovulatory follicles) $n = 43$; elapsed time 1 day (1-day-old postovulatory follicles) $n = 35$; and elapsed time 3.5 days (nonspawning mature females) $n = 38$. The time from spawning in the last class was unknown. We assigned the midpoint of the interval 2-5 days to this class because all fish classified as nonspawning would fall within this interval if the spawning cycle were 6 days. The mean diameter of oocytes in the second mode was estimated only for nonspawning females. In these more mature females, most of the oocytes in the second mode were >0.2 mm, whereas, in less mature fish a significant proportion of the oocytes in the second mode were <0.2 mm, and thus below the lower limit of our measurements.

The average diameter of eggs in the ovary in the most advanced mode immediately after spawning was 0.46 mm; 1 day after spawning it had increased to 0.51 mm and was 0.59 mm in nonspawning females. Figure 4 illustrates how growth in the diameter of eggs in the most advanced mode and

TABLE 5.—Sex ratio in samples (females/(males + females)) and percent of spawning northern anchovy taken in February 1978 off southern California.

Sex ratio			Percent of females			Number females classified
Sex ratio class	Class mean	Number samples[1]	Spawning on night of capture[2]	Spawned day before capture[3]	No evidence of spawning	
0.10-0.39	0.25	7	39	15	46	72
0.40-0.69	0.54	10	16	12	75	101
0.70-0.99	0.84	12	10	20	70	122

[1] Twenty-five fish per sample were used to calculate sex ratio and 10 or 11 females were examined histologically.
[2] Includes females with hydrated eggs and those with recent postovulatory follicles.
[3] Females with 1-day-old postovulatory follicles.

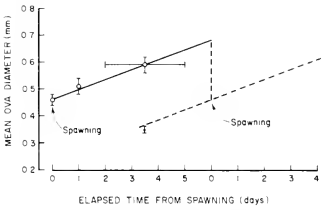


FIGURE 4.—Growth of oocytes in female northern anchovy during an assumed 6-day spawning cycle. Open circles are the mean diameter of eggs in the most advanced mode for: females with hydrated eggs (hydrated eggs excluded) combined with those with recent postovulatory follicles ("spawning"); females with day-old postovulatory follicles (second open circle); and for nonspawning females (third open circle). Horizontal bar indicates period in a 6-day cycle that females would be classified as nonspawning; and the point is plotted at the midpoint of that interval. Vertical bars are ±2 SE of mean and solid circle indicates the mean diameter of eggs in the least advanced mode for the nonspawning class.

that in the second mode could produce a 6-day spawning cycle, the second mode becoming the most advanced mode at the time of spawning. The mean diameter of the eggs in the most advanced and the second mode for the nonspawning class, when plotted at 3.5 days, seems in a reasonable position relative to the other points, indicating that the cycle may be about 6 days. A linear trajectory of oocyte growth of 0.04 mm/day indicates spawning at a diameter between 0.6 and 0.7 mm, in keeping with laboratory findings. This analysis indicates that the mean diameter of yolked oocytes of females in various reproductive stages is consistent with a 6-7 day spawning cycle.

Batch Fecundity

MacGregor (1968) estimated the number of eggs in the most advanced mode in northern anchovy ovaries to be 574 eggs/g wet weight, from an analysis of frequency distribution of eggs in 19 females. Norberg (see footnote 5) concluded that northern anchovy fecundity was 556 eggs/g, from an examination of 119 females. The supposition underlying both estimates was that the number of eggs in the most advanced mode represents the number of eggs spawned. Owing to the importance of batch fecundity in any estimate of spawning biomass from egg and larval production, we decided to reexamine spawning batch fecundity in the northern anchovy.

The assumptions underlying batch fecundity estimates are: all eggs in the most advanced mode are spawned; fecundity is directly proportional to weight; and no bias exists in the estimation of the number of eggs within the most advanced mode nor in the selection of mature females for analysis. We consider these assumptions for females taken in February 1978 using fecundity estimates for each reproductive class.

Histological examination of females with postovulatory follicles indicated that very few hydrated eggs were retained after spawning. Thus, the number of hydrated eggs within ovaries prior to ovulation (females with no postovulatory follicles) should give the most accurate estimate of the number of eggs spawned. Another advantage of using hydrated eggs was that they stand out as an isolated class, distinct from all others; they differ in appearance and are as much as 2-3 times larger than yolked oocytes. Hence, they only need to be counted; neither statistical techniques nor one's judgment need be used to separate overlapping modes.

The mean number of hydrated eggs per gram of female (ovary free) was 389±59 (±2 SE) eggs and was only 7% less than that estimated for females with the most mature ovaries (nonspawner class) (Table 6). Thus, nearly all eggs in the most advanced mode were destined to be hydrated and spawned. Fecundity estimates were substantially higher and more variable in the other three reproductive classes. Many of the females in these classes had only one mode of yolked eggs whereas about 90% of those classified as nonspawners had two modes. Fecundity estimates for the less mature females tend to be higher because the eggs destined to form a second mode have not grown sufficiently to be separated from the rest of the yolked oocytes. More variability exists because of variation among females in the extent of the differentiation of the second modal group of eggs.

In summary, we believe our most accurate estimate of batch fecundity is 389 hydrated eggs/g ovary-free female weight. If an estimate based on total female weight is needed, we recommend the one for nonspawning fish (Table 6) reduced by the fraction of eggs which may not be hydrated (7%). The adjusted fecundity for nonspawners is 368 eggs/g female weight.

Fecundity as estimated above is a function of female weight, ovary weight, and the number of

TABLE 6.—Fecundity (eggs per gram female) estimates for northern anchovy females collected in February 1978 off southern California.

Sample	Number of females	Fecundity: Ovary-free female weight $\bar{x}$	Ovary-free female weight SD	Total female weight $\bar{x}$	Total female weight SD	Percent of females with two modal groups of nonhydrated eggs
Most advanced nonhydrated eggs of females with						
Hydrated eggs[1]	23	530	360	462	309	39
Day 0, postovulatory follicles[2]	13	693	387	497	201	69
Day 1, postovulatory follicles	19	613	313	592	294	69
None of the above (nonspawners)	33	418	186	396	171	91
Hydrated eggs	23	389	141	340	114	—
MacGregor (1968)	19	606	151	574	131	—

[1]Only the nonhydrated eggs in most advanced mode are included.
[2]Females having both hydrated eggs and postovulatory follicles were included.

advanced eggs in a weighed sample of the gonad. The number of hydrated eggs per gram of ovary did not vary with fish weight and was 2,880 ± 373 (± 2 SE) eggs/g of ovary. If any weight-related bias existed, it probably was related to the gonad weight-female weight relation. To ascertain how ovary weight varied with female weight, we separated the data into three classes on the basis of mean diameter of eggs in the most advanced mode and plotted ovary weight as a function of female weight for each class (Figure 5). The relation was slightly curvilinear; the departure from linearity was most obvious in the 0.51-0.60 mm egg diameter class. Considering the variability in the number of mature eggs per gram of ovary, and the slight departure from linearity, no practical purpose is achieved in expressing fecundity as a function of female weight rather than as a direct proportion of weight, although direct proportionality is somewhat less accurate for extreme weight classes.

The relation between gonad weight and female weight differed somewhat among the diameter classes as can be seen in Figure 5. This might be expected because the weight of the ovary should increase somewhat with the average diameter of the eggs in the most advanced mode. We analyzed the data using multiple regression to determine if the ln (log e) gonad weight (G) could be estimated from the diameter of eggs in the most advanced mode (D), ln ovary-free female weight (W), and the interaction term ($D \ln G$). Both female weight and the interaction term had a significant effect on gonad weight, whereas diameter alone did not. The final multiple regression equation was:

$$\ln G = -4.213 + 1.069 \ln W + 0.555\, D \ln W$$

where $r^2 = 0.92$. Solving for diameter we obtain

$$D = \frac{\ln G + 4.213 - 1.069 \ln W}{0.555 \ln W}.$$

This equation may be useful for estimation of maturity stages for anchovy from weight relationships: 60% of the estimates of mean diameter were within ±0.1 mm of the observed values and the residuals were distributed evenly. The equation is more useful than gonad index (ovary weight / female weight), which is commonly employed to assess maturity, because it produces a number that can be directly related to reproduction and avoids a weight bias for extreme weight classes. The weight bias in gonad index is apparent by examination of data in Figure 5 (lowest); a 30 g female with eggs of 0.65 mm in the most advanced mode has a gonad index of 0.064 whereas that of a 10 g female at the same stage of maturity has an index of 0.040. The equation also identifies females with hydrated eggs; the average diameter of eggs estimated by the equation for females with hydrated eggs was 1.20 ± 0.12 mm (n = 22) and is close to the mean of spawned eggs (1.34 mm). Obviously, such equations would be specific to populations having similar weight relations, but it does seem a useful approach for assessing maturity.

DISCUSSION

This paper provides a method for direct estimation of the frequency of spawning of a multiple spawning pelagic fish population. From such estimates it may be possible to directly estimate spawning biomass from the abundance of eggs and larvae over a short segment of the breeding season. One of the major assumptions underlying the estimate is that a representative sample of females is obtained. Spawning frequency would be overestimated if nonspawning females were in re-

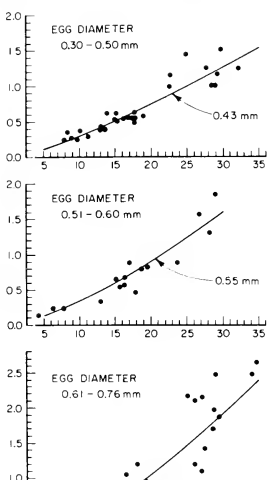


FIGURE 5.—Relation between wet weight of ovary and ovary-free wet weight of female northern anchovy classed into three groups, based on the mean diameter of eggs in the most advanced mode. Each point is a value for a single female. The lines represent multiple regressions, described in the text, for the mean egg diameters given by the arrows.

gions or at depths not sampled by the trawl or commercial purse seine. Studies need to be conducted at other times of the year and employing other sampling techniques to answer these questions.

This paper also describes a new method for estimation of batch fecundity in a multiple spawning fish. Our estimation for northern anchovy based on hydrated eggs (389 eggs/g female weight, less ovary), was substantially less than that of MacGregor (1968) (606 eggs). This difference could be attributed to annual variation in fecundity because variations of this size are known to occur in fishes (Bagenal 1973). On the other hand, our selection of females on the basis of reproductive state also may have been responsible for at least part of the difference. Our estimates for females that had recently spawned (day 0 and day 1 postovulatory follicles, Table 6) were close to MacGregor's estimate. In recently spawned females, modal groups of eggs were less distinct, and often one mode was considered to exist when the eggs may have been destined to form two spawning batches. If MacGregor (1968) used such females, this could explain in part why his estimate was higher than our estimates based on hydrated eggs or on fish classed as nonspawning. In addition, our technique of partitioning eggs occurring between two modal groups according to an assumed normal distribution may have decreased our estimate somewhat relative to past methods. Use of hydrated eggs avoids these problems, but it does require histological examination to insure that none of the females used for the estimate have begun ovulation. Apparently, some of the females we captured were spawning because their ovaries contained many new postovulatory follicles as well as many hydrated eggs. We usually examined only one set of histological sections to determination if ovulation had occurred; histological examination of an entire ovary was impractical. We believe our examination was adequate because our estimate based on hydrated eggs was close to the one based on females with the most advanced ovaries (nonspawning).

In addition to the obvious application to the estimation of spawning biomass, this work provided insights into the reproductive biology of *E. mordax*. The high spawning frequency, the ability to rapidly mature new batches of yolked oocytes, and the long breeding season of the northern anchovy (Lasker and Smith 1977), indicate that energy reserves and the availability of food may set the limit to the number of spawnings and hence to total fecundity. The analysis has also provided a possible explanation for the variability in the sex ratio of catches of anchovy.

ACKNOWLEDGMENTS

We thank Kenneth Mais (California Department of Fish and Game) for providing the specimens and data on sexual composition of schools from his February 1978 cruise. We are indebted to Roger Leong (Southwest Fisheries Center (SWFC)) who maintained and spawned anchovy in

the laboratory. Beverly Macewicz (University of California, San Diego) did all microtechnique work and assisted in the histological classification of the ovaries. Thomas Mickel (University of California, San Diego) assisted in the analysis of fecundity and estimation of ovum diameters. We thank James Zweifel (SWFC) for permitting us to use his unpublished method for estimating confidence intervals for the mean of a negative binomial distribution and for his analytical work on estimating ovum diameters from the gonad weight-female weight relation.

LITERATURE CITED

ABRAMSON, N. J.
1971 Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101:1-11,(1):2.10.

BAGENAL, T. B.
1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:186-198.

BOWERS, A. B., AND F. G. T. HOLLIDAY.
1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Mar. Res., Dep. Agric. Fish. Scotl. 1961(5):1-16.

BREWER, G. D.
1978. Reproduction and spawning of the northern anchovy, *Engraulis mordax*, in San Pedro Bay, California. Calif. Fish Game 64:175-184.

CLARK, F. N.
1934 Maturity of the California sardine (*Sardina caerulea*) determined by ova measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 p.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. Calif. Fish Game 38:189-207.

COLLINS, R. A.
1969 Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67 and 1967-68 seasons. Calif. Dep. Fish Game, Fish Bull. 147:56-74.

CUNNINGHAM, J. T.
1898 On the histology of the ovary and of the ovarian ova in certain marine fishes. J. Mier. Seig, New Ser., 40:101-163.

DEVLAMING, V. L.
1972 Reproductive cycling in the estuarine gobiid fish, *Gillichthys mirabilis*. Copeia 1972:278-291.

FULTON, T. W.
1898 On the growth and maturation of the ovarian eggs of Teleostian fishes. Annu. Rep. Fish. Board Scotl. 16:88-124.

GOKHALE, S. V.
1957. Seasonal histological changes in the gonads of the whiting (*Gadus merlangus* L.) and the Norway pout (*G. esmarkii* Nilsson). Indian J. Fish. 4:92-112.

GOLDBERG, S. R.
1977 Seasonal ovarian cycle of the tidewater goby, *Eucyclogobius newberryi* (Gobiidae). Southwest. Nat. 22:557-558.

IVANKOV, V. N.
1976. The formation of ultimate fecundity in intermittently spawning fish with reference to the southern onefinned greenling, *Pleurogrammus azonus* and the wild goldfish, *Carassius auratus gibelio*. J. Ichthyol. 16:56-62. (Translated from Vopr. Ikhtiol.)

JOHNSON, N. L., AND S. KOTZ.
1970 Continuous univariate distributions-2. Houghton Mifflin Co., Boston, 306 p.

KLINGBEIL, R. A.
1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off Southern California. Calif. Fish Game 64:200-209.

LAMBERT, J. G. D.
1970. The ovary of the guppy, *Poecilia reticulata*. The atretic follicle, a *Corpus atreticum* or a *Corpus luteum praeovulationis*. Z. Zellforsch. 107:54-67.

LASKER, R., AND P. E. SMITH.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

MACER, C. T.
1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish. Biol. 6:415-438.

MACGREGOR, J. S.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.

MAGNUSON, J. J., AND J. H. PRESCOTT.
1966. Courtship, locomotion, feeding, and miscellaneous behavior of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14:54-67.

MOSER, H. G.
1967. Seasonal histological changes in the gonads of *Sebastodes paucispinus*, an ovoviviparous teleost (Family Scorpaenidae). J. Morphol. 123:329-353.

NIKOLSKY, G. V.
1963. The ecology of fishes. Academic Press, N.Y., 352 p.

QASIM, S. Z.
1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. J. Cons. 21:144-154.

SCOTT, D. B. C.
1974. The reproductive cycle of *Mormyrus kannume* Forsk. (Osteoglossormorpha, Mormyriformes) in Lake Victoria, Uganda. J. Fish. Biol. 6:447-454.

WHEELER, J. F. G.
1924. The growth of the egg of the dab (*Pleuronectes limanda*). Q. J. Microsc. Sci. 68:641-660.

YAMAMOTO, K.
1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. J. Fac. Sci. Hokkaido Univ., Ser. 6, Zool. 12:362-373.

YAMAMOTO, K., AND F. YAMAZAKI.
1961. Rhythm of development in the oocyte of the goldfish, *Carassius auratus*. Bull. Fac. Fish., Hokkaido Univ. 12:93-110.

YAMAMOTO, K., AND H. YOSHIOKA.
1964. Rhythm of development in the oocyte of the medaka, *Oryzias latipes*. Bull. Fac. Fish., Hokkaido Univ. 15:5-19.

UTILIZATION OF THE NANAIMO RIVER ESTUARY BY JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

M. C. HEALEY[1]

ABSTRACT

Chinook salmon are considered, normally, to spend from a few months to a year rearing in freshwater before migrating to sea. Although large downstream movement of fry, recently emerged from spawning gravels, has been observed in several river systems, it has been suggested that most of these migrant fry are lost to the population. This report describes the fate of downstream migrant chinook salmon fry in the Nanaimo River, British Columbia. In 1975 and 1976 most of the potential fry production from the river system was estimated to have passed by a trapping location near the river mouth. Many of these fry were subsequently found rearing in the intertidal area at the river mouth where salinity was commonly above 20‰. Very few chinook salmon fry were captured at other sampling sites within a 10 km radius of the river mouth. Juvenile chinook salmon were present in the intertidal area of the estuary from March to July each year, but peak numbers occurred in April and May. Peak estuary population was estimated to be 40,000-50,000 in 1975 and 20,000-25,000 in both 1976 and 1977. While in the estuary, chinook salmon grew about 1.32 mm per day or 5.8% of their body weight per day. Individual fish probably spent an average of about 25 days rearing in the estuary and left the estuary when about 70 mm fork length. While in the estuary, juvenile chinook salmon fed on harpacticoid copepods, amphipods, insect larvae, decapod larvae, and mysids. After leaving the estuary, they fed mainly on juvenile herring. The stomach content of chinook salmon captured in the estuary averaged 5% of body weight or less, and varied seasonally and between years. It appears that in the Nanaimo and probably in other systems with well-developed estuaries, that the estuary is an important nursery for chinook salmon fry.

After they emerge from the spawning gravel in early spring, chinook salmon, *Oncorhynchus tshawytscha*, are considered, normally, to spend from a few months to a year in freshwater before migrating to sea (Reimers and Loeffel 1967; Stein et al. 1972; Mehan and Siniff 1962; Lister and Walker 1966). Recently, Reimers (1971) and Dunford (1975) showed that juvenile chinook salmon may also spend considerable time rearing in estuaries after their downstream migration and before moving into high salinity water. Although juvenile chinook salmon are known to occur in a number of British Columbia estuaries (Goodman[2]; Hoos and Vold[3]; Bell and Kallman[4]; Bell and Kallman[5]), the importance of estuarine habitats as nursery areas for young chinook salmon is not well documented. The purpose of this report is to present information on the utilization of the Nanaimo River estuary and adjacent marine areas by juvenile chinook salmon and to consider the importance of the estuary to the stock. Specifically, I shall discuss the timing of downstream movement and abundance of chinook salmon fry in the river; their distribution, abundance, and length of residence in the estuary and in marine waters adjacent to the estuary; and their growth rate and food habits. In this report the term "fry" refers to juvenile chinook salmon that recently emerged from the spawning gravel, often still with externally visible yolk.

METHODS

River Sampling

Downstream migrating chinook salmon fry were captured in seven inclined plane fry traps

[1]Department of Fisheries and Oceans, Resource Services Branch, Pacific Biological Station, Nanaimo, B.C., Canada V9R 5K6.

[2]Goodman, D. 1975. A synthesis of the impacts of the proposed expansion of the V.I.A. and other developments on the fisheries resources of the Fraser River estuary. Unpubl. manuscr., 137 p. + append. Environ. Can., Fish. Mar. Serv., Vancouver.

[3]Hoos, L. M., and C. L. Vold. 1975. The Squamish River estuary: Status of environmental knowledge to 1974. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 2, 361 p.

[4]Bell, L. M., and R. J. Kallman. 1976. The Cowichan-Chemainus River estuaries: Status of environmental knowledge to 1975. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 4, 328 p.

[5]Bell, L. M., and R. J. Kallman. 1976. The Nanaimo River estuary: Status of environmental knowledge to 1976. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 5, 298 p.

Manuscript accepted March 1979.
FISHERY BULLETIN VOL. 77, NO. 3, 1980

anchored in two narrow stream channels near the mouth of the Nanaimo River (Figure 1). (These traps were similar in design to those described by Lister et al. 1969.) The mouth opening of each trap was 30 cm wide by 60 cm deep. Four traps were set side by side in one channel and three in the other. Nylon netting of 5 cm mesh was run between the traps and shore in an attempt to lead additional fry into the traps. The traps were operated in 1975 and 1976 and were set and fished the same way each year. In 1975 the traps were in place from early March to late May, while in 1976 they were in place from early April to late May. Although the main river flow was down a third channel to the west of the traps, a significant fraction of the chinook salmon run passed down the trapping channels and, as will be shown later, the traps captured about 1.5% of the run.

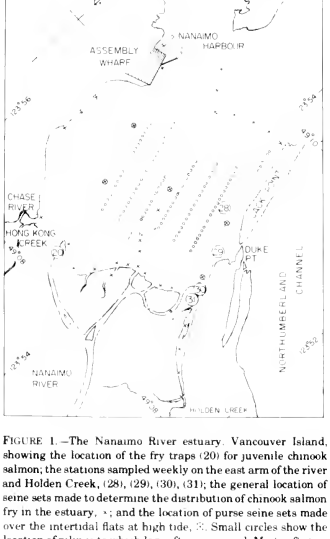


FIGURE 1.—The Nanaimo River estuary, Vancouver Island, showing the location of the fry traps (20) for juvenile chinook salmon; the stations sampled weekly on the east arm of the river and Holden Creek, (28), (29), (30), (31); the general location of seine sets made to determine the distribution of chinook salmon fry in the estuary, +; and the location of purse seine sets made over the intertidal flats at high tide, ○. Small circles show the location of pilings to which log rafts are moored. Most raft storage is on the west side.

Fry captured in the traps between 0800 h of 1 day and 0800 h of the next were counted as a single day's catch. In 1975 the fry were held in live pens in the river and marked a few hours after capture by spraying with fluorescent grit (Healey et al.[6]). After they were sprayed, the fry were held a further 24 h to recover and then were released in the late evening into the river about 2.5 km upstream from the traps. Most mortality from marking occurred in 24 h and was normally <5% (Healey et al.[7]). Each daily catch was examined for marked fry, and total daily run was estimated by mark recapture techniques (Ricker 1975; Healey et al. see footnote 7). In 1976 the fry captured each day were counted and released downstream from the trapping site.

By changing the color of marking grit several times during the run I determined that, on average, 75% of recaptures from a single release were made the night of release, a further 17% on the next night, and the remaining 8% over the next 14 nights. I assumed that these percentages represent the proportions of the marked fry which migrate the night of release or delay migration one or more days. Also, <100% of sprayed fry received a mark. Samples of marked fry examined a few days after spraying showed that usually 95% or more of the fry were marked. The total number of marked fry migrating downstream each night was, therefore, estimated to be the number of fry released, corrected for the proportion unmarked, minus the number expected to delay migration, plus the number expected to be migrating from previous releases. Total daily run was estimated as the product of daily catch and the estimate of marks migrating divided by the number of recaptures. Trap efficiency was the ratio of recaptures to estimated marks migrating.

During about half the trapping days in 1975 no recaptures were made. On these days the run was estimated as the trap catch divided by the overall estimate of trapping efficiency for the year (total recaptures total marks migrating). Total run in 1976 was estimated from the overall estimate of efficiency for 1975.

[6]Healey, M. C., F. P. Jordan, and R. M. Hungar. 1976. Laboratory and field evaluating of fluorescent grit as a marking material for juvenile salmonids. Fish. Res. Board Can. Manuscr. Rep. 1392, 17 p.

[7]Healey, M. C., R. V. Schmidt, F. P. Jordan, and R. M. Hungar. 1977. Young salmon in the Nanaimo area 1975: 1. Distribution and abundance. Fish. Res. Board Can. Manuscr. Rep. 1369, 161 p.

During April and May 1975, samples of downstream migrant chinook salmon were measured for fork length (millimeters) and wet preserved weight (±0.01 g) to provide an estimate of the body size of downstream migrants.

During 1975 and 1976 the temperature of the river near the trapping site was measured morning and evening. Daily discharge of the river was available from Inland Waters Directorate, Environment Canada, Ottawa. The measurements were made about 12 km upstream from the traps.

Estuary Sampling

In the intertidal area of the estuary most sampling was by beach seine (18 m long × 3 m deep of 12 mm mesh). Stream channels crossing the intertidal mud flat and the delta front were sampled at low tide, and the edges of the tidal marshes at high tide. During March and April 1975 widely scattered locations on the estuary were sampled, but during the latter half of April and May, sampling was concentrated in the east channel of the river and Holden Creek (Figure 1) at low tide. During 1976 and 1977 four specific sampling sites were established in the east channel of the river and Holden Creek and these were fished weekly (Stations 28-31; Figure 1) except that Station 28 was not fished until June 1976, and fishing at Stations 30 and 31 was discontinued after the chinook salmon disappeared from these stations. Sampling at other locations at high and low tide was performed occasionally, as time permitted, to determine the distribution of chinook salmon in the estuary. In addition to beach seining, five sets with a 90 · 7 m hand-hauled purse seine were made over the intertidal mud flat at high tide on 12 May 1976 to determine if juvenile chinook salmon remained over the mud flat at high tide. Catch data are presented as average catch-per-set (CPUE) in this report.

Estuary sampling began during the second or third week of March of each year. In 1975, sampling terminated in early June; in 1976, in mid-July; and in 1977, at the end of June. In 1975, samples of chinook salmon for analysis of length, weight, and stomach contents were preserved in only 6 of 12 sampling weeks. In 1976 and 1977, however samples of 20 or more were preserved each week.

In 1977, temperature (°C) and salinity (per mil) were measured at the time of beach seining at each sampling location in the east channel of the river and Holden Creek with a Yellow Spring Instruments Model 33 Thermister-Salinometer*.

In 1977 the total population of chinook salmon in the estuary was estimated twice by mark and recapture techniques. Between 18 and 21 April, 3,187 chinook salmon were captured along the east channel of the river and Holden Creek, mainly at Stations 30 and 31, marked with a left pelvic fin clip, and released at the point of capture. Catch and recaptures were recorded on 19-22 April, and on all subsequent sampling days. Between 16 and 19 May, 1,554 chinook salmon captured mainly at Stations 28 and 29 were marked with a right pelvic fin clip. Recaptures of these marks were recorded on 17-19 May, 22 May, and all subsequent sampling days.

Recaptures after the final mark release for each fin clip provided an estimate of the rate of disappearance of marked fish from the sampling area. This rate was assumed constant for each mark and was calculated as the slope of the regression of log$_e$ (CPUE marks) on days since marking. In calculating the rate for left pelvic clips, catches during the second marking period were ignored since sampling on these days was performed in a way to maximize catch, and was different from our normal sampling procedure. The number of marks released was reduced each day in accordance with these estimated rates of disappearance to give an estimate of the total marks present on each sampling day. Population estimates for each day were, therefore, the product of total catch and estimated marks present divided by recaptures. Left pelvic marks were still present at the time of the second marking, so that it was possible to make two independent estimates of population size at this time.

A sample of chinook salmon was preserved from those captured each day for marking, and these provided an estimate of the average size of marked fish at the time of release. Marked fry captured after the last release of each fin clip were preserved and their fork length and weight measured to provide an estimate of growth rate.

Marine Sampling

Up to 18 different locations within a 10 km radius of the river mouth were sampled in 1975 and 12 locations in 1976 (Figure 2). In 1975 nine

*Reference to trade names does not imply endorsement by Fisheries and Oceans, Canada, or by the National Marine Fisheries Service, NOAA.

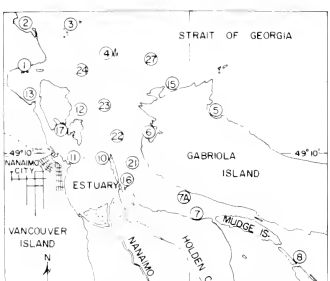


FIGURE 2.—Map of the Nanaimo area, Vancouver Island, showing the locations where beach seine and purse seine sets were made for juvenile chinook salmon (circled numbers).

locations (1, 2, 4, 5, 8, 9, 15, 16, 17; Figure 2) were sampled during the second and third week of May by beach seine (18 × 3 m). Twelve locations (1, 2, 5, 6, 7, 8, 9, 10, 11, 13, 15, 17; Figure 2), were sampled weekly from March to July by hand-hauled purse seine (90 × 7 m). Sixteen locations (1, 2, 3, 4, 5, 6, 7a, 8, 9, 10, 11, 12, 13, 21, 22, 23, 24; Figure 2) were sampled weekly from April to July by drum seine (216 × 18 m), except locations 21-24 which were sampled at 2-wk intervals from late May until early July. In 1976 seven locations (1, 2, 4, 5, 6, 16, 17; Figure 2) were sampled weekly from April to June by beach seine. Ten locations (1, 2, 4, 5, 6, 7a,10, 23, 24, 27; Figure 2) were sampled by drum seine weekly from early April until the end of July, then approximately monthly until March 1977. In 1977, Area 10 was sampled weekly from late April to late August by the 90 m hand-hauled purse seine.

Sample Processing

Fork length and weight of preserved fish were measured in all years, and in 1976 and 1977, stomach analyses were also performed. The lengths of fish in small catches at sea were occasionally measured at the time of sampling and the fish released. This was especially true of early catches in 1975. In 1977, fish captured by the hand-hauled purse seine in Area 10 were all measured for length, and a subsample of 15-20 was preserved for weight and stomach analyses. Scales of some of the preserved fish from both 1976 and 1977 were examined under 20 × magnification to determine age structure of the catch. Preserved samples were sometimes not analyzed until weeks or months after capture so preserved weights are likely to overestimate live weights. Length, however, is only slightly affected by preservation (Parker 1963).

Wet weights of the stomach contents of individual fish from the intertidal area of the estuary were measured in 1975. Sample size was small except for the 9 May sample (see Table 6). In 1976 and 1977, dry weight of the stomach contents of 10-20 fish from the estuary and a similar sample from off the estuary was recorded each week and converted to percent of body weight by assuming that preserved fish were 20% (average of ~20 determinations) dry matter.

Detailed taxonomic analysis of stomach contents was not made. However, in 1976 and 1977 the dominant components of the stomach contents of each sample were recorded.

DESCRIPTION OF STUDY AREA

The Nanaimo River discharges into the Strait of Georgia just south of the City of Nanaimo on the east coast of Vancouver Island (Figure 2). It supports spawning populations of chinook; coho, *O. kisutch;* and chum, *O. keta,* salmon as well as steelhead, *Salmo gairdnerii,* and cutthroat trout, *S. clarki.* Since 1950, chinook salmon escapement has averaged 2,100 spawners, and there has been a gradual decline in abundance from 3,700 spawners between 1950 and 1954 to 1,400 between 1972 and 1976 (Aro[9]; Canada, Fisheries and Marine Service[10]). Adult chinook salmon enter the river between April and October, and spawn from September to November (Aro see footnote 9). In 1974, 1975, and 1976 (the brood years reported in this study) escapement was estimated to be 2,400, 525, and 1,100 respectively.

The delta estuary of the river occupies about 9 km² of which about 6 km² is intertidal mud flat (Figure 1). At the southern margin of the delta the

[9]Aro, K. V. 1973. Salmon and migratory trout of the Nanaimo River and adjacent streams (Revised 1973). Fish. Res. Board Can. Manuscr. Rep. 1284, 15 p.

[10]Annual stream bank estimates of spawning escapement available from Fisheries and Oceans, Canada, Field Services Branch, 1090 West Pender Street, Vancouver, B.C..

river divides into two main channels which cross the intertidal mud flat on the east and west sides. The west channel carries most of the flow, however, and during low river flows in the spring and summer a gravel berm blocks the east channel, probably preventing any fish movement down this channel. Holden Creek flows across the delta on the east side and joins the east channel of the river about half way across the intertidal mud flat. Hong Kong Creek and Chase River enter the delta from the west and join the west channel of the river near the upper margin of the mud flat. The mud flat between the two main channels of the river is dissected by numerous small stream channels fed by seepage from the main river channels. The smaller streams contributing to the delta do not support chinook salmon spawning but do support chum and coho salmon.

Salt marshes at the top of the delta are dominated by black grass, *Juncus gerardii*. The intertidal area has three floral associations: *Fucus-Salicornia* in the upper tidal area, *Ulva-Enteromorpha* in the midtide area, and *Zostera-Ulva* in the low tide area (Foreman[11]). *Zostera* extends in a band across delta front, and well up the east channel of the river.

The intertidal area of the delta is used for log storage by local sawmills and a pulp mill. Part of the northwest corner of the estuary has been filled in during development and expansion of the Port of Nanaimo. Intermittent dredging occurs at the delta front to keep the shipping lane into Nanaimo Harbor open. Some dyking has occurred along the southern margin of the delta to create farm land. Further details of physical and biological features of the estuary and adjacent lands are given in Bell and Kallman (see footnote 5).

Seaward from the intertidal area of the delta a wide variety of habitats provide potential nursery area for juvenile salmon, from sheltered bays and lagoons to exposed rocky or sandy beaches. Many of these habitats were sampled during 1975 and 1976 to estimate the extent of utilization of habitats away from the river mouth as nursery areas (Figure 2). Some details of the physical and biological features of the habitats sampled are given by Healy et al. (see footnote 7). Apart from sampling locations 10, 11, and 17, within the Nanaimo Harbor area (Figure 2), salinity was usually above 27‰, while spring and summer temperature ranged 6°-15° C (Healey et al. see footnote 7).

RESULTS AND DISCUSSION

Downstream Run of Fry

Downstream movement of the chinook salmon fry had two peaks in 1975, the first on 19 April and the second 14 days later (Figure 3). Fry were moving in small numbers throughout March, but most movement occurred in April and May. A total of 10,876 fry entered the traps between 10 March and 24 May.

Trapping began on 8 April 1976, and chinook salmon were already moving downstream. One peak occurred in the 1976 run, although isolated large catches occurred before and after the peak (Figure 3). Only 4,360 fry entered the traps in 1976 suggesting that the total run was about half that in 1975.

Downstream migrants averaged 38.3 mm long (0.57 g) and ranged 33-45 mm long (0.33-1.02 g). Many of the fry still had visible yolk.

River discharge during the the fry run in 1975 ranged 16-100 m^3/s, and increases in fry run were generally associated with increases in discharge.

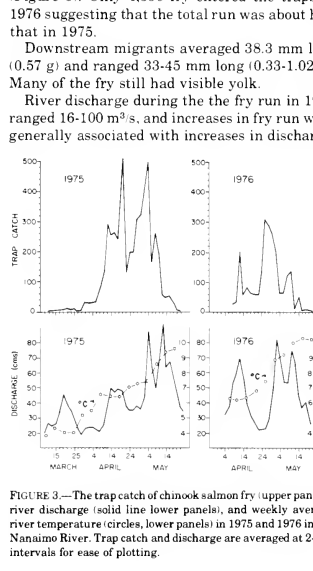


FIGURE 3.—The trap catch of chinook salmon fry (upper panels), river discharge (solid line lower panels), and weekly average river temperature (circles, lower panels) in 1975 and 1976 in the Nanaimo River. Trap catch and discharge are averaged at 2-day intervals for ease of plotting.

[11]Foreman, R. E. 1975. Nanaimo River estuary macrophyte study: Seasonal aspects of macrophyte distribution and standing crop on the Nanaimo River estuary mudflats. BERP Rep. 75-3, final report on Fish. Mar. Serv. Contract OSU4-0217 prepared by R. E. Foreman, Botany Dep., Univ. B.C., 41 p.

Temperature in 1975 ranged 3.1-11.2 C and was increasing during the run. Greatest fry movement in this year occurred when river temperature was 6-9 C (Figure 3). In 1976 discharge ranged 18-91 m^3/s and was higher early in the season than in 1975. Increases in the 1976 fry run often preceeded increases in discharge (Figure 3). River temperature ranged 5.0-13.3 C and greatest fry movement was when temperature was 8-11 C (Figure 3).

In addition to temperature and discharge, the catch of chinook salmon in the traps was probably influenced by tide. The traps were set very near the river mouth and at high tide flow past the traps was often negligible. To examine the potential contribution of discharge, river temperature, and tide height to variations in trap catch, I performed a stepwise multiple regression analysis on the data. The dependent variable was trap catch and the independent variables were river discharge, river temperature (morning and evening measurements averaged), average tide height during three periods of the "trapping day" (0800-1800 h, 1800-0000 h, 0000-0800 h), and Julian day of capture. I performed separate analyses on catches preceding and following the peak catch each year. The hypotheses tested were: 1) catch is positively correlated with discharge and temperature and negatively correlated with tide height for all data sets; 2) catch is positively correlated with day of capture prior to peak catch and negatively correlated after peak catch.

The regression analysis failed to confirm or reject either of these hypotheses unequivocally. Discharge was positively correlated with trap catch while catches were increasing, but was not correlated while catches were decreasing (Table 1). Temperature was not significantly correlated with catch in any of the analyses. Tide height was negatively correlated with trap catch while catches were increasing as predicted. While catches were decreasing, however, tide height was uncorrelated with trap catch in 1975 and positively correlated in 1976 (Table 1). The correlation of trap catch with Julian day was positive while catches were increasing and negative while catches were decreasing, as predicted, except that the correlation with increasing catch was not significant in 1976 (Table 1). The multiple correlation coefficients were highly significant and explained 50-79% of the variation in trap catch (R^2, Table 1). Some of the results, like the positive correlations between trap catch and tide height, were counterintuitive, however, and cast doubt on any interpretation of the regression analysis. In spite of these difficulties the regression analysis suggests that discharge and tide height may have influenced trap catch, while temperature probably did not.

Recaptures of marked fry in the traps in 1975 ranged 0-16.6% of the daily estimate of marks migrating. The ratio of recaptures to marks migrating for the whole run was 0.0175, indicating an overall trap efficiency of 1.75% (Table 2).

Peterson estimates of total daily run were made

TABLE 1.—Results of stepwise multiple regression analysis of fry trap catch of juvenile chinook salmon regressed on river discharge, river temperature, average tidal height during three daily time periods (0800-1800 h, 1800-2400 h, 2400-0800 h) and Julian day of capture. Only the regression coefficients for the variables that made a significant ($P<0.05$) contribution to the multiple regression are shown.

Independent variable	Partial Regression coefficient		Standardized partial regression coefficient		Multiple correlation coefficient (R)		R^2	
	1975	1976	1975	1976	1975	1976	1975	1976
Analysis 1: trap catch from first capture to maximum capture n = 53, 1975, n = 24, 1976								
Discharge	+0.20	+0.40	0.481	0.800				
Temperature	—	—	—	—				
Tidal height								
0800-1800	—	—	—	—				
1800-2400	—	−15.0	—	0.160				
2400-0800	−78.0	—	0.162	—				
Julian day	+6.3	—	0.507	—				
All significant variables					0.873	0.710	0.76	0.51
Analysis 2: trap catch from maximum capture to last capture n = 22, 1975, n = 31, 1976								
Discharge	—	—	—	—				
Temperature	—	—	—	—				
Tidal height								
0800-1800	—	+159.8	—	1.77				
1800-2400	—	+122.0	—	1.55				
2400-0800	—	—	—	—				
Julian day	−22.3	14.2	0.705	1.10				
All significant variables					0.705	0.891	0.50	0.79

TABLE 2.—Trap catch, estimate of marks migrating downstream, recaptures in the traps, and estimated daily run of chinook fry in the Nanaimo River in 1975. Population estimates in italics were derived from trap catch divided by average trap efficiency (0.0175). All other estimates are Peterson type estimates.

Date	Trap catch	Marks migrating	Recaptures	Population estimates	Date	Trap catch	Marks migrating	Recaptures	Population estimates
Mar 10	2	0	0	*114*	Apr 17	200	251	3	16,733
11	2	0	0	*114*	18	481	254	8	15,272
12	1	0	0	*57*	19	776	206	10	15,986
13	6	0	0	*342*	20	261	265	21	3,294
14	6	1	0	*342*	21	152	569	9	9,610
15	2	2	0	*114*	22	100	309	4	7,725
16	3	5	0	*171*	23	166	179	0	9,474
17	2	3	0	*114*	24	227	116	2	13,166
18	4	3	0	*228*	25	372	162	8	7,533
19	7	2	0	*400*	26	56	120	0	*3,196*
20	11	4	0	*628*	27	425	107	0	*24,255*
21	9	6	1	*54*	28	190	66	0	*10,844*
22	6	10	0	*342*	29	249	333	2	41,459
23	8	8	0	*457*	30	396	210	2	41,580
24	15	6	0	*856*	May 1	324	233	6	12,582
25	5	8	1	*40*	2	509	337	5	34,307
26	6	11	0	*342*	3	822	326	2	133,986
27	2	6	0	*114*	4	167	383	6	10,660
28	2	6	0	*114*	5	202	684	19	7,272
29	9	3	0	*514*	6	133	284	4	9,443
30	11	3	0	*628*	7	272	202	5	10,989
31	61	1	0	*3,481*	8	234	144	4	8,424
Apr 1	14	15	0	*799*	9	497	238	11	10,753
2	49	49	0	*2,797*	10	440	218	6	15,987
3	27	22	0	*1,541*	11	312	409	2	63,804
4	54	39	0	*3,082*	12	104	397	2	20,644
5	36	29	1	1,044	13	48	327	2	7,848
6	57	49	3	931	14	65	150	1	9,750
7	75	37	0	4,280	15	51	78	0	*2,911*
8	67	35	0	*3,824*	16	47	60	1	2,820
9	92	64	2	*2,944*	17	48	59	0	*2,739*
10	173	66	2	5,709	18	66	48	0	*3,767*
11	194	81	0	*11,072*	19	20	45	0	*1,141*
12	381	138	1	52,578	20	14	59	0	799
13	293	177	2	25,930	21	5	29	1	145
14	215	311	3	22,288	22	4	18	0	228
15	276	288	3	26,496	23	3	6	0	*171*
16	256	210	3	17,920	24	1	6	0	*57*

for 37 days of the 1975 run and ranged 40-133,986 fish day. The sum of these estimates was 687,568 chinook salmon, and total trap catch for the days when estimates were made was 9,188. The ratio of catch to total run for the Peterson estimates was 0.013, indicating only 1.3% trap efficiency. This estimate was strongly influenced, however, by the large population estimate for 3 May, which resulted from a large catch in which there were few recaptures (Table 2). Ignoring this estimate, the ratio of trap catch to Peterson population estimates was 0.0151, closer to the average efficiency based on mark recaptures.

Population estimates for all days of the run totaled 784,155 in 1975. Assuming trap efficiency was similar in 1976, the run was about 300,000 during the trapping period.

Although most chinook salmon are expected to go to sea after about 2 mo of residence in their natal stream, downstream movement of fry shortly after emergence has been observed in other systems. In the Big Qualicum River, 100 km north of the Nanaimo, between 3,000 and 241,000 fry migrated downstream mainly in March and April from 1961 to 1965, although the time of greatest movement varied from late March to early May (Lister and Walker 1966; Lister and Genoe 1970). The fry migration was followed by a fingerling migration in June which was usually larger than the fry migration. In the Cowichan River, 50 km south of the Nanaimo River, a large downstream movement of fry was recorded during March and April in 1966 and 1967 followed by a smaller fingerling movement in June (Lister et al.[12]). The survival of these fry and their contribution to the adult population were unknown, but presumed to be slight (Lister and Walker 1966).

The number of chinook salmon fry, estimated to have migrated downstream in the Nanaimo River in 1975 and 1976, was 5-10 times greater than in the Big Qualicum River which has a similar escapement (Lister and Walker 1966). This

[12]Lister, D. B., C. E. Walker, and M. A. Giles. 1971. Cowichan River chinook salmon escapement and juvenile production 1965-1967. Can. Dep. Fish. For. Tech. Rep. 1971-3, 48 p.

raises the question: What proportion of the fry population migrates out of the Nanaimo River each year? Information on sex and age of the 1974 and 1975 spawning population in the Nanaimo River is not available so egg deposition can only be surmised. If one assumes, however, that of the 2,400 escapement in 1974, 800-1,000 were females, and that of the 525 spawners in 1975, 200-225 were females, and that the fecundity of Nanaimo River chinook salmon is in the range 6,000-8,000 (Godfrey[13]; Schutz[14]), then potential egg deposition in 1974 was on the order of 6-6.5 million, and in 1975 on the order of 1.2-1.6 million. (The female population was estimated to be ~50% of the escapement because of the "jacks.") In the winters of 1974 and 1975 there were no extreme freshets, so survival was probably quite good, perhaps as high as 15-20% (Lister and Walker 1966; Coots[15]). Fry production may be estimated to be, therefore, on the order of 0.9-1.3 million in 1975 and 0.18-0.32 million in 1976. These values are similar to the estimated fry migration each year and indicate that a high proportion of Nanaimo River chinook salmon left the river as recently emerged fry.

Distribution and Relative Abundance of Chinook Salmon in the Estuary

Sampling in the intertidal area of the estuary revealed chinook salmon were abundant there in spring and early summer of each year (Figure 4). Juvenile chinook salmon were first captured at the beginning of April 1975, were most abundant in May, and had declined in abundance by early June when sampling terminated (Figure 4). Chinook salmon were captured from mid-March until late July 1976 but increased in abundance later than in 1975, and were generally less than half as abundant as in 1975. Juveniles were already abundant in the estuary when sampling began in late March 1977 and reached maximum abundance in early April, 3 wk earlier than in 1975 and 1976 (Figure 4).

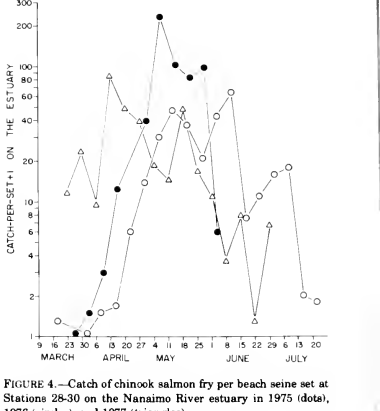


FIGURE 4.—Catch of chinook salmon fry per beach seine set at Stations 28-30 on the Nanaimo River estuary in 1975 (dots), 1976 (circles), and 1977 (triangles).

Greatest catches of chinook salmon were in the east channel of the Nanaimo River and Holden Creek. Catches in other stream channels crossing the intertidal mud flat and along the delta front at low tide were small by comparison. Catches in the stream channels in the center of the mud flat averaged only two fish/set, and on the west side of the delta only one chinook salmon was captured in eight sets.

Catches across the delta front at low tide averaged eight fish/set. At the same time catches in the east channnel and Holden Creek averaged 20-40 chinook salmon/set. Catches along the edges of the salt marshes at high tide were lower than in the east channel in 1975, but of similar size in 1977. Purse seine sets over the intertidal flats at high tide, even near locations 29 and 30 where chinook salmon were abundant at low tide, produced no chinook salmon (Figure 1).

Catches at Stations 28-31 in 1976 and 1977 indicated that the area of greatest concentration of juvenile chinook salmon moved seaward along the channel as the season progressed (Table 3). The difference in time of maximum abundance between Station 31 and Station 28 was about 5 wk.

Physical conditions during low tide at the sampling stations along the east channel and Holden

[13]Godfrey, H. 1968. Ages and physical characteristics of maturing chinook salmon of the Nass, Skeena, and Fraser rivers in 1964, 1965 and 1966. Fish. Res. Board Can. Manuscr. Rep. 967, 38 p.

[14]Schutz, D. C. 1975. Rivers Inlet chinook sport fishery, 1971-1974. Environ. Can. Fish. Mar. Serv. Tech. Rep. PACT-75-9, 24 p.

[15]Coots, M. 1957. The spawning efficiency of king salmon (*Oncorhynchus tshawytscha*) in Fall Creek, Siskiyou County 1954-55 investigations. Calif. Dep. Fish Game, Inland Fish. Branch, Inland Fish. Adm. Rep. 57-1 1-15.

TABLE 3.—Catch of juvenile chinook salmon per beach seine set at different points along the east channel of the Nanaimo estuary during 1976 and 1977. Station locations are shown in Figure 1.

Sampling week starts	Station 28	29	30	31	Sampling week starts	Station 28	29	30	31
Mar 21, 1976					Mar 20, 1977		22 5	5 5	4 0
28					27		16 0	22 0	30 0
Apr 4		0 0	0 5	1 0	Apr 3	6 5	7 5	1 5	18 5
11		0 3	0 0	0 5	10	0 5	158 5	76 5	99 5
18		0 5	3 5	8 0	17	12 0	31 4	76 0	58 9
25		20 0	13 0	10 0	24		12 0	79 5	23 0
May 2		2 0	15 5	37 0	May 1	35 0	35 0	7 5	1 5
9		34 5	63 7	31 0	8	20 0	24 0	11 5	0 0
16		64 5	24 0	3 0	15	63 8	47 9	3 5	2 0
23		50 0	9 0	1 0	22	31 0	23 0	7 5	2 0
30		68 0	0 0		29	36 0	0 5	1 5	1 5
June 6	85 7	32 5			June 5	6 0	4 5	0 0	0 0
13	3 0	7 3			12	13 5	0 5		
20	1 5	25 0			19	0 0	1 0	0 0	0 0
27	31 5	5 0			26	11 5	0 0		
July 4	21 5	13 0							
11	2 0	0 0							
18	1 0	0 5							

Creek varied considerably with season in 1977. Temperature ranged 9.5°-26.0° C and salinity 2-24‰ (Table 4). In general, temperature increased at all stations from April through June, but this was strongly influenced by variations in river discharge and weather conditions on the day of sampling. Salinity increased throughout the season, but was also dependent on river discharge and local conditions. Large, local variation in physical conditions was indicated by measurements of temperature and salinity at two locations at Stations 28 and 30 in May and June. At Station 28 a small steam channel joined the main east channel. Temperature of the river above where this stream entered was usually lower, and on one occasion 4.5° C lower, than below the entrance. Salinity above the entrance of this stream channel was sometimes higher and sometimes lower than below the entrance, the greatest observed difference being 6‰ (Table 4). At Station 30, Holden Creek joined the east channel of the river. The river was usually cooler than Holden Creek, although on one occasion it was warmer, and salinity of the river was usually lower than Holden Creek. Temperature and salinity values reported, therefore, should be taken as indications of the kind of conditions in which the fish lived at low tide, with considerable latitude for selection by the fish.

The appearance of juvenile chinook salmon in the intertidal area of the estuary was coincident with the buildup of the downsteam run and the rate of increase in catch on the estuary was similar to the cumulative increase in the number of chinook salmon which had moved downstream. In both 1975 and 1976 the estuary population continued to increase after the peak in the downstream run. These observations indicated that the fry which migrated downstream remained in the estuary for some time.

TABLE 4.—Temperature (° C) and salinity (‰) at sampling locations for juvenile chinook salmon on the Nanaimo estuary during 1977. Station locations are shown in Figure 1.

Sampling week starts	Station 28		Station 29		Station 30		Station 31	
	°C	‰	°C	‰	°C	‰	°C	‰
Apr 3	12 0	16 0	12 0	14 8	13 0	9 5	12 0	10 5
10	10 5		9 5		15 5		15 3	
17	13 0	20 0	13 6	17 8	12 7	13 0	17 8	11 0
24			11 8	2 0	17 0	10 4	17 2	11 3
May 1	17 0	22 8	15 0	12 8	15 8	14 3	20 0	17 0
8	18 0	20 8	18 2	19 8	21 3	21 6	21 4	20 4
					17 0	18 1		
15	16 7	[1]22 1	16 1	22 2	15 0	[2]19 0	15 4	17 8
	18 2	24 5			14 6	20 0		
22	15 8	[1]20 0	15 2	20 8	15 6	[2]22 2	16 9	18 3
	18 2	24 5			15 1	20 4		
29	13 0	[1]20 0	13 2	21 6	13 3	[2]20 6	13 8	19 1
	13 0	14 0			15 1	20 4		
June 5	19 0	[1]17 5	19 0	20 0	25 1	[2]19 8	26 0	19 4
	23 5	14 0			19 9	18 9		
12	19 0	[1]17 8	18 7	18 2	—	—		
	19 3	17 4			19 9	[2]18 9		
19	21 0	24 6	20 2	24 6	20 5	24 0	24 0	24 0
26	21 0	[1]22 3	19 0	22 0	—	—		
	20 3	23 2			19 9	[2]18 9		

[1]Upper measurement above small tributary, lower below small tributary
[2]Upper measurement in Holden Creek, lower in main river channel

At low tide the chinook salmon population in the estuary was clearly concentrated in the east channel of the river and Holden Creek. Some juveniles were found in stream channels crossing the center of the mud flat, and some also found their way down to the delta at low tide. The channels crossing the western side of the mud flat, however, were little used by juveniles.

With the incoming tide the chinook salmon moved to the landward margin of the mud flat and at high tide were found in scattered schools all

across the landward margin of the intertidal area. Apparently no chinook salmon, or very few, remained over the intertidal flats at high tide The redistribution of chinook salmon on each tidal cycle, and their concentration in one of several low tide refuges implied active habitat selection. Active selection of habitats at low tide is further indicated by the seaward movement of the center of the population in the east channel and Holden Creek as the season progressed.

The habitats in which chinook salmon were captured ranged from a few centimeters to a meter or more in water depth, on gravel, sandy, or muddy substrates, with and without eelgrass, *Zostera* sp. In the east river channel, concentrations of fry were found mainly in pools and back eddies. There were, however, no obvious qualitative differences between preferred sites in Holden Creek where chinook salmon were abundant and stream channels crossing the central and west sides of the intertidal area where chinook salmon were scarce. The upstream portions of the stream channels in the central area of the delta, where they cut through the marsh areas, were used as low tide refuges in early spring. Where these stream channels cross the intertidal mud flat deep pools are scarce and the water flow small. These features may have made them unsuitable as refuges during May. The absence of chinook salmon from the west branch of the river could not be explained in this way; however, disturbance of the estuary by log rafting is greatest along the west branch and this may have influenced chinook salmon distribution.

Temperature and salinity in the east channel of the river and Holden Creek indicated that the chinook salmon were tolerating moderate salinities and relatively high temperatures. Occasional measurements of temperature and salinity in other areas sampled at low and high tide were comparable with those in the east channel at low tide. Weisbart (1968) reported that juvenile chinook salmon (parentage not identified) were intolerant of direct transfer from freshwater to 31.8‰ seawater, but that they had greater resistance to seawater than either coho or sockeye salmon, *O. nerka*. McInerney (1964) reported that juvenile chinook salmon from the Samish hatchery, Washington State, avoided all salinites above 0‰ except for a brief preference for about 5‰ salinity in September tests. Presumably both tolerance and preference for salinity will vary among stocks of salmon, and Nanaimo River chinook salmon appear adapted to life in moderate salinity on the estuary. Temperatures experienced by the chinook salmon at low tide were within their tolerance range but were generally above the 12°-13° C reported to be their preferred temperature (Brett 1952).

Seasonal changes in the low tide distribution of chinook salmon were not obviously correlated with temperature and salinity in the east channel and Holden Creek. Temperature at the upstream stations often, though not always, exceeded that at the downstream stations. Chinook salmon were not captured at Stations 30 and 31 when temperature there exceeded 20° C. They were present at Stations 28 and 29, however, when temperature was 20°-21° C. Salinity was only slightly higher on the average at the downstream stations, and often the salinity at the upstream stations was the same or slightly higher than downstream (Table 4). Increasing adaptation to salinity, therefore, appeared not to be a factor in this seaward movement. Possibly the disappearance of chinook salmon from the shallow sampling stations in Holden Creek as the season progressed was an avoidance of the high temperatures that occurred there on sunny days.

The seasonal pattern of abundance of juvenile chinook salmon in the Nanaimo estuary was the same as that observed by Dunford (1975) in the Fraser River, but different from that in the Sixes River, Oreg. (Reimers 1971). In the Sixes River, most chinook salmon apparently spent some weeks in the river before moving into the estuary, although some were considered to have moved directly to the estuary, and some even directly to the sea. Reimers (1971) did not present information on the temperature and salinity of the estuary habitats he sampled. Dunford (1975) gave temperature measurements for two habitat types in the Fraser estuary, and these were lower than in similar areas of the Nanaimo River. Chinook salmon disappeared from Fraser River marsh habitats when temperature reached about 15° C (Dunford 1975).

Size and Growth of Chinook Salmon in the Nanaimo Estuary

Length and weight of chinook salmon captured in the intertidal area of the estuary were only slightly greater than those of downstream migrants throughout the fry run. Toward the end of the fry run, however, average length and weight of chinook salmon captured in the estuary increased rapidly and leveled off at around 70 mm fork

length (FL) and 4.2 g (Figure 5). Chinook salmon captured in 1976 were slightly smaller on the average, than those captured in 1975, while those captured in 1977 were the largest of all. Average size of chinook salmon captured in 1977 increased rapidly 3-4 wk earlier than in 1975 and 1976, in keeping with the apparently earlier downstream run in 1977. The differences in size of chinook salmon captured in the 3 yr were not large, at least early in the sampling, and probably reflected differences in the timing of migration rather than differences in growth rate. The small change in length and weight of chinook salmon in the estuary during March and April probably resulted from continued recruitment of downstream migrant fry to the estuary population, while the increase in May and June reflected growth of the fish residing in the estuary. Seventy millimeters fork length is apparently the size at which chinook salmon leave the estuary and disperse into the marine environment. No young-of-the-year <70 mm were captured away from the estuary. The smallest young-of-the-year captured in area 10 were 70-75 mm FL. Weisbart (1968) commented that 70 mm was about the size at which juvenile chinook salmon became physiologically capable of tolerating high salinity water.

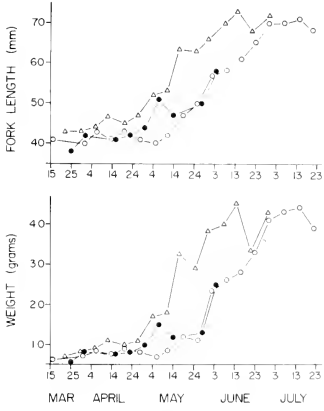


FIGURE 5.—Average fork length and round weight of juvenile chinook salmon captured on the Nanaimo River estuary in 1975 (dots), 1976 (circles), and 1977 (triangles).

The increase in size of chinook salmon on the estuary in June was not representative of their true growth rate, as it was influenced by both the continued immigration of small fish from the river and the emigration of fish reaching 70 mm FL. Recaptured fin clipped fish in 1977, however, provided an estimate of the growth rate of a known group of juveniles. Total mark recaptures sampled for length and weight were 36 left pelvic clips and 19 right pelvic clips. Left pelvic clips averaged 44 mm and 0.92 g when marked, and five of these recovered 47 and 57 days after marking averaged more than 100 mm and 13 g (Table 5). Right pelvic clips averaged 63 mm and 3.36 g when marked, and increased to more than 100 mm and 13 g after 29 days (Table 5). The linear regressions of length or log, weight on days since marking indicated no significant difference in the rate of growth between the two marked groups. The data were, therefore, combined by scaling to 0 length and weight at the day of release and growth rates were calculated for the combined data. Growth in length was 1.32 mm/day. Instantaneous daily growth in weight was 0.0566, or about 5.8% of body weight/day.

Estimates of Total Estuary Population

Although the beach seine samples taken in this study provided an adequate measure of distribution and relative abundance of chinook salmon, they do not permit an estimate of the total number of chinook rearing in the estuary. Mark and recapture estimates of abundance in 1977 provided a reference point for comparing catches between years and for comparing the downstream run of fry with the estuary population. Between 18 and 21 April 1977, 3,187 fish marked with a left pelvic clip were released at Stations 29-31 of the east

TABLE 5.—Size at release and recapture of fin-clipped juvenile chinook salmon in the Nanaimo River estuary in 1977.

Left pelvic clips				Right pelvic clips			
n	Days since marking	Average length	Average weight	n	Days since marking	Average length	Average weight
55	0	44	0 94	36	0	63	3.36
10	5	47	1 05	12	5	65	3 32
10	13	54	1 90	2	13	71	4 67
1	14	55	1 95	2	19	84	8 29
2	19	60	2 72	1	26	76	5 28
6	26	70	4 60	2	29	107	13 55
2	33	77	5 38				
4	47	103	13 80				
1	57	115	18 60				

channel. Sampling along the east channel and Holden Creek on 22 April showed that the marked fish occurred all along the east channel and Holden Creek but were most concentrated at Station 31 and for several hundred yards farther upstream. Sampling in subsequent weeks indicated that marked fish remained concentrated at Stations 30 and 31 as long as chinook salmon were abundant there. With the shift in population center to Stations 28 and 29, the marked fish also shifted downstream, but remained most abundant at Station 29. A few marked fish were also captured in samples taken across the delta front and across the landward margin of the mud flat at high tide, but none were captured in stream channels in the center of the mud flat at low tide. In spite of their twice daily migration up and down the delta with the tide, therefore, marked fish remained concentrated in the area of marking, so that population estimates from the recaptures referred only to the east channel and Holden Creek, and underestimated the population in this region as well.

The instantaneous rate of disappearance of marks from the sampling area after the April marking was 0.117, or about 11%/day, and after the May marking the rate was 0.137, or about 13%/day. These disappearance rates were used to correct the summed release of marks each day to an estimate of the marks remaining in the area and to calculate estimates of the marked population on all sampling dates following the last release of marks (Table 6).

Estimates of population size throughout the first period of marking were consistent, ranging only 14,675-17,133, and estimates for 25 April and 3 May were also similar (Table 6). On May 9, the population estimate dropped to 5,708 and remained at this level or lower throughout May. The first population estimate from right pelvic clips was on 17 May. Estimates based on this mark ranged 4,629-9,544 between 17 and 19 May and remained at this level throughout May. Estimates for the first 2 wk of June from recaptures of right pelvic clips were 2,352 and 1,204, respectively.

Estimates from right pelvic recaptures in May were twice as great, or greater, than estimates from left pelvic recaptures. Possibly this difference occurred because fishing during 17-19 May was concentrated where fry marked with left pelvic clips were most abundant, so that recaptures of this mark were high.

The estimates indicated that the population in the east channel and Holden Creek was 12,000-19,000 throughout April and early May and that the population declined to 5,000-10,000 in the latter half of May and declined further to about 2,000 in early June. These changes are consistent with changes in beach seine catches.

During the first week of May sampling was performed across the landward edge of the mud flat at high tide (13 sets) in the east arm and Holden Creek (8 sets), across the delta front at low tide (8 sets), and in the stream channels crossing the center of the mud flat (7 sets). Although this sampling was not at random with respect to either the distribution of chinook salmon or marks, it does permit a population estimate based upon sampling areas outside the east channel and Holden Creek. A total of 406 chinook salmon were captured, of which 12 were recaptures. The average

TABLE 6.—Release and recovery of fin-clipped chinook fry, estimates of marks available and population estimates for the Nanaimo River estuary in 1977. LV = left pelvic clip; RV = right pelvic clip. Population estimates are the product of total catch and estimated marks present divided by marks recaptured.

Date	Total catch	Total marks released		Marks recaptured		CPUE recaptures		Estimated marks present			Population estimates		
		LV	RV	LV	RV	LV	RV	LV	RV	Both	LV	RV	Both
Apr 18	589	370											
19	875	827		18				329			15,993		
20	858	791		55				1,028			16,037		
21	1,344	1,199		127				1,619			17,133		
22	609			104		8 00		2,506			14,675		
25	229			23		3 83		1,764			17,563		
May 3	168			10		1 25		692			11,558		
9	111			2		0 22		343			18,648		
16	233		203	6		0 75		151			5,708		
17	340		335	17	13	1 55	1 18	134	177	311	2,680	4 629	3,525
18	749		691	23	35	2 56	3 89	120	446	566	3,908	9 544	7,309
19	412		325	22	48	2 75	6 00	106	992	1,098	1,985	8 515	6,463
23	127			2	13	0 25	1 62	67	761	828	4,254	8,089	7,010
31	79			0	3	0 00	0 38	26	254	280		6,689	7,373
June 6	21			0	1	0 00	0 12	13	112	125		2,352	2,625
13	28			0	1	0 00	0 25	6	43	49		1,204	1,372
20	2			0	0	0 00	0 00	3	16	19			
28	13			0	0	0 00	0 00	1	5	6			

estimated marked population for the week was 655, giving a population estimate of 22,148 for the whole estuary. The average population of the east channel for the week was about 15,000, or about 68% of this estimate. Total estuary population may, therefore, be about 32% greater than the estimate for the east channel and Holden Creek.

Comparing beach seine catches for 1975-77 with the mark recapture estimates indicated that the peak population on the estuary was on the order of 20,000-25,000 in 1976 and 1977 but was probably closer to 40,000-50,000 in 1975. These estimates are comparable with a single day's fry migration in 1975 and 1976. However, the slow rate of disappearance of marked fry from the east channel indicated a relatively long residence of fry on the estuary (about 60 days). An accumulation of fry on the estuary during downstream migration would, therefore, be expected. Treating each daily run of fry as a single cohort arriving on the estuary, and reducing that cohort by 11-12%/day (the rate of disappearance of marked fry from the east channel), produced estimates for the estuary population of around 100,000 in 1975 and 50,000 in 1976, or about twice the estimate based on mark recapture results for 1977. Estimates of downstream run are for the release point of the marks, however, and significant mortality might occur between the release point and the estuary (Hunter 1959). Alternatively, the rate of disappearance of marked fry may underestimate the rate of disappearance of recent downstream migrants. A disappearance rate of 11-12%/day suggested an average residence time of about 60 days, whereas growth rates suggested that most fry should spend only 25 days in the estuary.

If downstream migrants spend only 25 days in the intertidal area, and their rate of disappearance is constant during that time, then peak estuary populations are 40,000 in 1975 and 20,000 in 1976, comparable with the estimate based on mark recaptures in 1977. The estimate of disappearance rate from mark returns has rather wide confidence limits, 25 days being within the range of 95% probability in estimates of residence time. The apparent discrepancy between mark recapture estimates of estuary population size and downstream run can be resolved by assuming residence of 25 days, therefore. The assumption of a constant rate of disappearance of chinook salmon from the estuary population, however, implies the disappearance of many juveniles <70 mm FL. Although high mortality of salmon fry is a common assumption, no predators or important diseases were obviously present in the Nanaimo estuary to justify the assumption of heavy losses of small fish. The tentative agreement between the various estimates of population size may therefore be spurious, and these estimates should be regarded as preliminary at best.

By comparison with the Fraser and the Sixes Rivers, chinook salmon were rare in the Nanaimo River. Dunford (1975) reported maximum densities in excess of 2 fish/m^2 in Fraser River marshes, compared with average densities of about 0.1 fish/m^2 in the east channel and Holden Creek. For the Sixes River estuary, an area about twice as large as the east channel and Holden Creek, Reimers (1971) reported maximum population estimates of 100,000-150,000. However, Reimers' estimates were made 5 days after the release of marked fish into the estuary, and, assuming his marked fish were disappearing at a rate similar to those in the Nanaimo River, the population in the Sixes River estuary may have been closer to half the values he reported. Nevertheless, this still represents a population significantly more dense than that in the Nanaimo estuary. In terms of suitable habitat, however, the Sixes River may not be greatly different from the Nanaimo River, as it is about twice as large as the east channel and Holden Creek, and probably supported about twice the population of chinook salmon.

Population of Juvenile Chinook Salmon Outside the Estuary

Beach seine samples in areas other than the intertidal area of the estuary produced few juvenile chinook salmon. In 1975, 19 sets made in mid-May yielded only 3 juveniles, and in 1976, 61 sets made during April-June yielded only 26. Twenty-four of these were captured in the lagoon behind Duke Point (area 16), adjacent to the estuary. Apparently onshore areas away from the estuary were not used by chinook salmon fry, although all the beaches sampled were used by pink and chum salmon fry.

Juvenile chinook salmon were captured in most locations sampled by the two purse seines in 1975 and 1976. Not all chinook salmon captured were young-of-the-year, however. Catches prior to May were mainly yearlings. In late May and early June there was a large influx of young-of-the-year and a subsequent decline in the catch of yearlings. The influx of young-of-the-year (Figure 6) coincided

with the decline in abundance of chinook salmon in the intertidal area of the Nanaimo estuary. The periodicity of catches in the estuary and adjacent marine areas is indicative of a stage movement away from the estuary and into deeper water by young-of-the-year. Sampling by drum seine after July 1976 indicated the persistence of moderate numbers of juvenile chinook salmon in the Nanaimo area until the end of October, after which catches declined to the low levels observed in spring (Figure 6).

Catches of chinook salmon by the 92 m purse seine in 1975 were mainly in area 10 (338 of 434 chinook salmon captured), with smaller catches in areas 6, 7, 8, and 11 and few elsewhere. Catches by the 218 m drum seine in 1975 were also mainly in area 10 (101 of 205 captured), with the remaining catch scattered throughout the sampling areas. Chinook salmon were more scattered in 1976, area 10 yielding only 79 of 245 captured by drum seine between April and July and areas 1, 2, 5, and 6 also providing good catches. Chinook salmon were of similar abundance in drum seine catches between April and June 1975 and 1976 (CPUE 0.73 in 1975 and 0.83 in 1976) but were significantly less abundant in July 1976 compared with 1975 (CPUE 3.30 in 1975 and 2.28 in 1976 $\chi^2 = 6.43$, $P < 0.05$). The greater catch in July 1975 presumably reflected the greater contribution of young-of-the-year from the estuary in 1975.

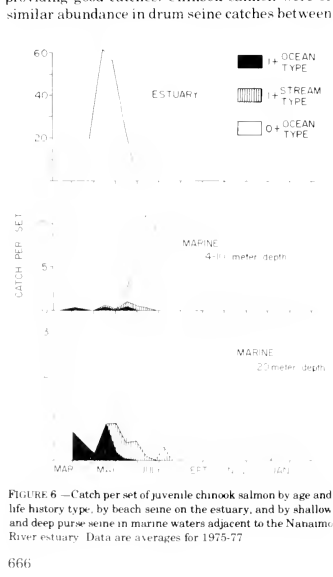


FIGURE 6.—Catch per set of juvenile chinook salmon by age and life history type, by beach seine on the estuary, and by shallow and deep purse seine in marine waters adjacent to the Nanaimo River estuary. Data are averages for 1975-77.

The presence of juvenile chinook salmon in the Nanaimo area throughout the year in 1976 indicates a local resident population that is supplemented by young-of-the-year in June. The appearance of juveniles in large numbers in area 10 coincident with their disappearance from the intertidal area of the estuary indicates that these fish were from the estuary population. The evidence is not conclusive however, and examination of the catch at area 10 in June and July 1977 for fin clips from the estuary produced only 8 marked fish out of 555 examined. This compares with approximately 10% of the estuary population marked in April and May. Possible reasons for the low number of marks in the catch at area 10 include differential mortality of marks (the percentage of mark returns in the estuary declined after each marking), rapid dispersal of chinook salmon away from the estuary, dilution of the fish of local origin by fish from other systems, or dilution of the estuary population by late migrants from the Nanaimo River. In my view the most likely explanations are rapid dispersal of juveniles from the estuary population, and dilution of the estuary population by late migrants from the Nanaimo River. Chinook salmon reared in the intermediate salinity of the estuary are probably already adapted to seawater by the time they are ready to leave the estuary while late migrants from the river might be expected to stay close to the river mouth for some time, adapting to salt water. Samples from area 10 may, therefore, contain a disproportionate number of late migrants.

An unknown proportion of the Nanaimo River population probably disperses rather quickly away from the Nanaimo area after leaving the river. Some young-of-the-year, however, remain in the Nanaimo area, at first concentrated rather close to shore, but later moving to more offshore sampling locations where they persist until at least November (Figure 6). During the winter these fish decline in numbers until by the following spring there are only a few 1+ ocean fish in the local area. Most of these disappear from the surface waters in May coincident with a small influx of yearling smolts from the Nanaimo River (Fig-

ure 6). The yearling smolts dominate samples taken in late May and early June, after which they disappear and are replaced by young-of-the-year, presumably from the Nanaimo River. This sequence of events in which 1+ ocean fish are replaced by 1+ stream fish which in turn are replaced by 0+ ocean fish is not unique to the Nanaimo area but appears to be typical for the Gulf Islands region as a whole (Healey[16]).

Food Habits and Feeding Rates

A growth rate in excess of 5% body weight/day implies good feeding conditions in the estuary (e.g., LeBrasseur 1969). Diets of juvenile chinook salmon were similar in 1976 and 1977, and five taxonomic groups made up the bulk of the diet in the estuary. Harpacticoid copepods were important in March and early April, decapod larvae and amphipods in April and May, and mysids and insect larvae in May-July. Off the intertidal area of the estuary fish larvae, chiefly herring, dominated the diet of juvenile chinook salmon from May through August, while calanoid copepods, decapod larvae, and insects were occasionally important. A shift from a predominantly invertebrate diet to a predominantly fish diet, therefore, occurred as the young chinook salmon dispersed away from the intertidal area of the estuary.

Average weights of stomach contents varied considerably from sample to sample; nevertheless, some generalizations appear possible. Weights of stomach contents of juvenile chinook salmon captured on the estuary in 1975 ranged about 3-5% of body weight in April but dropped rapidly to a low of about 0.1% of body weight as the chinook salmon population on the estuary increased in May (Table 7). Weights of stomach contents of juveniles on the estuary were uniformly low in 1976, never rising above 2.2% of body weight (Table 7). Stomach contents of juveniles captured in 1977 ranged 2-5% of body weight except during the peak of fry abundance when contents dropped to 0.5% of body weight (Table 7). Assuming that stomach contents are a reflection of feeding conditions, it appears that feeding conditions were poorest in 1976, better in 1977, and possibly best of all in 1975 when the population was greatest. Peak population densities were associated with a decline in stomach contents, and by inference, a decline in food intake in the years of good feeding conditions.

TABLE 7.—Stomach contents as a percent of body weight for juvenile chinook salmon captured in the intertidal area of the Nanaimo River estuary and off the intertidal area 1975-77. Sampling week dates are for 1976. Add 2 days for 1975 and subtract 1 day for 1977 to get the correct starting date for those years.

Sampling week starts	On the estuary						Off the estuary			
	1975		1976		1977		1976		1977	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Mar 14			1	1 4						
21					15	1 8				
28			1	1 7	19	3 4				
Apr 4	9	3 3	2	2 0	24	2 4				
11	3	4 1	6	1 0	20	2 6				
18	1	2 9	20	1 4	57	1 9				
25	5	5 0	20	1 7	15	0 6				
May 2	1	3 8	20	1 6	18	2 0				
9	25	0 1	20	2 2	20	2 2			25	2 6
16	3	2 3	20	1 2	36	4 1				
23			20	1 4	15	2 1				
30			20	1 1	12	4 0	5	2 5		
June 6			20	2 2	10	3 3	1	0 1		
13					6	5 0	13	2 0	14	2 5
20			20	1 9	2	2 0	3	1 3		
27			20	2 0	5	4 0			15	3 4
July 4			20	2 0			3	0 8	17	3 0
11			24	1 8			20	1 2		
18			3	1 0			24	1 3	29	2 7
25							8	1 2	19	1 4
Aug 15									4	2 3
22									10	1 2

Weights of stomach contents of juvenile chinook salmon captured away from the intertidal area of the estuary were similar to those in the estuary during May and early June, but in mid-June dropped below those from the estuary. Weights of stomach contents of chinook salmon captured offshore were lower in 1976 than in 1977, as was observed for the estuary population (Table 7).

The composition of the diet of juvenile chinook salmon in the Nanaimo estuary was similar to that reported by Sibert and Obrebski (1976) for the Nanaimo estuary in 1973 and to that recorded by Dunford (1975) in similar habitats on the Fraser estuary. The relative timing and importance of specific items in the diet was different than in the Fraser, but this probably reflects differences in abundance of the different diet items and the opportunistic feeding behavior of the fish. The change in diet of juvenile chinook salmon from invertebrates while in the intertidal area of the Nanaimo estuary, to larval fish when away from the intertidal area was consistent with observations on the Fraser estuary. Juveniles in the Fraser River and marsh area fed mainly on invertebrates, but those on Roberts and Sturgeon Banks fed mainly on juvenile herring (Goodman see footnote 2).

[16]Healey, M. C. 1978. The distribution, abundance and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fish. Mar. Serv. Tech. Rep. 788, 49 p.

Seasonal changes in the diet of chinook salmon in the intertidal area of the estuary indicated that a combination of size selection and availability influenced the diet. Very small organisms (harpacticoids and cladocerans) occurred in stomachs only in the early spring when the fish were 50 mm or less in length. Larger organisms (amphipods, mysids) were important later in the season when the fish were considerably larger. Insects were important diet items throughout, presumably because of their widespread availability in the habitats sampled.

CONCLUSIONS

The Nanaimo River population of juvenile chinook salmon is composed of fish which go to sea in their first year and fish which remain in freshwater for 1 yr, with those which go to sea in their first year most numerous. Chinook salmon which migrate to sea in their first year are the most common life history type in British Columbia (Milne[17]; Godfrey see footnote 13). In the Nanaimo River many of those chinook salmon which go to sea as young-of-the-year move downstream as recently emerged fry and rear to smolt size in the intermediate salinity of the estuary. Large numbers of chinook salmon fry are found in the marshes of the Fraser estuary in spring and summer (Dunford 1975) and in the estuaries of other rivers in which chinook salmon spawn (Healey unpubl. data). Estuaries, therefore, are important nursery areas for chinook salmon, a fact which has not hitherto been appreciated.

ACKNOWLEDGMENTS

Technical staff who contributed to the collection and analysis of data presented include R.V. Schmidt, F. P. Jordan, and R. M. Hungar. Fry trapping was performed by R. Wilson under contract. Robin Le Brasseur and T. G. Northcote criticized a draft of the manuscript.

LITERATURE CITED

BRETT, J. R.
1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9:265-323.

DUNFORD, W. E.
1975. Space and food utilization by salmonids in marsh habitats of the Fraser River estuary. M. Thesis, Univ. British Columbia, 81 p.

HUNTER, J. G.
1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.

LEBRASSEUR, R. J.
1969. Growth of juvenile chum salmon (*Oncorhynchus keta*) under different feeding regimes. J. Fish. Res. Board Can. 26:1631-1645.

LISTER, D. B., AND H. S. GENOE.
1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. 27:1215-1224.

LISTER, D. B., R. A. L. HARVEY, AND C. E. WALKER.
1969. A modified wolf trap for downstream migrant young fish enumeration. Can. Fish Cult. 40:57-60.

LISTER, D. B., AND C. E. WALKER.
1966. The effect of flow control on freshwater survival of chum, coho and chinook salmon in the Big Qualicum River. Can. Fish Cult. 37:3-25.

MCINERNEY, J. E.
1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish Res. Board Can. 21:995-1018.

MEHAN, W. R., AND D. B. SINIFF.
1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. Trans. Am. Fish. Soc. 91:399-407.

PARKER, R. R.
1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Board Can. 20:1441-1455.

REIMERS, P. E.
1971. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Fish Comm. Oreg. Res. Briefs, 99 p.

REIMERS, P. E., AND R. E. LOEFFEL.
1967. The length of residence of juvenile fall chinook salmon in selected Columbia River tributaries. Fish Comm. Oreg. Res. Briefs 13:5-19.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

SIBERT, J., AND S. OBREBSKI
1976. Frequency distributions of food item counts in individual fish stomachs. *In* C. Simenstad and S. Lipovsky (editors), Fish food habits studies. 1st Pacific Northwest Technical Workshop Proceedings, p. 107-114. Washington Sea Grant, Univ. Wash., Seattle.

STEIN, R. A., P. E. REIMERS, AND J. D. HALL.
1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. J. Fish. Res. Board Can. 29:1737-1748.

WEISBART, M.
1968. Osmotic and ionic regulation in embryos, alevins, and fry of the five species of Pacific salmon. Can. J. Zool. 46:385-397.

[17]Milne, D. J. 1964. Sizes and ages of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the British Columbia troll fisheries (1951-1959) and the Fraser River gillnet fisheries (1956-1959). Fish. Res. Board Can. Manuscr. Rep. 776, 36 p.

COMPOSITION, ABUNDANCE, AND DISTRIBUTION OF ZOOPLANKTON IN THE NEW YORK BIGHT, SEPTEMBER 1974-SEPTEMBER 1975

DAVID C. JUDKINS,[1] CREIGHTON D. WIRICK,[1] AND WAYNE E. ESAIAS[2]

ABSTRACT

Zooplankton taxa were counted in 8 to 19 samples from each of 11 cruises in the New York Bight between September 1974 and September 1975. Major seasonal events were an influx into the region of tropical-subtropical copepod species during autumn 1974 and summer 1975, an offshore (>50 m water depth) zooplankton abundance maximum in March dominated by the pteropod *Limacina retroversa*, a second offshore maximum in May characterized by high abundance of the copepods *Pseudocalanus* sp., *Calanus finmarchicus*, and *Oithona similis*, and an onshore (<50 m water depth) maximum in July characterized by high abundance of the copepods *Centropages typicus* and *Temora longicornis*. The offshore maxima occurred during or shortly after the local spring phytoplankton bloom (March-April). Advection of pteropod and copepod stocks into the region from the northeast probably contributed to these peaks. The July *C. typicus-T. longicornis* peak was associated with summer warming of the water column within the highly productive waters in the Bight apex and off the New Jersey coast. Comparison of our results with those of a study conducted in 1959-60 shows that the most abundant species of copepods were essentially the same during the two periods.

The New York Bight is the section of continental margin and overlying water within the bend of the Atlantic coastline bounded by Long Island on the north and New Jersey on the west (Figure 1). It is one of the most heavily used coastal regions of the world for a variety of human activities, including transportation, fisheries, recreation, and waste disposal (Gross et al. 1976). Exploration for and exploitation of potential offshore petroleum deposits may place additional burdens on the region's environment. Efforts to document changes in the biota because of these activities have generally been inadequate, especially in regards to the zooplankton. In a recent review, Malone (1977) observed that studies of the zooplankton of the New York Bight generally have been restricted to small geographic areas and to short periods of time, and consequently little data on species abundance and distribution exist for most of this heavily exploited area.

In this paper, we examine seasonal and onshore-offshore trends in occurrence and abundance of zooplankton taxa in waters of the New York Bight. These observations are based on analysis of the most comprehensive set of zooplankton samples obtained to date within the region and thus are invaluable for comparison with future studies. We compare our results with previous studies for evidence of the year-to-year variations in mean abundance of dominant species and in timing of peaks in their standing stocks. Finally, we examine occurrences of offshore water within the study area, and discuss zooplankton abundance maxima in relation to seasonal and regional variations in temperature and phytoplankton standing stocks and the environmental requirements of the dominant species.

METHODS

The station grid (Figure 1) was occupied 13 times between 25 July 1974 and 15 September 1975, with a cruise every month except December 1974 and January 1975. These cruises were part of an ichthyoplankton survey by the National Marine Fisheries Service (NMFS) Laboratory at Sandy Hook, N.J., funded by the Brookhaven National Laboratory. Zooplankton were analyzed in collections from the 11 cruises between 24 September 1974 and 15 September 1975 (Table 1).

Standard NMFS MARMAP gear was used that consisted of 60 cm diameter paired 333 μm and 505 μm mesh nets mounted on a "bongo" sampler without an opening-closing mechanism. Sampling accessories (flowmeters, depth recorder, depressor, towing cable) were rigged as specified by Smith and Richardson (1977). To obtain better estimates of small-bodied copepods, nets with 253

[1]Oceanographic Sciences Division, Brookhaven National Laboratory, Upton NY 11973.
[2]Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794

Manuscript accepted February 1979.
FISHERY BULLETIN VOL. 77, NO. 3, 1980

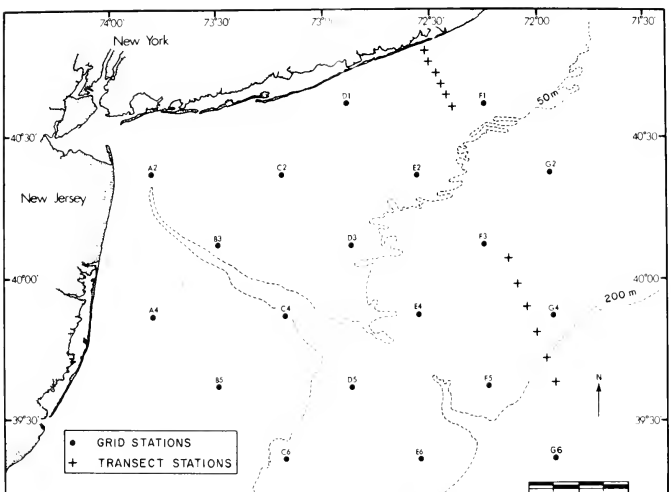


FIGURE 1.—New York Bight with stations for oblique net tows for zooplankton (grid) and chlorophyll, nutrient, and hydrographic measurements (grid and transect).

or 223 μm mesh were added to the sampling array in 1975. These nets were 20 cm in diameter and mounted as pairs on a bongo sampler rigged with a flowmeter in one mouth. The 20 cm sampler was attached to the towing wire immediately above the 60 cm frame, and the entire array was towed obliquely at 3.5 kn (6.5 km/h) from near bottom to surface, except at stations exceeding 200 m where tows were from 200 m to the surface. The samples from the two nets on the 20 cm frame were combined before preservation.

From 8 to 19 of the 20 grid stations (Figure 1) were sampled for zooplankton during the 11 cruises of the survey (Table 1). Samples were not available for every station because of gear failure, adverse weather, or contamination by algae or sediments. At all grid and transect stations (Figure 1) XBT's and nonmetallic sampling bottles were used to obtain temperature, salinity, nutrient, and chlorophyll data at discrete depths.

Samples were analyzed separately for chaetognaths, copepods, and "other" zooplankton (i.e., all taxa other than chaetognaths and copepods). We used only samples from 253 μm and 223 μm mesh nets to estimate the abundance of copepods and other zooplankton in 1975 but had to rely on 333 μm mesh nets for abundance estimates in 1974. In the separate analyses of copepods and other zooplankton, we removed aliquots from a sample with a piston pipette until a total of 500 or more individuals were identified and counted. We counted chaetognaths only in collections from 333 μm mesh nets, which retained most size classes of these large-bodied animals. We used a Folson plankton splitter to subsample collections with large numbers of chaetognaths until a total of 200

TABLE 1.—Zooplankton sampling data for the New York Bight region, 1974-75. Net mesh aperatures and mouth diameters indicated by letters: A, 333 μm, 60 cm; B, 253 μm (February 1975 only) or 223 μm, 20 cm. For station locations see Figure 1.

Station	Depth[1] (m)	Cruise 74-11 24-28 Sept	74-13 23-28 Oct	74-15 19-23 Nov	75-1 1-6 Feb	75-3 5-11 Mar	75-4 2-10 Apr	75-5 6-12 May	75-6 2-9 June	75-7 7-12 July	75-8 12-16 Aug	75-14 8-15 Sept
A2	27	A	A	—	A, B	A	A, B	A, B	A, B	A, B	A, B	B
A4	26	A	A	—	A, B	B	A, B	A, B	A, B	B	A, B	A, B
B3	40	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
B5	37	A	A	—	—	A, B	A, B	A, B	A, B	A, B	B	A, B
C2	33	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
C4	49	A	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B
C6	59	—	A	—	—	B	A, B	A, B	A, B	A	A, B	A, B
D1	29	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
D3	49	A	A	A	A, B	A	A, B	A, B	A, B	A, B	—	A, B
D5	64	A	A	—	A, B	A, B	A	A, B	A, B	A, B	A, B	A, B
E2	48	A	—	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
E4	66	A	A	A	A, B	A, B	A, B	A, B	B	A, B	A, B	A, B
E6	124	A	A	—	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
F1	49	A	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B
F3	71	A	A	—	A, B	A, B	—	A, B	A, B	A, B	A, B	A, B
F5	128	—	A	—	A, B	A, B	B	A, B	A, B	A, B	A, B	A, B
F7	2,800	A	A	—	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
G2	71	A	A	—	A, B	A, B	—	A, B	A, B	A, B	A, B	A, B
G4	146	A	A	—	A, B	—	A, B	A, B	A, B	—	A, B	A, B
G6	1,600	—	—	—	—	—	—	—	—	B	A, B	—

[1]Maximum sample depth = 200 m

or more individuals were counted. Abundances of taxa within individual samples and related data are available in a data report (Judkins[3]) and from the senior author. In our treatment of the cross-shelf distribution of zooplankton, we divided the study region into two sectors of equal area, an onshore zone shoreward of the 50 m depth contour and an offshore zone seaward of that contour. Each sector contained 10 zooplankton grid stations (Figure 1). This division yielded approximately equal numbers of onshore and offshore samples and provided an easy test for cross-shelf differences in species abundances.

In Tables 2 and 3, we list abundances as both concentrations (numbers/cubic meter) and standing stocks (numbers/square meter). We calculated concentrations primarily for comparison with the historical data which have been reported almost exclusively in that manner. However, it would be an error to compare concentrations from different locations in the New York Bight because of the wide range of depths of stations and the vertical stratification of zooplankton. Estimates of numbers/cubic meter from oblique tows are average values for the entire water column, and these would be adequate for comparisons of tows from different depths only if zooplankton were evenly distributed throughout the water column. However, if a species is restricted to a narrow depth stratum, then its concentration would be underestimated by deeper tows relative to shallower ones (Peterson and Miller 1977). Vertically discrete samples show that most species in the New York Bight are concentrated in the upper 20 to 30 m (Judkins unpubl. data). To avoid underestimating species abundances in samples that extended below about 30 m, we calculated standing stocks and were then able to obtain mean values for combinations of tows from different depths and to test for significant differences between these means.

[3]Judkins, D. C. Zooplankton sampling program and data. *In* E. Wold (editor), Atlantic coastal experiment survey cruises (July 1974-September 1975) data report Vol. 2. Zooplankton and ichthyoplankton, p. 2-129. BNL 24771. Brookhaven National Laboratory, Upton, N.Y.

RESULTS

Frequency of Occurrence of Zooplankton Taxa

We identified 88 copepod species, 10 chaetognath species, and 26 other holo- and meroplanktonic taxa (Table 4). By season, 100 taxa occurred in samples taken in autumn (September-November) 1974, 68 in samples from winter to spring (February-May) 1975, and 91 in samples from summer (June-September) 1975.

These taxa can be grouped on the basis of seasonal and cross-shelf patterns in occurrence. The taxa in one group occurred commonly during all seasons and included the copepods *Centropages typicus*, *Pseudocalanus* sp., *Calanus finmarchicus*, *Paracalanus parvus*, *Oithona atlantica*, *Metridia lucens*, and *Clausocalanus pergens*, the chaetognaths *Sagitta elegans* and *S. serratodentata*, and pteropods, appendicularians, medusae, polychaete larvae, bivalve veligers, and euphausiid furcilia and calyptopsis stages (Table 4). The copepod *O. similis* was uncommon only during au-

TABLE 2.—Mean abundance (no./m², no./m³, and percent total no./m²), frequency of occurrence (% of samples), average rank, and dominance of the 20 most abundant zooplankton taxa in the New York Bight, September 1974-September 1975. Taxa ranked within each sample on basis of number per square meter (1 = most abundant, ties averaged); ranks for each taxon averaged over all samples (n = 178 for chaetognaths, n = 183 for copepods and others). Dominance: proportion of samples in which taxon was among those making up 50% of the individuals; summation in each sample was begun with the most abundant species (Fager and McGowan 1963).

Taxa	Abundance			Frequency	Average rank	Dominance
	no./m²	no./m³	% total	%		
Pseudocalanus sp.	25,566	521	13.8	91	15.7	56
Pteropods	25,532	479	13.8	98	11.7	42
Centropages typicus	25,135	655	13.6	97	8.9	57
Paracalanus parvus	15,342	312	8.3	79	28.2	49
Penilia avirostris	14,613	454	7.9	28	82.9	15
Temora longicornis	11,365	373	6.2	61	50.8	11
Calanus finmarchicus	11,245	146	6.1	91	17.3	36
Oithona similis	8,293	146	4.5	81	28.7	9
Appendicularians	7,076	126	3.8	84	27.2	14
Gastropod veligers	4,833	113	2.6	61	52.3	5
Evadne spp.	3,901	91	2.1	46	65.9	9
Doliolids	3,600	90	2.0	32	79.5	6
Metridia lucens	2,498	21	1.4	58	52.4	8
Plutei	2,239	51	1.2	31	80.5	5
O. atlantica	1,979	22	1.1	72	36.7	17
Clausocalanus pergens	1,821	16	1.0	51	59.4	8
Medusae	1,419	27	0.8	74	40.7	0
Acartia tonsa	1,345	43	0.7	24	85.8	0
Sagitta elegans	1,311	26	0.7	96	30.9	3
Polychaete larvae	926	20	0.5	84	33.6	0
Total copepods	114,383	2,406	62.0			
Total chaetognaths	2,222	43	1.2			
Total "others"	67,769	1,511	36.8			
Grand total	184,174	3,960				

tumn 1974, and that may have been due simply to escapement of this small-bodied species through the coarse-mesh (333 μm) net used then. *Metridia lucens, C. pergens,* and euphausiid calyptopsis and furcilia stages were generally common only offshore, but all others in this group tended to be common throughout the Bight.

A number of taxa were common only during portions of the year. The oceanic copepod *Calocalanus tenuis*, cladocerans of the genus *Evadne*, hyperiid amphipods, and doliolids were common in autumn 1974 and again in summer 1975 but were uncommon during the intervening winter-spring period (Table 4). The neretic copepod *Temora longicornis*, ectoproct larvae, and copepod nauplii occurred commonly during autumn 1974 and winter-spring 1975 but were uncommon during summer 1975. The cold-water oceanic copepod *Pleuromamma borealis* occurred commonly only during the winter-spring period and then only offshore. Another oceanic copepod characteristic of warmer waters, *Mecynocera clausi*, was common offshore during winter-spring and summer 1975. Gastropod veligers were common both onshore and offshore during 1975 but were uncommon throughout the Bight in 1974. A large group of taxa were common only during autumn 1974. This assemblage consisted of copepods *Candacia armata, Oncaea venusta, Acartia tonsa, A. danae, Nannocalanus minor, Centropages bradyi, Rhincalanus nasutus, Eucalanus sewelli, Paracalanus aculeatus, Clausocalanus furcatus, C. jobei, Corycaeus clausi, C. speciosus, Temora stylifera, Scolecithrix danae,* and *Oithona plumifera*, the chaetognath *Sagitta enflata*, the cladoceran *Penilia avirostris*, echinoderm plutei, and siphonophores (Table 4). With the exception of the coastal-estuarine species *A. tonsa* and *P. avirostris* (and probably most of the plutei), members of this group typically inhabit the slope region and adjoining warm oceanic waters (Grice and Hart 1962; Owre and Foyo 1967; Bowman 1971).

The majority of copepods (61) and chaetognaths (7) were uncommon or rare in our samples, and most of these (43) were recorded most frequently or exclusively in autumn 1974 and/or summer 1975. Some of these rare and uncommon species are coastal-estuarine forms (e.g., *Centropages hamatus, Acartia longiremis, A. hudsonica, Paracalanus crassirostris, Tortanus discaudatus, Labidocera aestiva, Anomalocera opalus, Sagitta hispida*) and a few inhabit boreal offshore waters (e.g., *Calanus helgolandicus, Heterorhabdus norvegicus*), but the majority typically have

TABLE 3.—Seasonal variations in mean abundance (no./m² and no./m³) and frequency of occurrence (% of samples) of the 20 most abundant zooplankton taxa in the New York Bight, 1974-75. Values in parentheses are percents of total zooplankton (no./m²) during periods. Asterisks indicate significant differences in mean no./m² between periods (* = $P<0.05$, ** = $P<0.01$, NS = not significant, NT = not tested because of different mesh aperatures of nets used in 1974 and 1975).

		1974		1975			
		Sept	Oct.-Nov.	Feb.-Mar.	Apr.-May	June-July	Aug.-Sept.
No. samples (chaetognaths)		17	26	32	35	34	34
No. samples (copepods, others)		17	26	30	35	37	38
Taxa	Item						
Pseudocalanus sp.	No./m²	1,692 (1.0) NS	507(1.0) NT	116,340 (8.5)**	64,184 (24.1)*	40,855 (18.0)**	9,981 (6.3)
	No./m³	33	11	374	1,163	900	245
	% frequency	71	69	97	100	100	95
Pteropods	No./m²	712 (0.4)**	308 (0.6) NT	81,837 (42.4) NS	43,100 (16.2)**	12,553 (5.6)NS	5,801 (3.7)
	No./m³	13	8	1,215	937	335	149
	% frequency	100	100	100	100	95	97
Centropages	No./m²	16,818 (9.7) NS	19,838 (40.6) NT	30,077 (15.6) **	8,702 (3.3)*	50,801(22.4)NS	18,143 (11.6)
typicus	No./m³	445	606	700	104	1,498	451
	% frequency	100	92	100	97	97	97
Paracalanus	No./m²	2,834 (1.6) NS	6,168 (12.6) NT	17,388 (9.0) NS	5,402 (2.0) NS	13,820 (6.1)**	36,395 (23.2)
parvus	No./m³	74	188	299	41	295	784
	% frequency	94	96	90	31	73	100
Penilia avirostris	No./m²	74,658 (43.0)*	794 (1.6) NT	<1 (<0.1) NS	— NS	—*	36,434 (23.2)
	No./m³	2,278	24	<1	—	—	1,152
	% frequency	94	35	3	—	—	63
Temora longicornis	No./m²	139 (0.1) NS	246 (0.5) NT	855 (0.4)**	6,875 (2.6)*	48,173 (21.3)**	529 (0.3)
	No./m³	3	5	30	204	1,605	16
	% frequency	53	62	53	80	84	29
Calanus	No./m²	4,031 (2.3) NS	1,895 (3.9) NT	824 (0.4) NS	26,651 (9.8) NS	16,640 (7.3) NS	9,636 (6.1)
finmarchicus	No./m³	70	32	12	261	231	173
	% frequency	76	81	90	100	95	92
Oithona similis	No./m²	128 (0.1)*	34 (0.1) NT	11,199 (5.6) NS	18,947 (7.1)*	9,836 (4.3)**	3,739 (2.4)
	No./m³	3	<1	221	255	227	68
	% frequency	53	31	83	100	97	95
Appendicularians	No./m²	4,293 (2.5)*	561 (1.1) NT	11,894 (6.2) NS	19,205 (7.2)**	3,136 (1.4) NS	1,623 (1.0)
	No./m³	115	6	204	316	60	39
	% frequency	100	62	60	100	89	92
Gastropod veligers	No./m²	1(<0.1) NS	2(<0.1)NT	6,848 (3.5) NS	13,674 (5.1) NS	5,253 (2.3) NS	159 (0.7)
	No./m³	<1	<1	431	324	149	2
	% frequency	12	4	100	97	70	47
Evadne spp.	No./m²	3,846 (2.2)*	72 (0.1) NT	—**	13,116 (4.9)*	3,884 (1.7) NS	1,156 (0.7)
	No./m³	127	2	—	306	77	23
	% frequency	76	35	—	69	68	34
Doliolids	No./m²	22,022 (12.7)**	65 (0.1) NT	— NS	— NS	389 (0.1) NS	6,191 (4.0)
	No./m³	552	1	—	—	4	183
	% frequency	100	58	—	—	30	39
Metridia lucens	No./m²	221 (0.1) NS	247 (9.5) NT	1,533 (0.8)*	8,195 (3.1)*	1,683 (0.7) NS	1,327 (0.8)
	No./m³	2	4	23	58	15	12
	% frequency	32	62	70	69	47	58
Pluteı	No./m²	14,682 (8.5) NS	2,745 (5.6) NT	— NS	1,635 (0.6) NS	48 (<0.1) NS	784 (0.5)
	No./m³	308	90	—	22	1	21
	% frequency	59	54	—	54	14	21
O. atlantica	No./m²	1,354 (0.8) NS	1,742 (3.6) NT	1,498 (0.8) NS	2,350 (0.8) NS	1,963 (0.8) NS	2,497 (1.6)
	No./m³	18	31	27	18	14	24
	% frequency	88	88	100	57	41	76
Clausocalanus	No./m²	142 (0.1) NS	81 (0.2) NT	1,494 (0.8) NS	3,740 (1.4) NS	1,304 (1.4) NS	2,807 (1.8)
pergens	No./m³	1	1	21	27	15	21
	% frequency	41	50	80	29	43	63
Medusae	No./m²	128 (0.1) NS	540 (1.1) NT	511 (0.3)**	4,411 (1.7)*	1,927 (0.9)**	63 (<0.1)
	No./m³	4	16	10	67	33	2
	% frequency	65	85	70	97	78	50
Acartia tonsa	No./m²	4,195 (2.4) NS	435 (0.9) NT	— NS	41(<0.1) NS	—	4,264(2.7)
	No./m³	140	14	—	<1	—	132
	% frequency	71	58	—	6	—	39
Sagitta elegans	No./m²	1,006(0.6) NS	277 (0.6) NS	478(0.2)**	1,581 (0.6)**	2,850 (1.3)**	1,220 (0.8)
	No./m³	19	5	9	55	61	19
	% frequency	100	100	100	94	91	91
Polychaete larvae	No./m²	140(0.1) NS	71(0.1) NT	227 (0.1)**	2,835 (1.1)*	577 (0.3) NS	1,205 (0.8)
	No./m³	3	1	4	57	12	26
	% frequency	76	81	88	97	85	74
Total copepods	No./m²	49,149(28.3)NS	38,212(78.1) NT	89,074(46.2)*	159,725(60.0) NS	191,772 (84.6)*	96,930(61.8)
	No./m³	1,089	986	1,879	2,260	4,930	2,047
Total chaetognaths	No./m²	1,934(1.1) NS	1,721(3.5) **	797(0.4)**	2,627(1.0) NS	3,502(1.5) NS	2,393(1.5)
	No./m³	34	31	12	53	94	43
Total others	No./m²	122,617(70.6)**	8,975(18.4) NT	103,115(53.4) NS	104,226(39.1)**	31,386(13.8) NS	57,401(36.6)
	No./m³	3,441	215	1,582	2,138	733	1,662
Grand total	No./m²	173,697**	49,008 NT	194,238 NS	266,575 NS	226,313 NS	156,472
	No./m³	4,564	1,232	3,473	4,451	5,757	3,752

TABLE 4—Zooplankton taken in onshore (on) (≤50 m) and offshore (off) (>50 m) waters of the New York Bight during period 1 (September-November 1974), period 2 (February-May 1975), and period 3 (June-September 1975). Taxa within the major categories (copepods, chaetognaths, others) listed in order of decreasing overall frequency of occurrence. C = common, occurrence in >50% of samples; U = unusual, occurrence in ≤50% of samples; R = rare, occurrence in ≤3 samples.

Taxa	Period 1		Period 2		Period 3	
	On	Off	On	Off	On	Off
Copepods						
Centropages typicus	C	C	C	C	C	C
Pseudocalanus sp.[1]	C	C	C	C	C	C
Calanus finmarchicus	C	C	C	C	C	C
Oithona similis	U	U	C	C	C	C
Paracalanus parvus	C	C	U	C	C	C
O. atlantica	C	C	C	C	U	C
Temora longicornis	C	C	C	U	U	U
Metridia lucens	U	C	C	C	U	C
Clausocalanus pergens	U	C	U	C	U	C
Mecynocera clausi	U	U	U	C	U	C
Candacia armata	C	C	U	U	U	U
Calocalanus tenuis	C	C	—	U	—	C
Oncaea venusta	C	C	R	U	—	U
Pleuromamma borealis	R	U	U	C	—	U
Acartia danae	C	C	—	—	R	U
Nannocalanus minor	C	C	—	—	R	U
A. tonsa	C	U	R	—	U	U
Centropages bradyi	C	C	R	R	—	U
C. hamatus	R	—	U	U	U	U
Rhincalanus nasutus	U	C	R	U	—	R
Eucalanus sewelli	C	C	R	R	—	R
Paracalanus aculeatus	C	C	—	R	—	—
Clausocalanus furcatus	C	C	—	R	R	R
C. jobei	C	C	—	—	—	R
Corycaeus clausi	C	C	—	—	—	—
Scolecithrix danae	C	C	—	R	R	—
A. longiremis	—	—	U	U	U	U
Corycaeus speciosus	C	C	—	—	—	R
T. stylifera	C	C	—	—	—	—
C. danae	—	—	U	U	—	—
Tortanus discaudatus	—	—	U	U	U	—
Calocalanus styliremis	R	—	R	U	—	U
A. hudsonica	R	—	U	R	R	—
Oithona plumifera	C	R	—	—	—	—
R. cornutus	U	U	—	—	—	—
Oncaea mediterranea	U	U	—	—	—	—
E. pileatus	U	U	R	—	—	R
Labidocera aestiva	U	R	—	—	U	R
Aetideus armatus	—	R	—	R	—	U
Paracalanus crassirostris	R	—	—	—	U	U
Corycaeus venustus	R	U	—	R	—	R
Euchaeta marina	U	U	—	R	—	R
Undinula vulgaris	R	U	—	—	R	—
Calocalanus pavo	—	U	—	—	—	—
Ischnocalanus plumulosus	—	U	—	—	—	—
Calanus tenuicornis	R	R	—	R	R	R
O. conifera	R	U	—	—	—	—
Macrosetella gracilis	R	U	—	—	—	—
Clausocalanus parapergens	—	R	—	R	—	R
Sapphirina angusta	R	U	—	—	—	—
C. paululus	—	—	—	R	—	R
Eucalanus subtenuis	R	U	—	—	—	—
Pleuromamma robusta	—	—	—	—	—	R
Farranula gracilis	—	R	—	—	—	—
Calanus helgolandicus	R	—	—	—	R	R
Paracalanus pygmaeus	—	—	—	R	R	R
E. hyalinus	R	U	—	—	—	—
E. crassus	R	R	—	R	—	R
F. cannata	R	—	—	—	—	R
Clausocalanus lividus	—	R	—	R	—	R
Copilia mirabilis	—	R	—	—	—	—
Heterorhabdus norvegicus	—	—	—	—	—	R
H. papilliger	—	R	—	—	—	—
Clausocalanus arcuicornis	—	R	—	—	—	—
L. acutifrons	—	—	—	—	—	R
Corycaeus latus	R	R	—	—	—	—
Anomalocera opalus	—	—	—	—	R	R
Scolecithricella minor	—	—	—	—	—	R
Neocalanus gracilis	—	—	—	—	—	R
O. minuta	—	—	—	R	—	—
Clausocalanus mastigophorus	R	R	—	—	—	—
Corycaeus catus	R	—	—	—	—	—
C. elongatus	R	R	—	—	—	—
Pontella pennata	R	—	—	—	—	—
Sapphirina opalina	—	R	—	—	—	—
Lucicutia flavicornis	—	R	—	—	—	—
Calocalanus pavoninus	—	R	—	—	—	—
Scolecithricella vittata	—	R	—	—	—	—
Centropages velificatus	—	—	—	—	—	R
Paracalanus pusillus	—	—	—	—	—	R
Microsetella norvegica	R	—	—	—	—	—
Chiridius obtusifrons	—	—	—	—	—	R
Lubbockia squillimana	—	—	—	—	—	R
S. tenuiserrata	—	—	—	—	—	R
Scottocalanus securifrons	—	—	—	—	—	R
Sapphirina ovatolanceolata	—	—	—	—	—	R
P. quasimodo	—	R	—	—	—	—
Scottocalanus thomasi	—	—	—	—	—	R
Chaetognaths						
Sagitta elegans	C	C	C	C	C	C
S. serrodentata	C	C	C	C	U	C
S. enflata	C	C	R	U	R	U
Pterosagitta draco	R	U	R	—	—	R
Eukrohnia hamata	—	—	—	R	—	R
S. maxima	—	—	R	R	—	R
S. hexaptera	R	R	—	R	—	R
S. decipiens	—	R	—	—	—	R
S. hispada	—	R	—	—	—	—
E. fowleri	—	R	—	—	—	—
Others						
Pteropods	C	C	C	C	C	C
Appendicularians	C	C	C	C	C	C
Medusae	C	C	C	C	C	C
Decapod larvae	C	C	U	U	C	C
Polychaete larvae	C	C	C	C	C	C
Bivalve veligers	C	C	C	C	C	C
Euphausiid furcila stages	U	C	C	C	U	C
Gastropod veligers	—	R	C	C	C	C
Ectoproct larvae	C	C	C	C	U	U
Hyperiid amphipods	C	C	U	U	U	C
Copepod nauplii	C	C	C	C	U	U
Evadne spp	C	U	U	U	C	C
Anthozoan larvae	U	U	U	U	U	C
Euphausiid calyptopsis stages	R	C	U	C	R	C
Doliolids	C	C	—	—	C	C
Plutei	C	C	U	U	U	R
Siphonophores	C	C	R	R	U	U
Penilia avirostris	C	U	—	R	U	U
Conchoecia spp	U	C	R	U	—	U
Euphausiid nauplii	—	U	R	U	R	U
Barnacle cyprises	—	—	U	U	U	U
Heteropods	U	U	—	—	—	—
Podon spp	—	—	U	—	R	R
Salps	—	U	—	—	—	U
Barnacle nauplii	—	—	R	U	—	U
Stomatopod larvae	R	—	—	—	R	—

[1] Atlantic representatives of the genus *Pseudocalanus* are not adequately described. They are being studied by B. Frost, Department of Oceanography, University of Washington, Seattle.

warmwater oceanic distributions (Pierce 1953; Grice and Hart 1962; Jefferies 1967; Pennell 1976; Fleminger and Hulsemann 1977).

Mean Abundance, Frequency, Average Rank, and Dominance

We calculated mean abundances for various taxa and found that copepods, on the average, composed 62% of the zooplankton in our samples (Table 2). Pteropods and gastropod veligers together contributed 15% to the total, and cladocerans (*Penilia avirostris* plus *Evadne* spp.) and urochordates (doliolids and appendicularians) yielded another 10 and 6%, respectively. No other group (e.g., echinoderm plutei, medusae, polychaete larvae, chaetognaths), on the average, composed more than about 1% of the zooplankton. At the species level, *Pseudocalanus* sp. and *Centropages typicus* were codominant in 1974-75, their annual mean abundances (number/square meter) each equaling approximately 13% of the annual mean for total zooplankton. Pteropods composed another 13% of the zooplankton, and these consisted almost exclusively of one species, *Limacina retroversa* (Wormuth[4]). *Paracalanus parvus*, *Penilia avirostris*, *Calanus finmarchicus*, and *Temora longicornis* each composed between 5 and 10% of total zooplankton over the period, and several other taxa had values exceeding 1% (Table 2).

In addition to mean standing stocks and concentrations, we calculated frequency of occurrence, average rank (rank of most abundant taxon in a sample = 1), and an index of dominance (Fager and McGowan 1963) for the 20 taxa having the highest mean abundance in our samples (Table 2). These measures showed similar trends, and, in general, frequency of occurrence and dominance tended to decline and average rank to increase as mean abundance decreased. There were, however, a number of exceptions to this pattern. For instance, the highly seasonal species *P. avirostris* and *T. longicornis* had high mean abundances but disproportionately low frequency and dominance values and high average ranks. Conversely, other taxa, which were seldom abundant, nevertheless occurred frequently (e.g., *S. elegans*, *O. atlantica*, polychaete larvae, medusae).

[4]J. H. Wormuth, Department of Oceanography, Texas A&M University, College Station, pers commun. August 1978

Seasonality in Abundance

Total zooplankton in the New York Bight declined nearly fourfold in mean abundance between late summer (September) and autumn (October-November) 1974 (Table 3), primarily because of a drastic decline in the abundance of *P. avirostris* after September. In 1975, numbers of total zooplankton did not vary as greatly between seasons, and the highest mean value (April-May) differed from the lowest (August-September) by less than a factor of two. Copepods were least numerous in winter (February-March), but increased through spring (April-May) to an early summer (June-July) peak before declining in late summer (August-September). Other zooplankton combined exceeded copepods in mean abundance only during winter, and this primarily was due to the large standing stocks of the pteropod *L. retroversa* present in the Bight during that period.

We calculated mean abundances by season for the 20 taxa having the highest overall mean values in our samples (Table 2) and found that most of these taxa underwent marked and often statistically significant ($P < 0.05$) seasonal fluctuations in standing stock (Table 3). *Penilia avirostris*, doliolids, echinoderm plutei, and *Acartia tonsa* reached maximum or near maximum levels of abundance in late summer 1974 and again in late summer 1975. With the exception of echinoderm plutei, these taxa were virtually absent from our samples during the intervening winter and spring. The relatively low numbers of small copepods in 1974 may have been due to escapement through the coarse mesh (333 μm) nets used then. We found that *Paracalanus parvus*, *Pseudocalanus* sp., *O. similis*, and *Clausocalanus pergens* were significantly less abundant (paired sample *t*-test, $P < 0.05$) in collections from 60 cm diameter 333 μm mesh nets than in simultaneous samples from 20 cm diameter 253 and 223 μm mesh nets.

Only 1 taxa (*L. retroversa*) peaked in winter 1975, but 10 taxa (*Pseudocalanus* sp., *Calanus finmarchicus*, *O. similis*, *Metridia lucens*, *Clausocalanus pergens*, *Evadne* spp., appendicularians, gastropod veligers, medusae, and polychaete larvae) reached their highest levels of abundance during spring 1975. *Centropages typicus*, *T. longicornis*, and *S. elegans* attained maximum levels of abundance in early summer, and *Paracalanus parvus* peaked in late summer 1975. Among the 20 taxa listed in Table 3, *O. at-*

lontica varied the least in mean abundance during the study, showing only slight increases during spring and late summer 1975.

Onshore-Offshore Distribution

Several of the more abundant zooplankton taxa in the New York Bight showed statistically significant ($P<0.05$) differences in mean standing stocks between the onshore (<50 m) and offshore (>50 m) sectors of the region (Table 5). Taxa which on the average were significantly more abundant onshore during 1974-75 were *C. typicus, Penilia avirostris, T. longicornis, Evadne* spp., *A. tonsa,* and doliolids. Those which were significantly more abundant offshore were *Calanus finmarchicus, O. similis, O. atlantica, M. lucens,* and *Clausocalanus pergens.* Significant onshore-offshore differences on an annual basis were not observed for *Pseudocalanus* sp., pteropods, *Paracalanus parvus,* appendicularians, gastropod veligers, echinoderm plutei, medusae, and *S. elegans.* Neither total copepods nor total chaetognaths differed significantly between the two regions, but other zooplankton combined were significantly more abundant offshore (Table 5).

Substantial seasonal changes occurred in the onshore-offshore distribution of many of the aforementioned taxa (Figure 2). Certain copepod species which peaked or were otherwise very abundant in the offshore region during winter and spring were much less abundant onshore at those times. However, during the summer, onshore stocks of these species increased to levels approaching those in offshore waters. Species exhibiting this pattern were *M. lucens, C. pergens, O. atlantica, Calanus finmarchicus,* and *P. parvus* (Figure 2). Several other taxa which reached maximum levels of abundance during the spring tended to be equally abundant onshore and offshore during most times of the year. This group of ubiquitously abundant taxa included *Pseudocalanus* sp., *O. similis, S. elegans,* medusae, appendicularians, pteropods, gastropod veligers, and polychaete larvae (Figure 2). Doliolids and the coastal-estuarine species *Penilia avirostris, T. longicornis,* and *A. tonsa* all peaked in the onshore environment during summer or autumn and were seldom, if ever, abundant offshore (Figure 2). Although *Centropages typicus* also reached its highest levels of abundance onshore during the summer, it was usually abundant offshore as well, especially during March and April (Figure 2). Echinoderm plutei peaked in onshore waters during autumn 1974 but also exhibited a secondary offshore peak during spring 1975 (Figure 2). *Evadne* spp. exhibited maxima in both the onshore and offshore environments during spring and summer 1975 but were abundant only onshore during autumn 1975 (Figure 2).

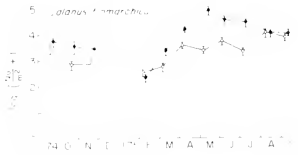
Zooplankton Maxima, Phytoplankton Blooms, and Temperature

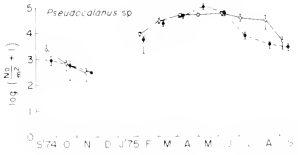
We observed distinct peaks in zooplankton abundance in both onshore and offshore environments in 1975 (Figure 3). In the offshore region, there were two maxima, in March and May. The March peak was dominated by *L. retroversa* which composed nearly 60% of all offshore zooplankton during that month. The remaining 40% of offshore zooplankton in March was composed primarily of the copepods *Pseudocalanus* sp., *O. similis, Paracalanus parvus,* and *M. lucens.* The May maximum was dominated by *Pseudocalanus* sp., *Calanus finmarchicus,* and *O. similis,* and these species tended to be most abundant over the outer shelf at the eastern end of the study area (e.g., stations F3, F5, G2, G4). The March pteropod-dominated maximum occurred similtaneously with the beginning of the spring phytoplankton bloom when chlorophyll *a* standing stock biomass (milligrams/square meters) was high (Figure 3) and discrete depth chlorophyll *a* concentrations exceeded 4 μg/l throughout the water column at virtually all stations. However, during May when copepods peaked in abundance offshore, the phytoplankton bloom was in decline (Figure 3). In the offshore region, water temperatures in the upper 20 m remained low ($\leq 10^{\circ}$ C) through May.

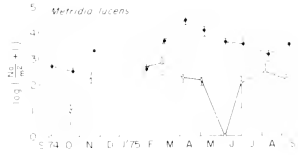
We observed a single peak in zooplankton abundance in the onshore environment during 1975 (Figure 3). This peak occurred in July and was the result of marked increases in the abundance of *Centropages typicus* and *T. longicornis.* In July, these two species constituted about 67% of all onshore zooplankton and were especially abundant at stations near the apex of the Bight and off the New Jersey coast (e.g., A2, A4, B3, B5). The early summer rise in *C. typicus* and *T. longicornis* stocks occurred during a period when surface water temperatures rose from about 10° to 20° C but when onshore chlorophyll *a* biomass was low (Figure 3). At other times during this study various other taxa were dominant onshore, e.g., *Penilia*

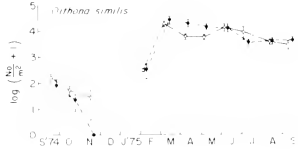
TABLE 5.—Onshore-offshore variations in mean abundance (no./m² and no./m³) and frequency of occurrence (%) of samples) of the 20 most abundant zooplankton taxa in the New York Bight, 1975, listed in order of overall mean abundance. Onshore: depth < 50 m, offshore: depth ≥ 50 m. Values in parenthesis after no./m² values are percents of total zooplankton. Asterisks indicate significant differences (Fisher-Behrens test, Campbell 1967) in mean no./m² between onshore and offshore (* = $P < 0.05$, ** = $P < 0.01$, NS = not significant).

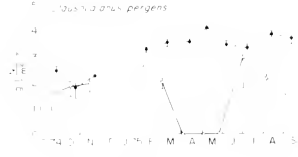
		Onshore	Offshore
No. samples (chaetognaths)		100	78
No. samples (copepods, others)		99	84
Taxa	Item		
Pseudocalanus sp.	No./m²	26 308(13.1) NS	24 691(14.9)
	No./m³	713	295
	% frequency	91	92
Pteropods	No./m²	21 487(10.7) NS	30 298(18.2)
	No./m³	564	379
	% frequency	99	98
Centropages typicus	No./m²	35 637(17.8)**	12 759(7.7)
	No./m³	1 071	165
	% frequency	98	96
Paracalanus parvus	No./m²	14 668(7.3) NS	16 136(9.7)
	No./m³	400	208
	% frequency	67	89
Pemilia avirostris	No./m²	26 829(13.4)**	217(0.1)
	No./m³	636	4
	% frequency	31	24
Temora longicornis	No./m²	20 455(10.2)**	651(0.4)
	No./m³	681	9
	% frequency	76	43
Calanus finmarchicus	No./m²	3 604(1.8)**	20,251(12.2)
	No./m³	82	220
	% frequency	85	98
Oithona similis	No./m²	5 415(2.7)**	11 686(7.0)
	No./m³	151	140
	% frequency	85	77
Appendicularians	No./m²	6 576(3.2) NS	7 666(4.6)
	No./m³	157	89
	% frequency	80	88
Gastropod veligers	No./m²	6 556(3.2) NS	2 804(1.7)
	No./m³	173	41
	% frequency	58	65
Evadne spp.	No./m²	5 891(2.9)**	1 557(0.9)
	No./m³	149	22
	% frequency	49	41
Doliolids	No./m²	6 497(3.2)*	185(0.1)
	No./m³	165	2
	% frequency	29	34
Metridia lucens	No./m²	178(0.1)**	5 232(0.3
	No./m³	4	41
	% frequency	37	83
Pluteı	No./m²	3 591(1.7) NS	680(0.4)
	No./m³	86	9
	% frequency	35	25
O. atlantica	No./m²	564(0.3)**	3 646(2.2)
	No./m³	13	31
	% frequency	57	90
Clausocalanus pergens	No./m²	161(0.1)**	3 777(2.3)
	No./m³	4	31
	% frequency	28	78
Medusae	No./m²	1 454(0.7) NS	1,378(0.8)
	No./m³	35	19
	% frequency	76	73
Acartia tonsa	No./m²	2 432(1.2)*	63(0.1)
	No./m³	78	1
	% frequency	35	11
Sagitta elegans	No./m²	1 407(0.7) NS	1,187(0.7)
	No./m³	34	17
	% frequency	95	96
Polychaete larvae	No./m²	989(0.5) NS	946(0.3)
	No./m³	26	13
	% frequency	65	68
Total copepods	No./m²	115,284(57.7) NS	113 104(68.2)
	No./m³	3,358	1 284
Total chaetognaths	No./m²	2 175(1.1) NS	2 282(1.4)
	No./m³	52	32
Total others	No./m²	82 510(41.3)*	50 396(30.4)
	No./m³	2,663	626
Grand total	No./m²	119 943 NS	165 590
	No./m³	6 073	1 942

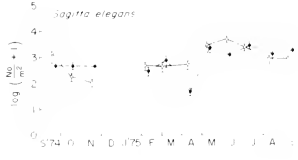

Calanus finmarchicus
log (N/m² + 1)
S '74 O N D J '75 F M A M J J A S


Pseudocalanus sp.
log (N/m² + 1)
S '74 O N D J '75 F M A M J J A S


Metridia lucens
log (N/m² + 1)
S '74 O N D J '75 F M A M J J A S


Oithona similis
log (N/m² + 1)
S '74 O N D J '75 F M A M J J A S

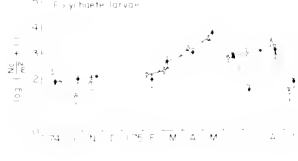

Oithona atlantica
log (N/m² + 1)


Sagitta elegans
log (N/m² + 1)


log (N/m² + 1)


Pteropods
log (N/m² + 1)


log (N/m² + 1)


log (N/m² + 1)

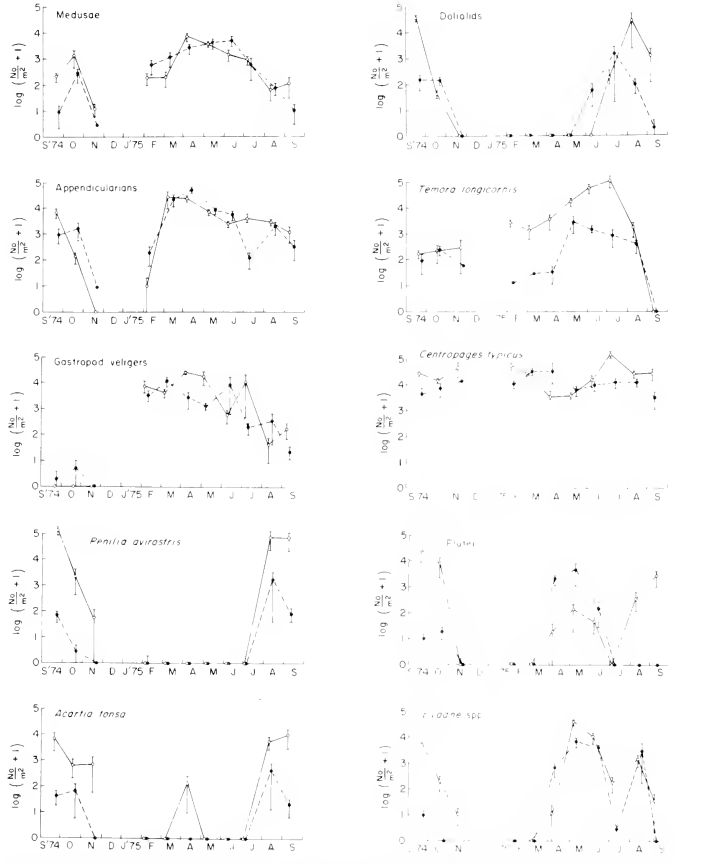


FIGURE 2.—Onshore (< 50 m) and offshore (> 50 m) monthly mean abundances of 20 most abundant zooplankton taxa in the New York Bight, September 1974-September 1975. Circles = onshore means, dots = offshore means, vertical bars = 1 SE above and below mean.

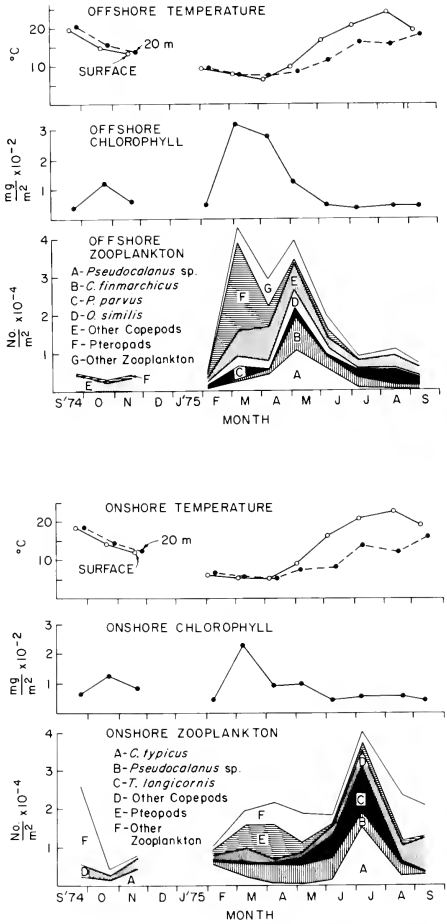


FIGURE 3.—Onshore (< 50 m) and offshore (>50 m) monthly means for temperature at surface and 20 m, chlorophyll *a* integrated water column biomass, and zooplankton abundance (showing cumulative contribution of dominant taxa) in the New York Bight, September 1974-September 1975.

avirostris (September 1974), *L. retroversa* (March, April), *Pseudocalanus* sp. (May), and *Paracalanus parvus* (August, September 1975).

DISCUSSION

Previous zooplankton studies in the New York Bight have been based on relatively few samples, usually taken from a restricted area over a limited period of time (cf. review in Malone 1977). Grice and Hart's (1962) study is closest to ours in taxonomic coverage, net mesh size, geography, and quantitative analysis. They collected a total of 14 samples with vertically hauled 230 μm mesh nets from New York Bight shelf waters on cruises in September and December 1959 and March and July 1960. These samples were part of a larger study of zooplankton along a transect between Montauk, N.Y., on eastern Long Island and Bermuda. Comparison of mean concentrations of several abundant species of copepods in their samples (table 4, Grice and Hart 1962) with our mean concentration values (Table 2) is informative. The eight most abundant copepods during 1959-60 (in order of decreasing abundance: *Pseudocalanus* sp., *C. typicus, O. similis, T. longicornis, Paracalanus parvus, Calanus finmarchicus, M. lucens, Candacia armata)* correspond closely with the eight most abundant species in 1974-75 (*Centropages typicus*, *Pseudocalanus* sp., *T. longicornis*, *Paracalanus parvus*, *Calanus finmarchicus*, *O. similis, Acartia tonsa, O. atlantica)*. Furthermore, the mean densities of the two most abundant copepods in both studies, *Centropages typicus* and *Pseudocalanus* sp., were very similar for both species during the two periods (i.e., the mean density of *C. typicus* was 450/m^3 in 1959-60 and 650/m^3 in 1974-75; the mean density of *Pseudocalanus* sp. was 560/m^3 in 1959-60 and 520/m^3 in 1974-75). This comparison suggests that zooplankton in the New York Bight had not changed substantially in the 15 yr between the two studies. The degree of similarity is somewhat surprising in view of the evidence that considerable year-to-year variations may occur in the timing, duration, and amplitude of abundance maxima in important zooplankton taxa (Bigelow and Sears 1939; Sears and Clarke 1940).

Grice and Hart (1962) observed an influx of warmwater oceanic species into the New York Bight in September 1959, and this is similar to the high incidence of subtropical-tropical species in autumn 1974 and summer 1975. This apparently annual phenomenon is probably associated with intrusions of the Gulf Stream over the continental slope which occur most frequently during the warm seasons (Wright 1976; Bowman 1977). Our hydrographic data reveal the occurrence of salinities (≥36‰) characteristic of Gulf Stream water (Wright 1976) in the slope region during September 1974, and in June, August, and September 1975 (Figure 4), and the National Environmental Satellite photos show Gulf Stream water impinging along the outer edge of the study area in August 1974 and in May, July, and August 1975.

A shoreward increase in the abundance of several common offshore copepods (e.g., *Calanus finmarchicus, O. atlantica, Clausocalanus pergens, M. lucens*) also occurred during warm portions of the year. This onshore increase in abundance of common forms and the frequent occurrence over the shelf of less common oceanic species are probably the result of shoreward mixing of slope water with shelf water. Slope water is thought to move onshore along isopycnals during late summer and autumn (Wright and Parker 1976; Gordon et al. 1977), and during September 1974 we observed slope water (35‰ ≤salinity <36‰, Wright 1976) on the shelf (Figure 4).

Limacina retroversa, Pseudocalanus sp., *O. similis*, and *Calanus finmarchicus*, the species responsible for zooplankton abundance maxima in the New York Bight during spring 1975, are low-temperature forms whose distributions are centered north of the region (Fish 1936a, b, c; Redfield 1939; Bigelow and Sears 1939; Fleminger and Hulsemann 1977). Their geographical distribu-

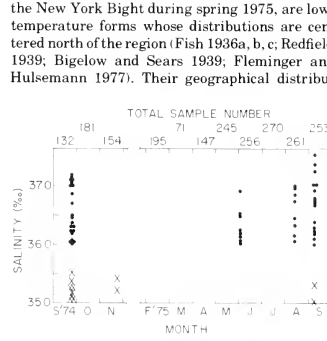


FIGURE 4.—Occurrences of Gulf Stream water (salinity ≥36‰) over slope (≥100 m), and of slope water (35‰< salinity <36‰) over the shelf in the New York Bight, September 1974-September 1975. Dots = Gulf Stream salinities over slope; × = slope salinities over shelf.

tions and the generally southward flow along this sector of the shelf (Bumpus 1973) suggest that a high proportion of individuals occurring in the Bight are advected into the region from the northeast. Irrespective of the origin of these populations, it can be assumed that they were major consumers of the spring phytoplankton bloom in 1975.

Centropages typicus and *Temora longicornis* are warm temperate species (Fleminger 1975), and their abundance in the New York Bight appears to be strongly influenced by temperature. Lawson (1969) found that *C. typicus* eggs failed to hatch when maintained at 5°-6° C, the prevailing water temperature in February through May (Figure 3), and Bigelow and Sears (1939) reported a northward seasonal shift in abundance of *C. typicus* beginning in the Chesapeake Bay-Delaware Bay region in the spring, progressing to the New York area in July, and finally reaching coastal waters off New England in autumn. The geographical distribution of *T. longicornis* corresponds closely to that of *C. typicus* (Fleminger 1975), and it is likely that it exhibits similar seasonal trends in abundance. In the New York Bight in 1975, *C. typicus* and *T. longicornis* increased in abundance from April to July as water temperature rose from about 5° to 20° C (Figure 3). These species appear to be especially well adapted for exploitation of coastal environments where high food levels persist into the warm season. Their peak abundances in 1975 occurred in or near the apex of the Bight where primary production in July can exceed 1-3 g C/m^2 per day (Malone 1976).

ACKNOWLEDGMENTS

We thank the numerous people at the Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, who participated in the survey, especially A. Kendall for his cooperation in adding smaller mesh nets to the original sampling array and for providing hydrographic data. We are grateful to E. Schwarting, S. Hoerscher, P. Pepe, R. Hautsch and especially D. Ninivaggi at the Brookhaven National Laboratory (BNL) for assistance in analysis of the zooplankton. Thanks also go to numerous individuals from BNL and the Marine Sciences Research Center, State University of New York, Stony Brook, for assistance in collecting and processing chlorophyll samples on survey cruises, to J. Wartha, Environmental Products Group, National Environmental Satellite Service, NOAA, for providing Gulf Stream analyses cited in the study, and to A. Fleminger, Scripps Insitution of Oceanography, for identifying specimens of *Calanus helgolandicus*. A. Kendall, S. Smith (BNL), and M. Dagg (BNL) offered helpful suggestions towards improvement of the manuscript. This research was supported by the U.S. Department of Energy under contract no. EY-76-C-02-0016.

LITERATURE CITED

BIGELOW, H. B., AND M. SEARS
1939. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Mus. Comp. Zool., Har. Univ. 54:179-378.

BOWMAN, M. J.
1977. Hydrographic properties. MESA New York Bight Atlas Monogr. 1. N.Y. Sea Grant Inst., Albany, 78 p.

BOWMAN, T. E.
1971. The distribution of calanoid copepods off the southeastern United States between Cape Hatteras and southern Florida. Smithson. Contrib. Zool. 96, 58 p.

BUMPUS, D. F.
1973. A description of the circulation of the continental shelf of the east coast of the United States. Prog. Oceanogr. 6:111-157.

CAMPBELL, R. C.
1967. Statistics for biologists. Camb. Univ. Press, Camb., 242 p.

FAGER, E. W., AND J. A. MCGOWAN.
1963. Zooplankton species groups in the North Pacific. Science (Wash., D.C.) 140:453-460.

FISH, C. J.
1936a. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. Biol. Bull. (Woods Hole) 70:118-141.
1936b. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. Biol. Bull. (Woods Hole) 70:193-216.
1936c. The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. Biol. Bull. (Woods Hole) 71:168-187.

FLEMINGER, A.
1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. *In* L. E. Cronin (editor), Estuarine research. Vol. 1. Chemistry, biology, and the estuarine system, p. 392-419. Acad. Press, N.Y.

FLEMINGER, A., AND K. HULSEMANN.
1977. Geographical range and taxonomic divergence in North Atlantic *Calanus* (*C. helgolandicus*, *C. finmarchicus* and *C. glacialis*). Mar. Biol. (Berl.) 40:233-248.

GORDON, A. L., A. F. AMOS, AND R. D. GERARD.
1976. New York Bight water stratification—October 1974. *In* M. G. Gross (editor), Middle Atlantic Continental Shelf and the New York Bight, p. 45-57. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2.

GRICE, G. D., AND A. D. HART.
1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287-309.

GROSS, M. G., R. L. SWANSON, AND H. M. STANFORD.
1976. Man's impact on the middle Atlantic continental shelf and the New York Bight—symposium summary. *In* M. G. Gross (editor), Middle Atlantic Continental Shelf and the New York Bight, p. 1-13. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2.

JEFFRIES, H. P.
1967. Saturation of estuarine zooplankton by congeneric associates. *In* G. H. Lauff (editor), Estuaries, p. 500-508. Publ. 83, Am. Assoc. Adv. Sci., Wash. D.C.

LAWSON, T. J., JR.
1969. *Centropages typicus*, Krøyer 1847 (Copepoda: Calanoida), its developmental stages and factors affecting its distribution. M.A. Thesis, Univ. North Carolina, Chapel Hill, 41 p.

MALONE, T. C.
1976. Phytoplankton productivity in the apex of the New York Bight: Environmental regulation of productivity/chlorophyll *a*. *In* M. G. Gross (editor), Middle Atlantic Continental Shelf and the New York Bight, p. 260-272. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2.
1977. Plankton systematics and distribution. MESA New York Bight Atlas Monogr. 13. N.Y. Sea Grant Institute, Albany, 45 p.

OWRE, H. B., AND M. FOYO.
1967. Copepods of the Florida Current. Fauna Caribbaea, Number 1. Crustacea, Part 1. Copepoda, 137 p.

PENNELL, W. M.
1976. Description of a new species of pontellid copepod, *Anomalocera opalus*, from the Gulf of St. Lawrence and shelf waters of the Northwest Atlantic Ocean. Can. J. Zool. 54:1664-1668.

PETERSON, W. T., AND C. B. MILLER.
1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon Coast. Fish. Bull., U.S. 75:717-724.

PIERCE, E. L.
1953. The Chaetognatha over the continental shelf of North Carolina with attention to their relation to the hydrography of the area. J. Mar. Res. 12:75-92.

REDFIELD, A. C.
1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. Biol. Bull. (Woods Hole) 76:26-47.

SEARS, M., AND G. L. CLARKE.
1940. Annual fluctuations in the abundance of marine zooplankton. Biol. Bull. (Woods Hole) 79:321-328.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

WRIGHT, W. R.
1976. The limits of shelf water south of Cape Cod, 1941 to 1972. J. Mar. Res. 34:1-14.

WRIGHT, W. R., AND C. E. PARKER.
1976. A volumetric temperature/salinity census for the Middle Atlantic Bight. Limnol. Oceanogr. 21:563-571.

DISTRIBUTION AND CATCH COMPOSITION OF JONAH CRAB, *CANCER BOREALIS*, AND ROCK CRAB, *CANCER IRRORATUS*, NEAR BOOTHBAY HARBOR, MAINE[1]

JAY S. KROUSE[2]

ABSTRACT

An analysis of research and commercial catch data of Jonah crab, *Cancer borealis*, and rock crab, *C. irroratus*, collected near Boothbay Harbor, Maine, revealed dissimilarities in the distribution of the two species. Jonah crabs were more numerous at the deeper, seaward sampling sites with rocky substrates, while rock crabs were more abundant on soft mud bottoms of the shallower estuarine stations. Distribution of both species is dependent upon the environmental factors of temperature, depth, and substrate type. Absence of Jonah crabs <67 mm carapace width in all collections, indicates that, unlike the rock crab, the nursery areas of the Jonah crab are not in nearshore waters. Sex ratios varied seasonally and spatially for rock crabs and seasonally for Jonah crabs. These variations seem to be related to changes in local abundance as the result of movement in association with the reproductive and molting cycles.

Jonah crab, *Cancer borealis*, and rock crab, *C. irroratus*, make up a small but increasingly important commercial fishery along the Maine coast. Since 1966, the price per pound of crabs paid to the fisherman has increased from 4¢ to 12¢ (Figure 1). As a result the Maine lobstermen have been selling their incidental catches of crabs to offset increasing operational costs (bait, fuel, etc.). In view of the current retail price of American lobster, *Homarus americanus*, which often exceeds $3.00/lb, the value of the very palatable crab may be expected to continue to increase. In fact, some dealers are now paying 20¢ to 25¢/lb for crab.

Despite the present economic value (reported 1977 landed value was $142,106) of Maine's crab fishery and its potential for future growth, there is little information on the biology of either of the cancrid crabs. While several investigators have studied various aspects of the life history of *C. irroratus*, very little work has been done on *C. borealis* other than by Haefner (1977) and Carpenter (1978) on the distribution and biology of *C. boreolis* on the continental shelf of the Mid-Atlantic Bight and by Sastry (1977) on the larval development of *C. borealis*.

To supplement these studies, I have: 1) examined the size and sex composition and distribution of Jonah crabs in commercial and research catches in Maine waters; 2) described the width-weight relationship of the Jonah crab; and 3) compared the distribution, size, and sex composition of Jonah and rock crabs from commercial and research catches.

METHODS

Jonah crabs were caught incidental to the lobster sampling program of the Maine Department of Marine Resources during which vinyl-coated wire (2.54 × 2.54 cm mesh) and conventional wooden lobster traps were fished at nine locations (Figure 2) near Boothbay Harbor, Maine, from July 1968 to December 1974.

At the time of capture, each crab was sexed and measured. Carapace width (CW), distance between the two outermost notches on the anterolateral border of the carapace, was recorded to the nearest millimeter.

Width-weight relations were calculated for 110 male (89-160 mm CW) and 90 female (96-131 mm) Jonah crabs caught by commercial fishermen near Boothbay Harbor, 1973 through 1976. Wet weights were recorded to the nearest 10 g. Linear regression of weight on carapace width was fitted by the method of least squares to logarithmically (base 10) transformed data, and analysis of covariance was used to evaluate the regression coefficients of males and females for differences.

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 5314.

[2]Maine Department of Marine Resources, West Boothbay Harbor, ME 04575

Manuscript accepted April 1979
FISHERY BULLETIN VOL. 77, NO. 3, 1980

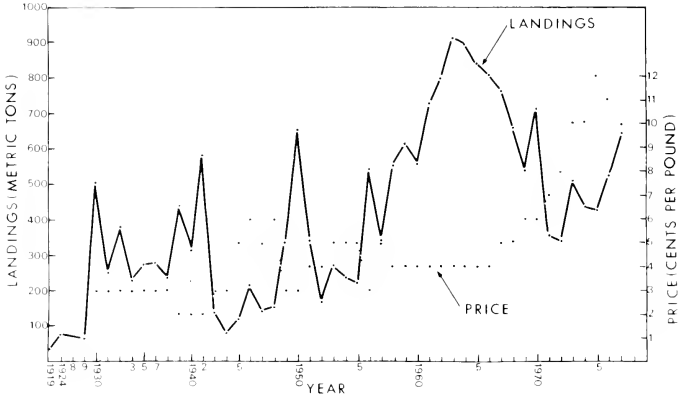


FIGURE 1.—Catch and ex-vessel price of Jonah and rock crabs (species combined) landed in Maine, 1919-77.

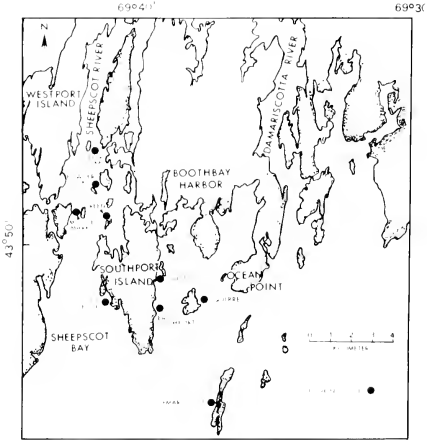


FIGURE 2.—Boothbay Harbor region and location of sampling sites.

Additional commercial catch data were provided by Joel Cowger, Maine Department of Marine Resources, West Boothbay Harbor, Maine, who obtained measurements of 299 commercially caught Jonah crabs from the Maine coast (September 1977-March 1978). Carapace widths were measured between the tips of the outermost anterolateral spines. These long carapace width measurements can be converted to short carapace width (distance between notches) by the linear regression $Y = -1.669 + 0.973X$ where Y = short CW and X = long CW (Carpenter 1978).

RESULTS AND DISCUSSION

Size Composition

Jonah crabs captured with research traps (mean 104.8 mm CW for females and 113.7 mm for males) were significantly smaller (t-test, $P<0.01$) than those crabs commercially landed at either Boothbay Harbor (mean 114.0 mm CW for females and 128.6 mm for males) or at other Maine ports (mean 114.0 mm CW for females and 141.1 mm for males) (Figures 3-5). At first it was thought that disparities in size composition might be associated to variations in selectivity of the research and commercial gear for crabs <95 mm CW; however, since similar proportions of small crabs appeared in both the research and commercial catches (Figures 3-5), the effects of gear selectivity must be minimal. The near total absence of crabs <95 mm CW in the commercial catch from Boothbay Harbor (Figure 4) was the result of fishermen discarding the smaller crabs before their landed catches were measured; whereas, the catches shown in Figures 3 and 5, which were measured at sea, included all crabs caught. Thus, I attribute these size disparities to spatial variations in the distribution of different size crabs. For instance, research traps were fished at depths of 3-20 m, whereas, most commercial traps were fished at depths of 12-91 m. In support of this contention, different size groups of Jonah crabs have been observed to be distributed within the Mid-Atlantic Bight according to depth (Haefner 1977; Carpenter 1978).

Male Jonah crabs averaged larger than females in all catches (Figures 3-5); similarly, male rock crabs generally averaged larger than females (Krouse 1972). Unlike female rock crabs, which have no commercial value because of their small size (rarely >100 mm CW, Krouse 1972), female Jonah crabs, which approximate the size of male rock crabs, are commercially harvested along with male Jonah crabs.

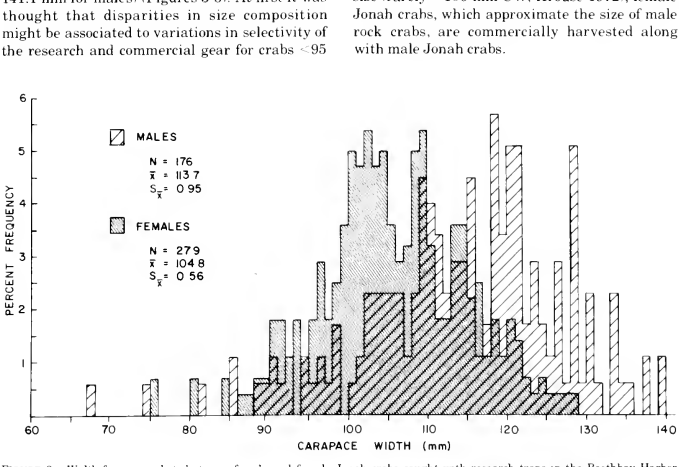


FIGURE 3.—Width-frequency distributions of male and female Jonah crabs caught with research traps in the Boothbay Harbor region, 1968-74

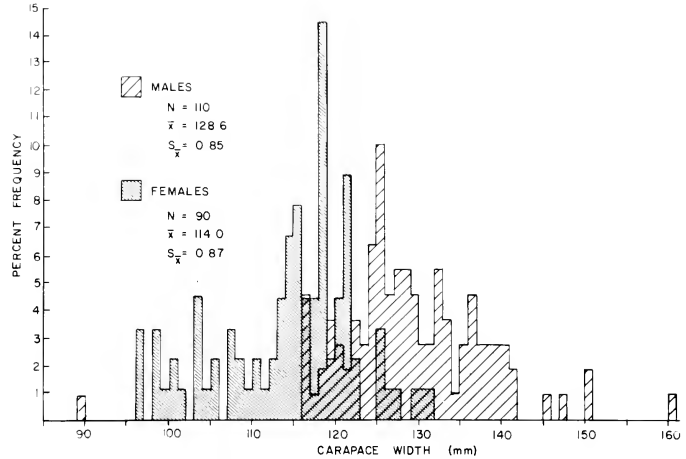


FIGURE 4.—Width-frequency distributions of male and female Jonah crabs caught by commercial fishermen in the Boothbay Harbor region, 1973-76.

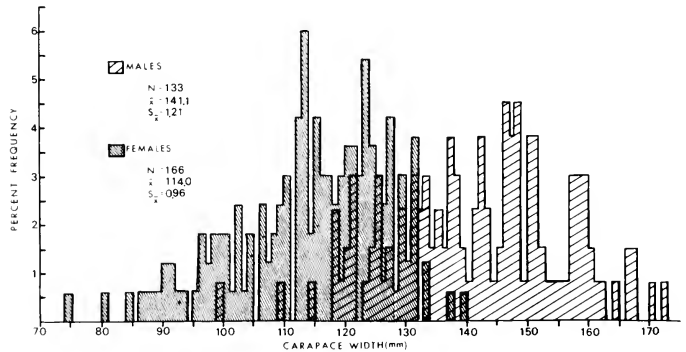


FIGURE 5.—Width-frequency distributions of male and female Jonah crabs caught by commercial fishermen at various locations along the Maine coast, 1977-78

The total commercial and research catch of 954 Jonah crabs included only 27 (2.8%) individuals 90 mm. This might be related to gear selectivity, but this explanation loses credibility given that numerous rock crabs (equivalent catchability to Jonah crab) from 40 to 60 mm CW have been sampled previously with conventional and modified lobster traps (Krouse 1976). Moreover, the fact that no Jonah crabs 67 mm CW were observed while hand-collecting 2,426 rock crabs (mean 23.9 mm CW) during a 3-yr intertidal study (Krouse 1976) or hauling research gear over a 9-yr period (juvenile rock crabs were frequently seen in traps) is evidence that small Jonah crabs in Maine waters, unlike juvenile rock crabs, inhabit deeper water exclusively. In the Mid-Atlantic Bight, Carpenter (1978) reported that Jonah crabs <30 mm CW were most abundant in depths 150 m, while Haefner (1976) found crabs 40 mm CW to be most numerous between 75 and 150 m. Both investigators noted that the maximum abundance of the larger crabs (40 mm) occured in the 150-400 m strata.

Distribution

From July 1968 through 1974, 459 Jonah crabs were captured in 7,055 trap hauls (0.07 crab/trap haul) with research gear fished near Boothbay Harbor (Table 1). Fluctuations in the catch in association with temporal and spatial variations in fishing effort were assessed by plotting mean monthly values of catch in numbers per trap haul (catch per unit of effort, CPUE) for each fishing area (Figure 6). In areas with relatively high CPUE (average >0.1), catches gradually increased throughout the summer, peaked in the fall, and then diminished rapidly. Because most crabs in the research catch were at least two molt increments larger than the lower size limit of the gear's selectivity range, the seasonal rise in CPUE may be explained by recruits migrating into the fishing areas. Conversely, the decline in CPUE in winter may be attributed to the effects of fishing mortality as well as emigration. Jonah crabs have been reported by Jeffries (1966) to move into the warmer waters of Narragansett Bay, R.I., from spring through fall, followed in winter by a movement to deeper, relatively warmer waters as inshore water temperature declined. The closely re-

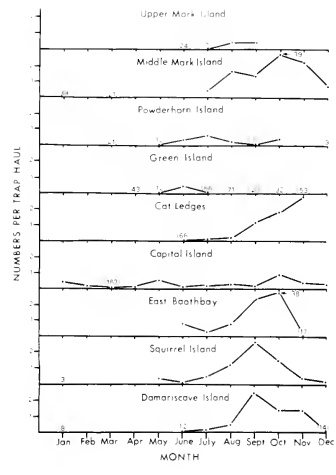


FIGURE 6.—Monthly catch per unit of effort values for Jonah crabs collected at various stations in the Boothbay Harbor region, 1968-74. Number of trap hauls are in parentheses. Catch per unit of effort outliers are marked by arrows.

TABLE 1.—Trap catch-effort values of Jonah and rock crabs caught in research traps at various stations near Boothbay Harbor, Maine, 1968-74

Area	Depth range (m)	Substrate	Hauls	Jonah crab: Total no. caught	Jonah crab: No. per haul	Rock crab: Total no. caught	Rock crab: No. per haul
Upper Mark Island	5-15	Mud	157	5	0.03	645	4.11
Powderhorn Island	3-10	Mud	271	8	0.03	2,062	7.61
Green Island	3-10	Mud	396	4	0.01	1,025	2.59
Middle Mark Island	10-20	Mud-rock outcroppings	522	65	0.12	671	1.29
Cat Ledges	5-15	Sand-bedrock	656	41	0.06	660	1.01
Capitol Island	5-15	Mud	2,794	75	0.03	4,869	1.74
East Southport	5-15	Mud-rock outcroppings	253	30	0.12	318	1.26
Squirrel Island	5-20	Mud-rock outcroppings	1,267	149	0.12	2,674	2.11
Damariscove Island	5-20	Sand-bedrock	739	82	0.11	535	0.72
Total	3-20		7,055	459	0.07	13,459	1.91

lated European edible crab, *C. pagurus*, have also been observed to undertake similar seasonal movements off the coast of England (Brown[3]). Limited population movements of Jonah crabs has also been suggested by Haefner (1977).

Although Jonah crabs were caught at each station, their relative abundance varied markedly by area as reflected by CPUE values which ranged from 0.01 to 0.12 (Table 1). Jonah crabs were more numerous at the generally deeper, more seaward stations (East Southport, Squirrel Island, and Damariscove Island) characterized by rocky substrates and within the Sheepscot River at Middle Mark Island where the fishing area borders relatively deep water (45 m) and the bottom is hard-packed mud interspersed with rock outcroppings. Conversely, Jonah crabs were sparsely distributed at the other stations in the Sheepscot estuary (Upper Mark Island, Green Island, and Powderhorn Island) which in contrast to Middle Mark Island are quite shallow with soft mud bottoms. Thus, the data indicate that the distribution and abundance of Jonah crabs reflects bottom type as well as depth.

Comparisons of CPUE for rock crabs with those for Jonah crabs at different sampling sites revealed an inverse relationship (Table 1). Rock crabs were very abundant at those stations within the Sheepscot River (CPUE: 2.6-7.6) where Jonah crabs were scarce; whereas, at other areas where Jonah crabs were more plentiful rock crabs were less common (CPUE: 0.7-2.1). Based on these observations, rock crabs seem to prefer inshore areas with mud bottoms while Jonah crabs favor seaward locations with rocky substrates. This agrees with Jeffries' (1966) findings that the same two cancrid crabs are separated spatially in Narragansett Bay according to bottom type: rock and Jonah crabs inhabit sand and rock substrates, respectively. Interestingly, in the more northern latitudes, juvenile rock crabs, unlike the adults, show preference for coarse, rocky bottoms (Scarratt and Lowe 1972; Krouse 1972; Reilly and Saila 1978), where protection from predators would be optimum.

Distribution of both cancrid crabs is not only related to substrate type and depth, but is also dependent upon water temperature. For example, in the mid-Atlantic region, Carpenter (1978) found Jonah crabs at temperatures from 5° to 15° C with maximum abundance between 6° and 12° C. Similarly, Haefner (1977) reported Jonah crabs to be most numerous in the temperature range of 8°-14° C. The more eurythermal rock crabs have been observed to be widely distributed over the continental shelf of the Mid-Atlantic Bight and most abundant inshore particularly during winter when temperatures are lowest (as low as 2° C) (Musick and McEachran 1972; Haefner 1976). In Chesapeake Bay rock crab abundance increases markedly in winter (2°-8° C) and declines in spring as temperatures warm (Shotton 1973; Terretta 1973). In view of these data, the distribution of the two cancrid crabs along the Maine coast may be further examined in relation to temperature. Rock crabs have been found to be most abundant in shallow nearshore waters where temperatures may vary from near 0° C in winter to 18° C in summer (Welch[4]); whereas, Jonah crabs are more numerous at greater depths where temperatures are more stable. Likewise, in the Gulf of St. Lawrence where the temperature regime is great (−2° to 20° C [Lauzier and Hull[5]]), rock crabs are common and Jonah crabs are nonexistent (Squires 1966; Scarratt and Lowe 1972).

Thus, it appears that the distribution of these congeneric species in the northern part of their range is dependent upon substrate, depth, and temperature.

Sex Ratios

Initially, I examined ratios of male to female Jonah crabs in monthly catches at each fishing site; however, due to the small sample sizes for several of the groups, area catches were combined by month (Table 2). The chi-square test, which was used only when the monthly N was >10, indicated that July through September ratios deviated significantly ($P < 0.05$) from 1:1. Males dominated in July while during August and September there was a preponderance of females. This shift in sex ratios may be attributed to an apparent movement of female crabs into warmer shoal water during summer and early fall as the result of behavior associated with molting and copulating. The closely related Dungeness crab, *C. magister*, and

[3]Brown, G. G. 1975. Norfolk crab investigations 1969-73: Lab Leafl. 30, 12 p. Fish. Lab., Lowestoft, Suffolk, England.

[4]W. R. Welch, Marine Resources Scientist, Maine Department of Marine Resources, West Boothbay Harbor, ME 04575, pers. commun. February 1979.

[5]Lauzier, L. M., and J. H. Hull. 1969. Coastal station data: temperatures along the Canadian Atlantic coast 1921-1969. Fish. Res. Board Can. Tech. Rep. 150, 25 p.

TABLE 2.—Monthly captures and sex ratios of Jonah crabs caught with research traps, 1968-74. Asterisks denote significant deviation from 1:1 (chi-square).

Month	♂	♀	Ratio (♂:♀)	Month	♂	♀	Ratio (♂:♀)
Dec.-Apr.	10	4	2.5 1NS	Aug.	39	81	1:2.1**
May	7	3	2.3 1NS	Sept.	38	117	1:3.1**
June	8	2	4 1NS	Oct.	44	45	1.1NS
July	24	7	3.4:1*	Nov.	11	19	1:1.7NS

NS = not significant
* = $P = 0.05$
** = $P = 0.01$

European edible crab have been reported to move inshore in spring and offshore in fall (Dewberry 1956; Hoopes 1973; Brown see footnote 3). In fact, mature female European edible crabs have been observed to move considerable distances (>225 km) along the coast of England (Brown see footnote 3).

Sex ratios of rock crabs caught with research gear varied not only by season but also by area (Figure 7). From July through September females generally outnumbered males, throughout the fall many of the sex ratios approximated a 1:1 relation, and then in winter males were dominant except in the upper Sheepscot River where they predominated only in May. Similar to Jonah crabs, seasonal variations in rock crab sex ratios may best be explained by changes in the crabs' availability and vulnerability to the research traps in association with shedding and mating behavior. For instance, peak catches of females during summer and early fall coincided with egg hatching (summer) and molting (fall) in Maine waters (Krouse 1972).

Higher proportions of male rock crabs in winter and spring catches may be attributed to: 1) recruitment of males as the result of winter-spring shedding (Krouse 1972) and, possibly, inshore movement (Haefner [1976] suggested that male rock crabs in the Mid-Atlantic Bight undertake seasonal inshore-offshore migrations); 2) increased feeding activity of newly molted crabs; and 3) a reduction in the availability and vulnerability of females during the winter spawning period (Dewberry [1956] noted that ovigerous female *C. pagurus* consume little food). Throughout summer the number of male rock crabs, particularly those >90 mm CW, diminished due to fishing mortality and, perhaps, an offshore movement.

The upper Sheepscot River sites, unlike the other locations, had a preponderance of females during fall and winter, yet in spring, similar to other areas, males were more numerous (Figure 7). Perhaps this relatively high abundance of

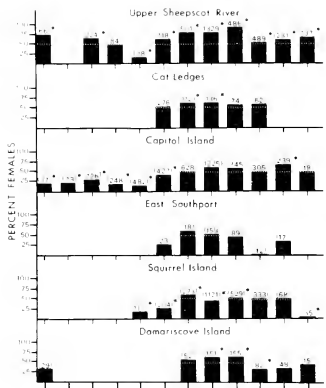


FIGURE 7.—Monthly percent frequencies of female rock crabs caught by research traps at different locations in the Boothbay region, 1968-74. Numbers in parentheses represent total number of males and females. Those ratios differing significantly from 1:1 ($P = 0.05$ by chi-square) are marked with asterisks. Blank bars represent no fishing effort.

females may be related to the Sheepscot River sites' soft mud substrate, which females apparently seek during the spawning season. From laboratory observations it appears that unless females are burrowed in the substrate at the time of egg extrusion, many eggs will not become attached to the pleopods resulting in a significantly reduced complement of eggs. Edwards and Early (1972) reported that female *C. pagurus* also show preference for soft substrates during the spring.

Lindsay (1973) also noted that sex ratios of Maine rock crabs vary by locality and season. He also found males to be more abundant in the winter and spring.

Width-Weight Relations

Because the overlap of data of males and females composed only a small segment of the total range of sizes, I applied analysis of covariance to the total regressions as well as the partial regressions derived from the data that

overlapped. Significant differences ($P = 0.05$) were found between the y-intercepts of either sex for both the complete and partial regressions, so males and females were treated separately. Plots of the predictive regressions show that male Jonah crabs averaged about 8% heavier than females of the same CW over the range 115-130 mm (Figure 8).

SUMMARY

From July 1968 through March 1978, 419 male (67-168 mm CW) and 535 female (74-136 mm) Jonah crabs were collected from research traps and commercial fishermen. Even though male Jonah crabs attain larger sizes (mean sample 113.7-141.1 mm CW) than females (mean sample 104.8-114.0 mm), many female Jonah crabs are harvested commercially whereas, rock crab landings are chiefly composed of males.

No Jonah crabs <67 mm CW were caught and only 2.7% of the total catch were <90 mm CW. This with other evidence indicates that small Jonah crabs inhabit greater depths (>20 m) than those sampled.

Catch per unit of effort values for Jonah crabs caught with research gear generally increased during summer, peaked in fall, and then declined sharply. Fluctuations in the catch were attributed primarily to movement. Catches were highest at the deeper, more seaward sampling sites where the substrate was predominantly rocky. In contrast, rock crabs were more abundant at those relatively shallow estuarine stations having soft

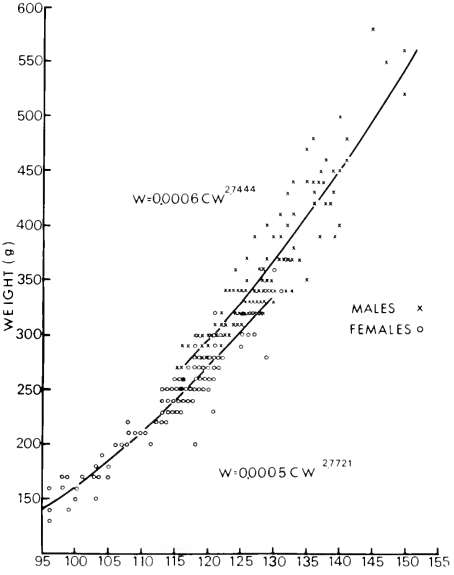


FIGURE 8.—Carapace width-weight relationships calculated for 110 male and 90 female Jonah crabs from the Boothbay Harbor region. Standard errors of the regression coefficients are 0.1793 (a) and 0.0850 (b) for males and 0.2023 (a) and 0.0984 (b) for females.

mud bottoms. Distribution of both cancrid crabs appears to be controlled by substrate type, depth, and temperature.

Male Jonah crabs outnumbered females in the catch in July; the opposite occured in August and September; during the remaining months, sex ratios did not differ significantly from 1:1. In comparison, female rock crabs generally predominated July through September, during fall most ratios approximated 1:1, and in winter and spring males usually dominated with the exception of most estuarine locations where males were only in the majority during May.

ACKNOWLEDGMENTS

I thank the many summer assistants who helped collect, compile, and tabulate several years data. I also thank Joel Cowger for providing me with his field data and Clarence Burke for drafting many of the figures.

LITERATURE CITED

CARPENTER, R. K.
1978. Aspects of growth, reproduction, distribution and abundance of the Jonah crab, (*Cancer borealis*) Stimpson, in Norfolk Canyon and the adjacent slope. M.A. Thesis, Univ. Virginia, Charlottesville, 68 p.

DEWBERRY, E. B.
1956. The characteristics, habits and life history of the edible crab. Naturalist (Leeds) 858:91-96.

EDWARDS, E., AND J. C. EARLY.
[1972.] Catching, handling and processing crabs. Dep. Trade Ind., Torry Res. Stn., Torry Advis. Note 26 (rev.), 17 p.

HAEFNER, P. A., JR.
1976. Distribution, reproduction and moulting of the rock crab, *Cancer irroratus* Say, 1917, in the mid-Atlantic Bight. J. Nat. Hist. 10:377-397.
1977. Aspects of the biology of the jonah crab, *Cancer borealis* Stimpson, 1859 in the mid-Atlantic Bight. J. Nat. Hist. 11:303-320.

HOOPES, D. T.
1973. Alaska's fishery resources — the Dungeness crab. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Fish Facts-6, 14 p.

JEFFRIES, H. P.
1966. Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47:477-481.

KROUSE, J. S.
1972. Some life history aspects of the rock crab, *Cancer irroratus*, in the Gulf of Maine. J. Fish. Res. Board Can. 29:1479-1482.
1976. Size composition and growth of young rock crab, *Cancer irroratus*, on a rocky beach in Maine. Fish. Bull., U.S. 74:949-954.

LINDSAY, B. P.
1973. Some aspects of mobility and feeding activity of the rock crab, *Cancer irroratus*. M.S. Thesis, Univ. Maine, Orono, 57 p.

MUSICK, J. A., AND J. D. MCEACHRAN.
1972. Autumn and winter occurrence of decapod crustaceans in Chesapeake Bight, U.S.A. Crustaceana 22:190-200.

REILLY, P. N., AND S. B. SAILA.
1978. Biology and ecology of the rock crab, *Cancer irroratus* Say, 1817, in southern New England waters (Decapoda, Brachyura). Crustaceana 34:121-140.

SASTRY, A. N.
1977. The larval development of the Jonah crab, *Cancer borealis* Stimpson, 1859, under laboratory conditions (Decapoda Brachyura). Crustaceana 32:290-303.

SCARRATT, D. J., AND R. LOWE.
1972. Biology of rock crab (*Cancer borealis*) in Northumberland Strait. J. Fish. Res. Board Can. 29:161-166.

SHOTTON, L. R.
1973. Biology of the rock crab, *Cancer irroratus* Say, in the coastal waters of Virginia. M.A. Thesis, Univ. Virginia, Charlottesville, 72 p.

SQUIRES, H. J.
1966. Distribution of decapod Crustacea in the northwest Atlantic. Ser. Atlas Mar. Environ. Am. Geogr. Soc. Folio 12, unpaged.

TERRETTA, R. T.
1973. Relative growth, reproduction and distribution of the rock crab, *Cancer irroratus*, in Chesapeake Bay during the winter. M.A. Thesis, Coll. William and Mary, Williamsburg, Va., 104 p.

EFFECTS OF DESICCATION AND AUTOSPASY ON EGG HATCHING SUCCESS IN STONE CRAB, *MENIPPE MERCENARIA*

The stone crab, *Menippe mercenaria*, is found from North Carolina to Yucatan, Mexico, Cuba, Jamaica, and the Bahamas; commercial fishing occurs principally in the State of Florida. Crabs are captured in wooden or plastic traps (40 × 40 × 28 cm) baited with available fish scraps. Present Florida laws allow harvest of both claws from all crabs, including ovigerous females, provided each claw is of legal size (70 mm propodus length). Sale of whole crabs is prohibited, and declawed crabs are released to allow regeneration of lost claws and renewal of fishable stocks. Regeneration of another legal claw can occur within 18 mo (Sullivan[1]).

The commercial season extends from 15 October to 15 May. Spawing occurs during the warmer months (Noe 1967; Cheung 1969), and females with large external egg masses (sponge) of up to 600,000 eggs are observed from early March to late November. Newly extruded eggs, attached to abdominal pleopods, are red-orange and progress to yellow then grey over a 9-12 day maturation period. Larvae generally hatch directly from eggs attached to pleopods. Most commercial operations maximize daily marketable claw yield by pulling traps continuously and declawing crabs only during the return trip to port. This necessitates keeping whole crabs in large fish boxes or containers on deck that are exposed to air for up to 8 h. Claw removal from air-exposed ovigerous females and desiccation of exposed egg masses may reduce larval hatching and recruitment. Since these procedures violate Florida law requiring crabs to be declawed immediately and released in the same area where captured, this study was conducted to provide scientific data to implement change in current fishing methods and protect future stocks.

Methods

Gravid stone crabs were captured in the Gulf of Mexico (5-9 m) west of Pass-A-Grille Beach, St Petersburg, Fla., between March and September 1977. Females with large egg masses were transported in 4 l containers by ship to the Florida Department of Natural Resources Marine Research Laboratory, St. Petersburg. Container water, exchanged frequently with Gulf water while sampling, was not changed for approximately 1½ h during transport through low salinity waters.

Unfed crabs were kept individually in plywood tanks divided into compartments (45.7 × 30.5 × 30.5 cm), sealed with fiber glass tape and epoxy, and leached 2-4 wk prior to use. Water in the closed system was maintained at 15 cm depth by removable standpipes, and overflows were directed into individual glass tanks where eggs or larvae were retained before water entered two 1,000 l undergravel filter vaults (Dugan et al. 1975) (Figure 1). Overflow splash and two airlift standpipes maintained aeration.

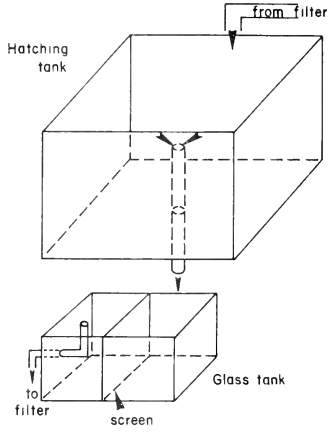


FIGURE 1.—Hatching tank (45.7 × 30.5 × 30.5 cm) and glass larval capture tank (15 × 15 × 30 cm) for desiccation and autospasy experiments with ovigerous stone crabs.

[1]J. R. Sullivan, Florida Department of Natural Resources, Marine Research Laboratory, pers. commun. May 1977.

Optimum survival conditions for egg development and hatching success for *M. mercenaria* (30 C and 34‰ salinity) were determined by Ong and Costlow (1970). Salinity in the present study varied between 32.0 and 36.0‰ and averaged 34.4‰ in all experiments. Air and water temperatures in the control room fluctuated from 27 to 33 C with water temperature generally 0.5-1.0 C lower. Dissolved oxygen levels were measured twice monthly. Nitrites and ammonia levels were evaluated weekly and never exceeded 0.089 and 0.073‰, respectively. Lighting was regulated for 16 h light: 8 h dark and utilized Vita-Lite[2] bulbs which simulated the natural spectrum of sunlight (Dugan et al. 1975).

Experiment I (13 April-31 July)

Crabs were divided into three test groups, with similar ranges of animal size and egg mass color (maturity) and were acclimated to tanks for at least 18 h. Initially, individual crabs were exposed to ambient indoor air conditions in separate cages. This procedure was modified after the first series to simulate commercial holding techniques more closely by placing crabs from a single group into loosely covered wooden slat boxes located in direct sunlight. After desiccation, crabs were returned to holding tanks and observed every 24 h until all eggs hatched. Group I (control) crabs remained in water throughout the experiment. Group II and Group III crabs were desiccated for 2 and 5 h, respectively. Total number of crabs for each group was: 35-Group I, 34-Group II, 33-Group III.

Experiment II (5 August-21 September)

Desiccation procedures were identical to modified procedures in Experiment I; added stress from claw removal was introduced after desiccation. Claws were removed using commercial harvesting methods by inducing autospasy (loss of appendage through externally applied pressure). In this technique, claws were grasped firmly and ventral pressure applied until the fused basis-chium stopped against the coxa. Further flexion strained the autotomizer muscle, and separation of the limb occurred at a natural fracture plane. Excessive hemorrhaging is prevented by swelling of a hypodermal diaphragm located at the fracture plane.

Group IV (control) crabs remained in water throughout the experiment and had similar treatment as Group I. Group V and Group VI crabs were desiccated for 2 and 5 h, respectively, then declawed. Declawed crabs were placed immediatedly into holding tanks and observed every 24 h as in Experiment I. Total number of crabs for each group was: 30-Group IV; 34-Group V; and 35-Group VI.

Crabs continuously discarded eggs from egg masses. Single eggs were shed when females raised their bodies on claws and legs and preened (combed) egg masses with rear legs. Egg stalks containing up to several hundred eggs (clumps) were also frequently shed. Aeration of eggs by rapid abdominal movement also occurred at this time. Detached eggs, larvae, and other egg mass products retained in individual glass tanks were removed daily and preserved in 10% Formalin prior to counting.

Analysis

Hatching occurred from 0 to 9 days after day of experimental stress. Complete hatching generally required 24-48 h, and organic matter retained in glass tanks after that time was principally dead eggs, deformed larvae, or empty egg cases cleaned from pleopods.

The day with highest number of normal first-stage larvae was called major hatch. Days before and following major hatch were called prehatch and posthatch.

Eggs from a single ovigerous female were observed microscopically to determine normal hatching process and identify normal first-stage larvae. Initial breaking of the chorion enabled larvae to emerge head first from the egg. Vigorous abdominal flexing by the larvae cast off the egg case and induced shedding of the prezoeal cuticle and full extension of the rostral and lateral spines. In a few instances, spinular extension was delayed until complete seperation from the egg, but all prezoea yielded normal, active free-swimming first-stage larvae within minutes of initial hatch. Eggs removed from the same female after desiccation were observed for comparison. Increased numbers of inviable eggs and partial hatches were evident. Numerous prezoea, unable to cast off prezoeal cuticles, died after continued struggle. Successful first-stage development was reduced, and

[2]Reference to trade names does not imply endorsement by the Marine Research Laboratory, FDNR or the National Marine Fisheries Service, NOAA

larval activity was sluggish, frequently ending in death.

Aliquots from individual daily crab samples (1 or 2 ml; count ≃ 200) were sorted under a dissecting microscope and classified. Normal first-stage larvae (Hyman 1925; Porter 1960) were denoted as viable; whole eggs, partially hatched eggs, prezoea (Hyman 1925; no rostral or lateral extension), and deformed first-stage larvae were denoted as inviable. Stein's two-stage sample test (Steel and Torrie 1960) indicated that six replicate aliquots from each sample provided reliable counts (within 95% confidence limits) of total numbers of viable and inviable eggs and larvae present each day. Because results of aliquot counts were inconsistent when samples contained clumps of eggs, 1-8 ml of chlorine bleach (5.25% sodium hypochlorite) were added to dissolve stalks and dissociate eggs uniformly before aliquots were taken.

Number of eggs carried by individual crabs at time of capture was estimated by combining daily totals of viable and inviable eggs and larvae. Total hatching success was expressed as percent of original egg mass that hatched viably. Total egg mass mortality was expressed as the percent not hatching or hatching inviably. Average daily mortality (per group) was calculated by dividing total mortality per day by the number of crabs yielding inviable eggs and larvae that day. Crabs not yielding any larvae were eliminated from analysis; two crabs in Group I and one crab each in Groups III, IV, and VI were so eliminated.

Comparison among groups was made by presenting prehatch, posthatch, and total egg mass mortality for each group. I chose this method because inviable eggs and larvae were evident in some form in all daily samples, but viable larvae were present for only 24-48 h.

Results and Discussion

Experiment 1

Initial egg loss from crabs in Group I (Figure 2) was probably caused by handling at capture and stress from transport to laboratory. With acclimation to holding tanks, average daily mortality decreased until major hatch, when highest egg and larval mortality coincided with maximum first-stage larval survival.

Crabs desiccated for 2 h (Group II) showed immediate preening activity upon return to water and daily prehatch mortality peaked at 3.6%, 3 days after desiccation (Figure 2). Thereafter, daily percent mortality decreased until major hatch. Posthatch mortality was similar to, but slightly higher than that of Group I. Total prehatch mortality (12.1%) was four times greater than that of Group I (Table 1) and posthatch mortality (9.3%) was nearly twice that of Group I. Total mortality for Group II (21.4%) was 13.0% higher than control (Group I).

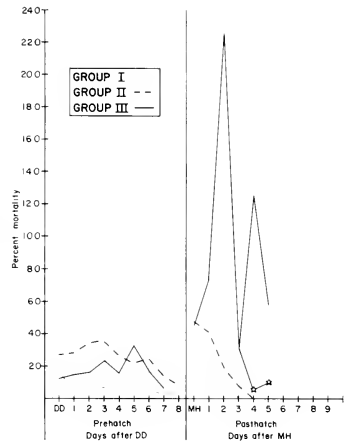


FIGURE 2.—Average daily percent egg mortality in ovigerous stone crabs as related to desiccation. Group I crabs untreated (control). Group II crabs exposed to 2-h desiccation and Group III crabs exposed to 5-h desiccation. DD - day of desiccation; MH - day when major hatching occurred; Prehatch - days following DD. Posthatch - days following MH. Starred points represent percent mortality excluding one of three crabs which accounted for 96% total mortality on posthatch days 4 and 5.

Desiccation for 5 h (Group III) caused temporary lethargy in crab mobility; sponge care and initial mortality were below those of Group I (Figure 2). Crabs recovered slowly during prehatch, resulting in 5 days of generally increasing daily egg mortality. Maximum daily egg and larval mortality usually occurred on the day of major hatch, but was delayed 2 days for most Group III crabs. Improper maternal care of eggs during prehatch and through posthatch may have prolonged oxygen

TABLE 1.—Percent egg mortality in ovigerous stone crabs as related to desiccation and autospasy. Experiment I compares egg mortality after effects of desiccation and experiment II compares egg mortality after desiccation followed by removal of both claws (autospasy).

Group and treatment	Crabs (no.)	Prehatch	Posthatch	Total
Experiment I				
I (control)	33	3.3	5.1	8.4
II (2-h desiccation)	34	12.7	9.3	21.4
III (5-h desiccation)	32	5.9	33.8	39.7
Experiment II				
IV (control)	29	7.0	6.7	13.7
V (2-h desiccation autospasy)	23	8.5	18.1	26.6
VI (5-h desiccation autospasy)	16	9.8	50.4	60.2

deficiency within the egg mass and lack of abdominal movement may have hindered successful larval hatching. Davis (1965) separated eggs from female blue crab, *Callinectes sapidus*, and noted a decrease in hatching success if eggs remained in small clusters, presumably due to insufficient oxygen. Rice and Williamson (1970) found that decapod larvae hatched from ovigerous females were weakened if oxygenated water could not be replenished.

Prehatch mortality for Group III (5.9%) was less than that of Group II, but was still greater than that of Group I (Table 1). Posthatch mortality (33.8%) was considerably higher than Group I or Group II. Total mortality for Group III (39.7%) represented a mean increase of 18.3% mortality above that of Group II and a mean increase of 31.3% above that of Group I (Table 1).

Experiment II

Autotomizer muscle reflexes were adversely affected in crabs subjected to air exposure, and declawing often resulted in jagged wounds and severance of the artery proximal to the hypodermal diaphragm. Unrestricted hemorrhaging caused death in 8 crabs in Group V and 14 crabs in Group VI. Death in seven additional crabs (three in Group V, four in Group VI) could not be explained as above, but also occurred after declawing. Resulting 100% egg mass mortality for 34.4% of Group V and 52.9% of Group VI notably reduced group mean hatching success related to control Group IV (Table 1).

Wood and Wood (1932) found any treatment which weakened brachyurans affected muscular responses, preventing normal autotomic reflex. they further stated that American crayfish (Astacidae) held captive for any length of time were vitiated and lacked normal reflex. Davis[3] related wound size and body fluid loss in reporting 53.7% death in *M. mercenaria* held for 10 days in laboratory tanks and then declawed using commercial methods.

Loss of both claws after desiccation reduced preening of eggs by surviving crabs, resulting in an apparent initial egg mass mortality below that of Group IV (Figure 3).

Group V crabs (2-h desiccation) recovered quickly and compensated for claw loss by propping themselves against sides of compartments; rocks and shells common where stone crabs occur may be used similarly in nature. Prehatch mortality peaked 3 days after desiccation. Posthatch mortality was higher and more erratic than that of control Group IV. Prehatch mortality (8.5%) was slightly higher than that of Group IV (7.0%), but posthatch mortality (18.1%) was almost three times higher than that of control group (Table 1). Total mortality for Group V (26.6%) was 12.9% above control (Group IV).

[3]Davis, G. E. Interim report June, 1977. National Park Service Stone Crab Study. Everglades National Park, Box 279, Homestead, FL 33030.

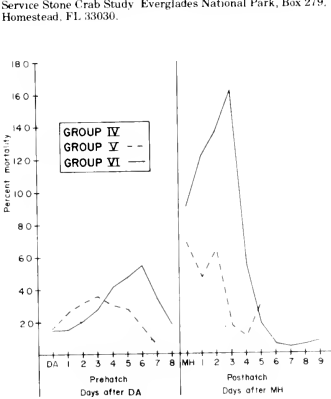


FIGURE 3.—Average daily percent egg mortality in ovigerous stone crabs as related to desiccation and autospasy. Group IV crabs were untreated (control). Group V crabs had both claws removed (autospasy) after 2-h desiccation, and Group VI crabs had both claws removed after 5-h desiccation. DA - day of desiccation and autospasy, MH - day when major hatching occurred. Prehatch - days following DA. Posthatch - days following MH.

After 5-h desiccation, surviving declawed crabs (Group VI) recovered more slowly than did crabs of Group V. Maternal preening was delayed and egg mortality during prehatch did not peak until 6 days after desiccation (Figure 3). As noted previously, maximum egg and larval mortality normally occurred at major hatch, but difficulty in maintaining body elevation probably inhibited preening for Group VI during posthatch. Consequently, maximum egg and larval mortality occurred 3 days after major hatch and time needed to clean pleopods was extended to 9 days.

Group VI recovery from stress was sufficient to produce prehatch mortality of 9.8%, an increase of 2.8% above control Group IV (Table 1). Extended posthatch yielded 50.4% egg and larval mortality, the highest of any group. Total mortality for surviving crabs in Group VI (60.2%) was a marked increase of 46.5% above that of control Group IV (Table 1) even excluding 100% mortality values from 18 dead crabs.

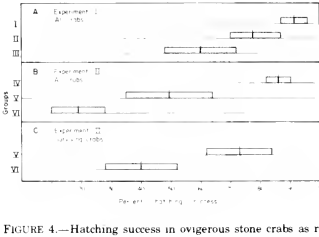


FIGURE 4.—Hatching success in ovigerous stone crabs as related to desiccation and autospasy. Mean (vertical line), range (horizontal line) and 95% confidence intervals (bar) about the mean. Set A includes untreated Group I crabs, Group II crabs exposed to 2-h desiccation and Group III crabs exposed to 5-h desiccation; Set B includes untreated Group IV crabs, Group V crabs, both claws removed after 2-h desiccation and Group VI crabs, both claws removed after 5-h desiccation; Set C includes only crabs that survived desiccation and autospasy in Groups V and VI

Mean Hatching Success

Mean hatching success for control crabs in Experiment I (Group I) was 91.6%. Desiccation from air exposure for 2 h (Group II) decreased success to 78.6% and desiccation from 5-h air exposure (Group III) decreased success to 60.3%. Mean hatching success for control crabs in Experiment II (Group IV) was 86.3%. Stress from 2-h desiccation plus autospasy (Group V) decreased success from Group IV to 49.6% and stress form 5-h desiccation plus autospasy (Group VI) decreased success to 18.8% (Figure 4).

Summary

Desiccation of eggs by air exposure of ovigerous females caused reduction in larval hatching success that was directly related to length of exposure. Desiccation weakened normal crab autotomic muscular reflex, and experimental declawing resulted in death of 34.4% of crabs exposed 2 h and 52.9% of crabs exposed 5 h.

Stress from autospasy after 2-h desiccation did not increase mean egg and larval mortality for surviving crabs above that for crabs desiccated only. Related to controls, Group II (2-h desiccation) and Group V (2-h desiccation autospasy) had nearly identical total mortalities, 12.9% and 13.0%, respectively. Claw loss delayed maternal egg mass preening, and reversed the prehatch posthatch egg mortality ratio of crabs desiccated 2 h from 12.1:9.3 (Group II) to 8.5:18.1 (Group V).

Effects of stress after 5-h air exposure were less definitive. Egg and larval mortality for surviving declawed crabs exposed to 5-h desiccation was 15.5% higher than was mortality for similarly exposed whole crabs when related to controls. Maternal egg preening by declawed crabs was obviously affected by claw loss, but small sample size (16) in surviving declawed crabs and overlap in confidence intervals for the 5-h desiccation groups made differences in mortalities inconclusive.

The stone crab fishery, unlike the blue crab fishery which allows permanent removal of whole animals, realizes high stability and recruitment by release of reproductively active crabs capable of claw regeneration. Present harvesting techniques adversely affect this stability by subjecting crabs to air exposure and desiccation. When crabs are ovigerous, desiccation causes a definite reduction in larval hatching success and is related to crab death and reduced overall population recruitment. Protection of ovigerous females by immediate release or by use of methods to dampen crabs while on deck is therefore warranted.

Acknowledgments

This study was funded in part by the U.S. Department of Commerce, NOAA, National Marine Fisheries Service under PL 88-309, Project No.

2-278-R. I thank F. S. Kennedy, Jr., M. E. Berrigan, J. R. Sullivan, D. G. Barber, and S. M. Foster for helping to collect and process the data, J. Hinkle and D. Richardson for laboratory assistance, and W. G. Lyons, D. K. Camp, and J. A. Huff for editorial review. Special thanks to Deb, my wife, who spent immeasurable time assisting me on weekends.

Literature Cited

CHEUNG, T. S.
1969. The environmental and hormonal control of growth and reproduction in the adult female stone crab *Menippe mercenaria* (Say). Biol. Bull. (Woods Hole) 136:327-346.

DAVIS, C. C.
1965. A study of the hatching process in aquatic invertebrates: XX. The blue crab, *Callinectes sapidus*, Rathbun. XXI. The Nemertean, *Carcinonemetes carcinophica* (Kölliker). Chesapeake Sci. 6:201-208.

DUGAN, C. C., R. W. HAGOOD, AND T. A. FRAKES.
1975. Development of spawning and mass larval rearing techniques for brackish-freshwater shrimps of the genus *Macrobrachium* (Decopoda Palaemonidae). Fla. Mar. Res. Publ. 12, 28 p.

HYMAN, O. W.
1925. Studies on the larvae of crabs of the family Xanthidae. Proc. U.S. Natl. Mus. 67(3), 22 p.

NOE, C. D.
1967. Contributions to the life history of the stone crab *M. mercenaria* with emphasis on the reproduction cycle. M.S. Thesis, Univ. Miami, Coral Gables, Fla., 55 p.

ONG, K. S., AND J. D. COSTLOW, JR.
1970. The effect of salinity and temperature on larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory. Chesapeake Sci. 11:16-29.

PORTER, H. J.
1960. Zoeal stages of the stone crab *Menippe mercenaria* (Say). Chesapeake Sci. 1:168-177.

RICE, A. L., AND D. I. WILLIAMSON.
1970. Methods for rearing larval decapod crustacea. Helgol. wiss. Meersunters. 20:417-434.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics, with special reference to biological sciences. McGraw-Hill, N.Y., 481 p.

WOOD, F. D., AND H. E. WOOD.
1932. Autotomy in decapod Crustacea. J. Exp. Zoöl. 62:1-55.

RODRIC A. SCHLIEDER

Florida Department of Natural Resources
Marine Research Laboratory
100 Eighth Avenue SE
St. Petersburg, FL 33705

FIRST RECORDS OFF OREGON OF THE PELAGIC FISHES *PARALEPIS ATLANTICA*, *GONOSTOMA ATLANTICUM*, AND *APHANOPUS CARBO*, WITH NOTES ON THE ANATOMY OF *APHANOPUS CARBO*[1]

The species covered in this report are common in parts of the Atlantic Ocean and all are known to occur in the Pacific Ocean. We fill a gap in knowledge of the distribution of two species known formerly only north and south of Oregon, extend the northward range of *Gonostoma atlanticum* Norman, and report inshore occurrences of *Paralepis atlantica* Krøyer. The unusual gross anatomy surrounding the gas bladder of *Aphanopus carbo* Lowe is worthy of description.

Methods

Counts and measurements followed those of Hubbs and Lagler (1958) and all measurements were taken to the nearest 0.1 mm. Specimens are catalogued in the fish collections of the Department of Fisheries and Wildlife (OS) or the School of Oceanography (OSUO), Oregon State University. Anatomical terminology follows that of Lagger et al. (1962) and Romer (1970). Four specimens of *A. carbo* from Oregon were dissected and two were radiographed. Two specimens from the Atlantic Ocean off Madeira were dissected and radiographed. Complete vertebral counts could not be made from the radiographs due to poor resolution of the small posterior caudal vertebrae.

Notes on Distribution and Morphology

Paralepis atlantica has been recorded in the eastern Pacific from Baja California and California (Rofen 1966) and from the vicinity of Willapa Bay, Wash. (Kajimura 1969). Bakkala (1971) reported the species from surface waters of the central Pacific at lat. 48°00′ N, long. 165°00′ W.

Two specimens of *P. atlantica* were found on shore in northwestern Oregon. One (OS 956:456 mm SL) was taken alive on the beach at Netarts, Tillamook County, on 7 October 1963. Another (OS 5160:466 mm SL) was found dead on the beach 29 km north of Seaside, Clatsop County, on 16 May 1960. A specimen of *G. atlanticum* (OSUO 2402:59 mm SL) was captured on 30 July 1977, 65

[1]Technical Paper No. 5082, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

km west of Newport (lat. 44°38′ N), between 335 and 400 m deep with a small Cobb midwater trawl (10 m mouth opening) with an opening and closing cod end (Pearcy et al. 1977). This female fits the descriptions by Grey (1960, 1961, 1964) and Mukhacheva (1972). Maximum diameter of eggs in the ovary was 0.16 mm. Grey (1964) considered fish of this size to be mature.

Gonostoma atlanticum is usually distributed in warm water of the Atlantic, Pacific, and Indian Oceans. It is found in the eastern and central North Atlantic, and it has usually been recorded from equatorial waters in the Pacific and Indian Oceans. The northernmost previous record (lat. 34°18.6′ N) for its occurrence in the Pacific Ocean was that of Berry and Perkins (1966), who captured several individuals off southern California. The temperature of the water in which the OSUO specimen was captured was 5.37°-5.70° C. Backus et al. (1965) reported the occurrence of *G. atlanticum* in the Atlantic Ocean in waters of 10°-11° C.

Aphanopus carbo was first reported from the Pacific Ocean off Bodega Bay and Fort Bragg, Calif., in 1969 (Fitch and Gotshall 1972). Peden (1974) reported a specimen from off the Strait of Juan de Fuca. Clarke and Wagner (1976) collected larvae and juveniles off Hawaii. Five specimens were taken off Oregon in 1976: OS 5381 (476 mm SL), about 29 km off Cape Meares, at about 183 m; OS 6115 (639 mm SL), about 37 km off Florence, at about 146 m; OSUO 2352 (570 mm SL), 2353 (558 mm SL), 2354 (547 mm SL), 120 km west of Newport, at about 400-480 m, in an opening and closing net.

Our specimens compared with those from Madeira, had slightly smaller horizontal orbit, slightly wider suborbital head width, and slightly shorter anal spines. Otherwise the Atlantic and Pacific Ocean specimens are very similar.

Gas Bladder Anatomy in *Aphanopus carbo*

Although Maul (1954) mentioned that on retrieval to the surface the gas bladder in *A. carbo* expands greatly, causing the skin of the abdomen to split, none of our specimens exhibited this characteristic. Shepel[2] stated that none of the specimens examined by him had their skin split, but that the stomach in most specimens (all from the Atlantic Ocean) were everted. Only one of our specimens had an everted stomach. These differences led us to examine the gas bladder and associated structures in *A. carbo*.

Bone (1971) described the anatomy and histology of the gas bladder of *A. carbo*. Tucker (1953) briefly mentioned the ribs and provided partial radiographs of the ribs and vertebral column in *A. carbo* and *A. schmidti*. However, we found no descriptions of the relationship of the bladder to the vertebral column, ribs, kidneys, and coelom. Our examination of *A. carbo* shows that the gas bladder of this species, and the structures associated with it, has several unusual characteristics. Little variation in anatomy was noted in our specimens.

The position of the gas bladder in *A. carbo* is typical of that in most fishes; it is ventral to the vertebral column and kidneys and dorsal to the peritoneal (abdominal) cavity (i.e., retroperitoneal) (Figure 1). The anterior end of the gas bladder is below the sixth vertebra. From it, two minute extensions proceed anterolaterally at 45°, but the size of the extensions did not allow us to trace them forward more than a few millimeters. Posteriorly, the gas bladder extends to a blunt end between vertebrae 42 and 45, directly dorsal or slightly anterior to the vent. Although the dorsoposteriad portion of the peritoneal cavity narrows and curves ventrally, the gas bladder continues to parallel the vertebral column except for a slight dip near the posterior end. The region between the gas bladder and the peritoneal cavity is filled with hypaxial muscle. The bladder is slightly narrowed at its anterior and posterior ends. It is oval in cross section and slightly smaller than the diameter of vertebral centra in our preserved specimens (Figure 1).

The kidneys extend anteriorly from the region dorsal to the vent to the posterior portion of the skull. They are enlarged in the area above the vent, and between the anterior of the gas bladder and posterior of the skull, and lie ventrolateral to the vertebral column and dorsolateral to the gas bladder. They terminate in a urinary duct that appears to empty into a urogenital sinus.

The ventral ribs are intimately associated with the gas bladder and kidneys. A pair of ventral ribs is present on all trunk vertebrae, but those anterior to the gas bladder are short and thin. These ribs are difficult to find but may be seen readily in radiographs. From immediately anterior to the gas bladder to about the ninth vertebra the ribs become progressively longer and

[2]L. I. Shepel, Fishery Reconnaissance, Murmansk, U.S.S.R., pers. commun. 15 November 1977.

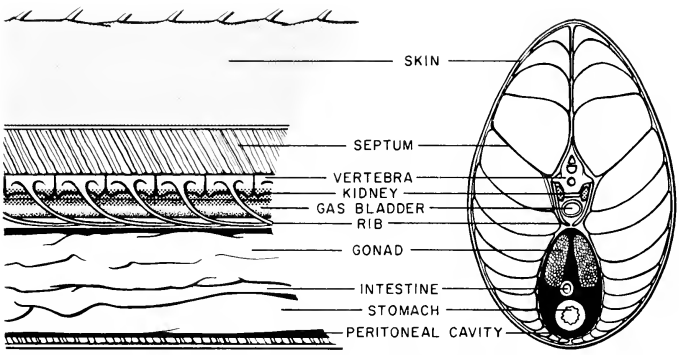


FIGURE 1.—Gross anatomy of the gas bladder and surrounding region in the black scabbardfish, *Aphanopus carbo*. Left: Partial sagittal section in region of the 14th-19th vertebrae. Muscle and other tissue have been removed from the region ventral to the indicated septum. Right: Cross section in the region of the 14th vertebra.

thicker. From that point posteriorly to the first caudal vertebra, all the ribs, except the last two to four, are of the same size, shape, and relative position. All the ribs extend laterally around the kidneys but the last few extend farther ventrally to encage the enlarged posterior portion of the kidneys. Where the ribs contact the gas bladder laterally, they turn abruptly posteriad and almost parallel the bladder while remaining in contact with it. In doing so, they curl beneath the bladder. Each rib extends posteriorly a distance almost equal to two vertebrae (Figure 1). Each rib appears to join a myocomma, then connect to the ventrolateral wall of the bladder. The gas bladder is thus surrounded by a "rib cage."

The hypaxial muscles, in conjunction with the ribs, surround the gas bladder almost completely. The only gap is a narrow medial band of connective tissue to which the ribs attach, present between the peritoneal membrane and the gas bladder (Figure 1).

The unusual anatomy of *A. carbo* invites speculation concerning its significance. The enclosure of the gas bladder in a rib cage apparently reinforces the gas bladder wall, which Bone (1971) has shown is composed of thick connective tissue. The combination of a thick, tough wall reinforced by muscle and bone seems likely to prevent the expansion of the gas bladder when ambient pressure decreases more rapidly than the gas contained in the bladder can be absorbed into the bloodstream. This species is known to feed on cephalopods (Zilanov and Shepel 1975). Possibly the anatomical modifications of its gas bladder and associated structures allow *A. carbo* individuals to pursue prey into significantly shallower water without having to adjust bouyancy and/or absorb gas.

Acknowledgments

For supplying us with specimens, we thank D. Demory, B. Dixon, K. Martinson, and F. Sumner. Robert Rofen kindly verified the identification of *P. atlantica*. Four specimens of *A. carbo* collected off Madeira, Portugal, were lent to us by G. E. Maul, Museu Municipal do Funchal, Madeira. The radiographs of *A. carbo* were gratuitously done by G. Walters, Good Samaritan Hospital, Corvallis. Jim Long and Tom Rasmussen rendered various aids. Bonnie Hall drew the illustrations. Howard Horton and Carl Schreck reviewed the manuscript. The work of the second author was supported in part by the Office of Naval Research Contract #N00014-67-A-0369-007 under Project NR083-102 and the work of the first and third authors by the Agricultural Experiment Station, Oregon State University.

Literature Cited

BACKUS, R. H., G. W. MEAD, R. L. HAEDRICH, AND A. W. EBELING.
1965. The mesopelagic fishes collected during Cruise 17 of the R/V Chain, with a method for analyzing faunal transects. Bull. Mus. Comp. Zool. Harv. Univ. 134:139-158.

BAKKALA, R. G.
1971. Occurrence of the barracudina, *Paralepis atlantica* Kroyer, in the central North Pacific Ocean. Fish. Bull., U.S. 69:881.

BERRY, F. H., AND H. C. PERKINS.
1966. Survey of pelagic fishes of the California Current area. U.S. Fish Wildl. Serv., Fish. Bull. 65:625-682.

BONE, Q.
1971. On the scabbard fish *Aphanopus carbo*. J. Mar. Biol. Assoc. U.K. 51:219-225.

CLARKE, T. A., AND P. J. WAGNER.
1976. Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. Fish. Bull., U.S. 74:635-645.

FITCH, J. E., AND D. W. GOTSHALL.
1972. First record of the black scabbardfish, *Aphanopus carbo*, from the Pacific Ocean with notes on other Californian trichiurid fishes. Bull. South. Calif. Acad. Sci. 71:12-18.

GREY, M.
1960. A preliminary review of the family Gonostomatidae, with a key to the genera and the description of a new species from the tropical Pacific. Bull. Mus. Comp. Zool. Harv. Coll. 122:57-125.
1961. Fishes killed by the 1950 eruption of Mauna Loa, Part V Gonostomatidae. Pac. Sci. 15:462-476.
1964. *Family* Gonostomatidae. *In* Y. H. Olsen (editor), Fishes of the western North Atlantic. Part four, p. 78-240. Sears Found. Mar. Res., Yale Univ., Mem. 1.

HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes region. Revised ed. Univ. Mich. Press, Ann Arbor, 213 p.

KAJIMURA, H.
1969. Northern range extension for *Paralepis atlantica* Kroyer in the eastern North Pacific. Calif. Fish Game 55:246-247.

LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER.
1962. Ichthyology. John Wiley and Sons, Inc., N.Y., 545 p.

MAUL, G. E.
1954. Notes and exhibitions. [A sketch of Madeiran ichthyology with observations on the ecology of the most important fishes.] Proc. Zool. Soc. Lond. 123:901-903.

MUKHACHEVA, V. A.
1972. On the systematics, distribution and biology of the *Gonostoma* species (Pisces, Gonostomatidae). [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 93:205-249.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

PEDEN, A.
1974. Rare fishes, including first records of thirteen species, from British Columbia. Syesis 7:47-62.

ROFEN, R. R.
1966. Family Paralepididae. *In* Fishes of the western North Atlantic. Part five, p. 205-461. Sears Found. Mar. Res., Yale Univ., Mem. 1.

ROMER, A. S.
1970. The vertebrate body. 4th ed. W. B. Saunders Co., Phila., 601 p.

TUCKER, D. W.
1953. The fishes of the genus *Benthodesmus* (Family Trichiuridae). Proc. Zool. Soc. Lond. 123:171-197.

ZILANOV, V. K., AND L. I. SHEPEL.
1975. A contribution to the ecology of black scabbardfish *Aphanopus carbo* Lowe in the North Atlantic. [In Russ.] Vopr. Ikhtiol. 93:737-740.

KEVIN M. HOWE

Department of Fisheries and Wildlife
Oregon State University, Corvallis, OR 97331

DAVID L. STEIN

School of Oceanography
Oregon State University, Corvallis, OR 97331

CARL E. BOND

Department of Fisheries and Wildlife
Oregon State University, Corvallis, OR 97331

CHANGES IN RIBONUCLEIC ACID, DEOXYRIBONUCLEIC ACID, AND PROTEIN CONTENT DURING ONTOGENESIS IN WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, AND EFFECT OF STARVATION

Normal development of most embryonic and prolarval (yolk-sac) teleosts depends on material stored in the yolk for a source of both energy and biosynthetic precursers. After hatching there is a transition period when larvae shift from dependence on yolk to an exogenous food supply. The availability of sufficient prey of the proper quality and the ability of larvae to capture and assimilate it are critical to survival during the larval stage. Since differential mortality during the larval stage could be important in determining the year-class size of marine fish, a method for determining the nutritional condition of fish larvae in plankton samples could aid in determining larval survival and prediction of subsequent year-class size. In the past, weight-length relationships (Blaxter 1971), morphometric (Ehrlich et al. 1976), chemical (Ehrlich 1974a, b), and histological (O'Connell 1976; Theilacker 1978) methods have been used with varying degrees of success. All four approaches have limitations and diagnosis of the starving condition in sea-caught larvae is difficult.

Bulow (1970) used RNA-DNA (ribonucleic acid-deoxyribonucleic acid) ratios as indicators

of recent growth rates in golden shiner, *Notemigonus crysoleucas*, adults. He reported that RNA-DNA ratios were very sensitive to changes in feeding levels. The RNA content of a wide variety of organisms have been related to growth rate (Sutcliffe 1970). Sutcliffe (1965) was able to predict quite accurately the growth rates of laboratory populations of brine shrimp, *Artemia salina*, and mud snail, *Nassarius obsoletus*, larvae using a growth-RNA relation determined on whole amphipod *Orchestia platesis*. Dagg and Littlepage (1972), however, concluded that the general positive relationship between growth rate and RNA content lacked sufficient specificity for determination of growth rate. A positive relationship is expected since growth in marine teleosts is accompanied by and is partially a function of protein synthesis, and certain types of RNA are directly involved in protein synthesis serving as both a template and organizer. The DNA content of an organism has been used as an indication of cell number since the DNA content of somatic cells is generally constant for a given species. Some eggs and early larvae, however, have been shown to contain large amounts of cytoplasmic DNA, greatly exceeding the amount of nuclear DNA (Neyfakh and Abramova 1974). This study was undertaken to determine the relationships between changes in DNA, RNA, and protein content and events in the development of winter flounder, *Pseudopleuronectes americanus*, and to determine if measurements of these classes of biochemicals could be used to determine the nutritional condition of winter flounder larvae.

Methods

Pseudopleuronectes americanus adults were caught by trawl net off Rhode Island and kept in a 1,900 l aquarium. Eggs were obtained, fertilized, and incubated according to methods previously described (Smigielski 1975). Larvae were maintained at 8° C in 38 l all black glass aquaria. Commencing 4 days after hatching the larvae were fed zooplankton collected in the Narragansett Bay area in excess of 2 organisms ml according to the methods of Laurence (1975). On days 3 and 28 a portion of the larvae were transferred to an identical aquarium containing seawater filtered through a 0.45 μm Millipore[3] filter. Wild winter flounder larvae were collected in Narrow River, R. I., with a 505 μm 0.5 m plankton net.

About 40 eggs or larvae were pooled per sample through day 11 after hatching; thereafter 10 larvae were pooled per sample except on days 43, 50, and 58 when only 5 larvae were used for the largest size group. All samples through day 36 were run in triplicate; thereafter samples were run in duplicate. Starting on day 28 the standard length of each larva sampled was determined using an ocular micrometer and 10 larvae were taken on each sampling day for dry weight determinations.

Eggs and larvae were homogenized in 2 ml of ice-cold distilled water immediately after sampling. Protein was determined on duplicate 0.1 or 0.05 ml samples of homogenate using a modification of the Lowry method (Hartree 1972). RNA and DNA were extracted and partially purified from 1.7 ml of homogenate using a modification of the Schmidt-Thannhauser method (Munro and Fleck 1966) adapted for the micro quantities present in larval fish and eggs. RNA concentration was estimated from the absorbancy at 260 nm of the acid-soluble, alkali-hydrolyzed fraction. The DNA content of larvae was determined from the absorbency at 260 nm of the alkali-stable, acid-hydrolyzed fraction. Because of the very small quantities of DNA in winter flounder eggs their DNA content was determined on the alkali-stable fraction using a modification of the 3,5-diaminobenzoic acid dihydrochloride florometric assay described by Holm-Hansen et al. (1968) and Hinegardner (1971). At the beginning of this study RNA was also determined using the orcinol method (Sutcliffe 1965) and DNA was determined using the indole method (Ceriotti 1952). These values were in good agreement with the values reported.

Results

DNA content per egg increased rapidly between fertilization and hatching (Figure 1). Upon hatching 10 days after fertilization, larvae contained slightly more RNA and DNA than unhatched eggs and retained 78% of the protein. During the period from hatching to the end of the yolk-sac stage (day 5), DNA and RNA content remained essentially constant while a decrease in protein was observed. Although plankton was added on day 4 to aquaria containing fed larvae, visual observation of the gut indicated that the majority of the larvae had

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

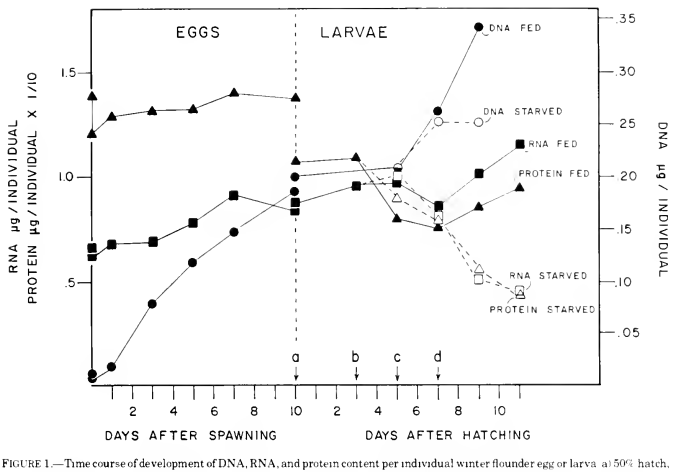


FIGURE 1.—Time course of development of DNA, RNA, and protein content per individual winter flounder egg or larva a) 50% hatch, b) starved larvae transferred to filtered seawater; c) most larvae showed no visible yolk, d) food visible in gut of fed larvae

not begun feeding until day 7. Between the end of the yolk-sac stage and initiation of feeding (day 7) DNA content increased sharply while RNA and protein decreased. Of the protein present in the egg just prior to hatching, 45% was lost by the time of feeding initiation. After feeding initiation DNA, RNA, and protein content increased steadily (Figure 1; Tables 1, 2).

The RNA and protein content of winter flounder larvae transferred to filtered seawater prior to feeding initiation continued to decrease until a 100% mortality was observed between day 11 and 14 (Figure 1). Starved larvae did show an increase in DNA content on day 7 similar to that observed in fed larvae. The RNA-DNA ratio of both starved and fed larvae decreased from the end of the yolk-sac stage through day 9. However, the RNA-DNA ratio was significantly higher in fed larvae than starved larvae on day 9.

The RNA content of a second group of larvae transferred to filtered seawater 28 days after hatching decreased within 2 days, while both DNA and protein content appeared to increase (Table 1). After 4 days a decrease in all three components was observed. A 50% mortality, consisting almost entirely of the smaller individuals

TABLE 1.—RNA, DNA, and protein content of starved and fed winter flounder larvae 28 to 36 days after hatching

Age (days)	Starvation time[1] (days)	Standard length[2] (mm)		RNA[3] (µg larva)		DNA[3] (µg larva)		Protein[3] (µg larva)		RNA DNA[3]	
		Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
28	0	5.61 ± 0.60		3.85 ± 0.67		0.91 ± 0.21		36 ± 7		4.27 ± 0.42	
30	2	5.83 ± 0.72	5.64 ± 0.56	4.74 ± 0.73	3.32 ± 0.51	0.99 ± 0.13	1.04 ± 0.11	37 ± 3	44 ± 5	4.81 ± 0.56	3.16 ± 0.26
32	4	5.84 ± 0.66	5.68 ± 0.54	4.75 ± 0.14	2.59 ± 0.61	1.21 ± 0.16	0.93 ± 0.13	79 ± 4	36 ± 7	3.99 ± 0.50	2.78 ± 0.29
	C[4]	5.44 ± 0.80		3.95 ± 0.22		0.99 ± 0.05		43 ± 4		3.98 ± 0.06	
36	8	6.53 ± 0.92	6.41 ± 0.45	8.91 ± 0.66	3.70 ± 0.50	2.17 ± 0.41	1.73 ± 0.18	94 ± 4	60 ± 8	4.19 ± 0.43	2.14 ± 0.16
	C[4]	6.23 ± 0.94		8.15 ± 2.67		1.92 ± 0.46		86 ± 24		4.20 ± 0.34	

[1]Number of days starved fish were in filtered seawater
[2]Data are means ± 1 SD for 40 to 50 larvae
[3]Data are means ± 1 SD of three replicates containing 10 larvae each
[4]Fish removed from fed population and transferred to filtered seawater 18 h prior to sampling to clear stomach contents

TABLE 2.—RNA, DNA, and protein content of wild and cultured (fed) winter flounder.

Age (days after hatching)	Standard length (mm) Range	Mean	SD	RNA (μg/larva)	DNA (μg/larva)	Protein (μg/larva)	RNA/DNA
Cultured larvae[1]							
42	4.98–6.07	5.60	0.39	3.55 ± 0.23	—	44 ± 1	—
	6.27–6.89	6.50	.20	9.19 ± 0.75	1.99 ± 0.06	99 ± 10	4.61 ± 0.09
	7.00–8.77	7.77	.57	21.83 ± 1.98	3.91 ± 0.70	200 ± 15	5.62 ± 0.52
43	5.26–6.35	5.76	.30	3.35 ± 0.61	**0.82 ± 0.13**	44 ± 5	4.10 ± 0.07
	6.36–7.26	6.82	.26	7.75 ± 0.98	**1.85 ± 0.25**	91 ± 5	4.18 ± 0.03
	7.29–8.54	8.19	.33	27.42 ± 0.28	**4.64 ± 0.00**	274 ± 5	5.67 ± 0.06
50	4.10–6.54	6.01	.55	5.32 ± 0.40	1.27 ± 0.08	49 ± 4	4.19 ± 0.03
	6.31–7.69	7.00	.34	11.08 ± 0.29	2.52 ± 0.02	115 ± 1	4.40 ± 0.08
	7.50–8.67	8.83	.56	32.82 ± 2.83	6.19 ± 0.69	370 ± 37	5.31 ± 0.14
58	5.79–6.91	6.31	.27	5.70 ± 0.03	1.35 ± 0.07	64 ± 1	**4.23 ± 0.20**
	6.67–8.35	7.27	.47	14.33 ± 1.03	**3.18 ± 0.08**	153 ± 1	**4.50 ± 0.21**
	7.40–8.49	7.33	.31	37.08 ± 1.02	**7.05 ± 0.10**	434 ± 3	**5.26 ± 0.07**
Wild larvae[2]							
Group I	7.29–7.45	7.34	.09	19.05	**4.19**	212	**4.55**
II	5.80–6.71	6.41	.53	—	**2.48**	131	—
III	6.54–7.54	6.95	.41	25.36 ± 3.20	**5.45 ± 0.34**	376 ± 43	**4.65 ± 0.41**

[1]Standard length data for cultured larvae are means ± 1 SD for 50 to 150 larvae. Chemical data are for two replicates consisting of 10 larvae each except for the largest size group on days 43, 50, and 58 when only 5 larvae were used per replicate.
[2]In this sample, 6 of the 10 fish had metamorphosed.
[3]In this sample, all fish had metamorphosed.
[4]Data for Groups I and II represent values for pools of three larvae each. Data for Group III are means ± 1 SD for five larvae analyzed individually.

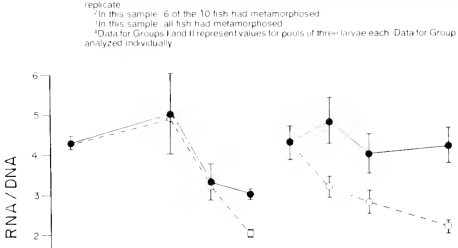


FIGURE 2.—RNA-DNA ratios of starved and fed winter flounder larvae. Open circles indicate values for larvae transferred to filtered seawater on day 3 and day 28. Brackets indicate ± 1 SD.

in the group, occurred 7 days after transfer to filtered seawater, accounting for the high DNA, RNA, and protein values observed on the final day of sampling (day 36). The RNA-DNA ratio of larvae transferred to filtered seawater decreased continually until a 100% mortality was observed. No significant change in the RNA-DNA ratio of fed larvae was observed during the same period (Figure 2). The DNA, RNA, and protein content of different size groups of wild and cultured larvae through metamorphosis is shown in Table 2.

Discussion

The DNA, RNA, and protein content of winter flounder eggs reported in this study are total values for the yolk plus the embryo. Any increase in the amount of a particular component must therefore result from synthesis rather than transfer from the yolk to the embryo. The continual net accumulation of DNA from fertilization to hatching is probably correlated with an increase in cell number (Regnault and Luquet 1974) although the content of DNA per cell may decrease (Neyfakh and Abramova 1974). The small increase in protein content during the same period is evidence that protein is not an important energy source during early development in winter flounder. The 46% decrease in protein content between the maximum 3 days prior to hatching and the

minimum at initiation of feeding on day 7 indicates that protein is probably an important energy source during this period although this includes a 22% decrease in protein upon hatching, the majority of which may be lost with the chorion. Two periods of decrease in RNA content were observed. One occurred just prior to hatching; the other just prior to feeding initiation. No significant net decrease in the DNA content of eggs or fed larvae was observed between any sampling periods.

The decrease in protein and RNA content (Figure 1) as well as the decrease in the RNA-DNA ratio (Figure 2) prior to feeding initiation resembles the pattern observed for starved larvae. Even in the presence of excess food the RNA-DNA ratio fell from 4.9 at the end of the yolk-sac stage to 3.0 at initiation of feeding on day 7. The critical importance of food availability at the initiation of feeding capability was demonstrated 2 days later when fed larvae contain almost 100% more RNA and 55% more protein than larvae held in filtered seawater.

The RNA-DNA ratio was the most reliable and sensitive index of nutritional state evaluated in this study which included relationships between RNA, DNA, protein, standard length, and dry weight. RNA content was the most labile, decreasing within 2 days after removal of food. DNA content was generally conserved except in the final stages of starvation prior to death. The protein-DNA ratio, which is an index of the amount of protein per cell, generally decreased as starvation progressed and the protein-RNA ratio generally increased. The RNA-DNA ratio was particularly useful as an indicator of condition since unlike other indices it fell within well-defined limits throughout most of the period studied. Winter flounder larvae established a mean RNA-DNA ratio of between 4.0 and 4.8 3 wk after initiation of feeding (Figure 2). This range is similar to the RNA-DNA ratio values reported by Bulow (1970) for golden shiners. The RNA-DNA ratio was not greatly affected by either the age or size of the larvae until metamorphosis when the RNA-DNA ratio increased to between 5.3 and 5.7 and remained at this level until the experiment was terminated on day 58 (Table 2). This is particularly important since the age of sea-caught larvae is difficult, if not impossible, to establish and a large size range is observed in larvae of the same age. This point was demonstrated on day 36 when a large mortality of smaller larvae resulted in an increase in the mean DNA, RNA, and protein content of starved larvae. The RNA-DNA ratio, however, was unaffected by the change in size distribution and continued to decrease. Results from larvae transferred to filtered seawater 18 h prior to sampling and allowed to empty their stomachs (Table 1) indicate that the RNA-DNA ratio is not significantly affected by stomach contents at the time of sampling.

The RNA-DNA ratios of winter flounder larvae captured in Narrow River fell within the range of values observed for fed winter flounder in the laboratory. The high RNA-DNA ratios indicated that the larvae were in good nutritional condition. This observation is supported by visual examination of the larvae and the high growth and survival rates of laboratory-reared winter flounder held in situ in Narrow River with a semiopen environmental chamber (Laurence et al. 1979).

Before measurements of RNA-DNA ratios are useful in the field, the effect of changing environmental conditions such as temperature, salinity, and possibly various pollutants as well as low prey concentrations and intermittent feeding should be evaluated. Although adult golden shiners, larval winter flounder, and larval cod, *Gadus morhua*, (Buckley unpubl. data) showed a similar decline in RNA-DNA ratio when food is withheld, the response of other species should be determined.

Acknowledgments

I would like to thank G. C. Laurence and E. Jackim for their critical review of the manuscript.

Literature Cited

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 160:128-136.

BULOW, F. J.
1970. RNA-DNA ratios as indicators of recent growth rates of a fish. J. Fish. Res. Board Can. 27:2343-2349.

CERIOTTI, G.
1952. A microchemical determination of desoxyribonucleic acid. J. Biol. Chem. 198:297-303.

DAGG, M. J., AND J. L. LITTLEPAGE.
1972. Relationships between growth rate and RNA, DNA, protein and dry weight in *Artemia salina* and *Eucheata elongata*. Mar. Biol. (Berl.) 17:162-170.

EHRLICH, K. F.
1974a. Chemical changes during growth and starvation of larval *Pleuronectes platessa*. Mar. Biol. (Berl.) 24:39-48.

1974b. Chemical changes during growth and starvation of herring larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 301-323. Springer-Verlag, Berl.

EHRLICH, K F, J H S BLAXTER, AND R PEMBERTON
1976 Morphological and histological changes during the growth and starvation of herring and plaice larvae Mar Biol (Berl.) 35 105-118
HARTREE, E F
1972 Determination of protein A modification of the Lowry method that gives a linear photometric response Anal Biochem 48 422-427
HINEGARDNER, R T
1971 An improved fluorometric assay for DNA Anal Biochem 39 197-201
HOLM-HANSEN, O, W H SUTCLIFFE, JR., AND J SHARP
1968. Measurement of deoxyribonucleic acid in the ocean and its ecological significance. Limnol. Oceanogr. 13:507-514.
LAURENCE, G C
1975 Laboratory growth and metabolism of winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures Mar Biol (Berl.) 32 223-229
LAURENCE, G C, T A HALAVIK, B R BURNS, AND A S SMIGIELSKI.
1979. An environmental chamber for monitoring "in situ" growth and survival of larval fishes. Trans. Am. Fish. Soc. 108:197-203.
MUNRO, H N, AND A FLECK
1966 The determination of nucleic acids Methods Biochem Anal 14:113-176
NEYFAKH, A A, AND N B ABRAMOVA
1974 Biochemical embryology of fishes *In* M. Florkin and B T Scheer (editors), Chemical zoology, Vol VIII, p 261-286 Acad Press, N.Y
O'CONNELL, C P
1976 Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard J Exp Mar Biol Ecol 25:285-312
REGNAULT, M, AND P LUQUET
1974 Study by evolution of nucleic acid content of prepuberal growth in the shrimp *Crangon vulgaris* Mar Biol (Berl.) 25 291-298
SMIGIELSKI, A S
1975 Hormonal-induced ovulation of the winter flounder, *Pseudopleuronectes americanus* Fish Bull, U S 73:431-438
SUTCLIFFE, W H, JR
1965 Growth estimates from ribonucleic acid content in some small organisms Limnol Oceanogr. 10 R253-R258
1970 Relationship between growth rate and ribonucleic acid concentration in some invertebrates J Fish Res. Board Can 27 606-609
THEILACKER, G H
1978 Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae Fish Bull, U S 76 403-414

L J BUCKLEY

Northeast Fisheries Center Narragansett Laboratory
National Marine Fisheries Service, NOAA
R R 7A, Box 522A
Narragansett, RI 02882

EGGS AND EARLY LARVAE OF SMALLMOUTH FLOUNDER, *ETROPUS MICROSTOMUS*

Smallmouth flounder, *Etropus microstomus* (Gill), ranging from early postlarvae to adult were described and illustrated in detail by Richardson and Joseph (1973). Eggs and larvae through yolk-sac absorption had yet to be identified.

During a 1975-76 ichthyoplankton survey of Block Island Sound conducted by Marine Research, Inc. small unidentified planktonic fish eggs were taken. Through subsequent rearing of a number of these eggs and completion of a length series with larger, known larvae, we identified the specimens as *E. microstomus* eggs. Our descriptions of eggs and yolk-sac larvae together with the work of Richardson and Joseph (1973) provide a complete developmental series for identification of this species.

Methods

Sampling was conducted in Block Island Sound at five stations along each of three transects running from Charlestown and East Beach, R.I., to Block Island, a distance of approximately 14.8 km. Collections were made with 60 cm, 0.505 mm mesh, bongo nets. All tows were made obliquely, bottom to surface at approximately 2.5 kn for about 5 min. Digital flowmeters provided volume estimates and quantitative density estimates. Periodically, a 30 cm, 0.505 mm mesh, plankton net was fixed above the bongo net to collect samples of live eggs. These were returned to the laboratory in aerated 4 l thermos jugs and incubated at 20 -21 C. *Etropus microstomus* eggs and larvae were stored in 3-5% buffered Formalin[1] solutions before examination.

Descriptions of the Egg

Etropus microstomus eggs (Figure 1, Table 1) are small, 0.561-0.740 mm in diameter ($\bar{x}$ = 0.64) with a single small oil globule, 0.051-0.165 mm ($\bar{x}$ = 0.12). The egg is spherical with a transparent, unsculptured chorion. The oil globule is also spherical. Occasonally two oil globules were noted or a single one with several surrounding oil particles were found. This condition has commonly been noted for other species (Ahlstrom and Ball

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

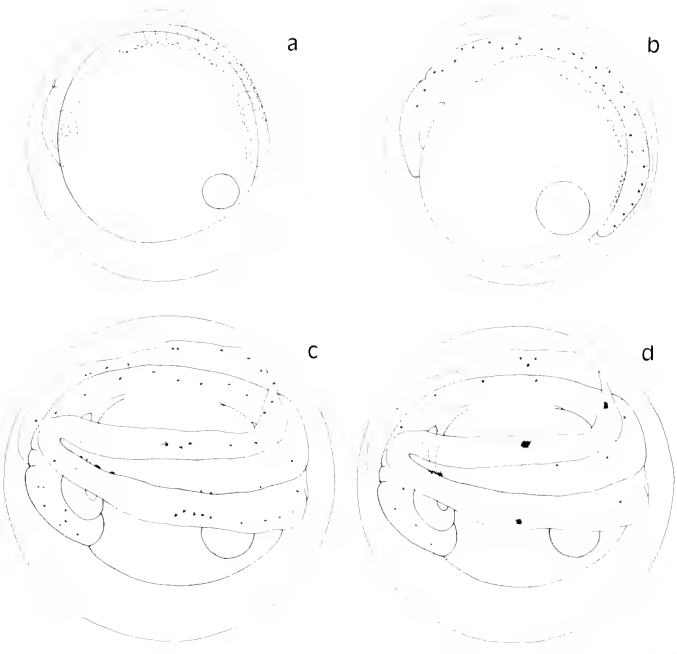


FIGURE 1.—*Etropus microstomus* eggs, mean diameter 0.64 mm: a) middle stage, b-d) development of pigmentation during late stage.

TABLE 1.—Egg, yolk, and oil globule diameters (millimeters) for *Etropus microstomus* eggs taken in Block Island Sound, 1975.

	Egg diameter				Oil globule diameter				Yolk diameter			
Stage	*n*	Mean	SD	Range	*n*[1]	Mean	SD	Range	*n*[1]	Mean	SD	Range
Early	449	0.64	0.02	0.59-0.73	435	0.12	0.01	0.08-0.17	111	0.52	0.03	0.43-0.59
Middle	261	0.65	0.02	0.59-0.71	257	0.11	0.01	0.05-0.13	239	0.55	0.03	0.49-0.61
Late	111	0.65	0.03	0.56-0.74	102	0.11	0.02	0.08-0.15	103	0.56	0.05	0.49-0.69
Total	821	0.64	0.02	0.56-0.74	794	0.12	0.02	0.05-0.17	453	0.54	0.04	0.43-0.69

[1]Discrepancies in sample sizes resulted from shattered oil globules and yolks which were not measured.

1954; Smith and Fahay 1970; Berrien 1975) and is generally believed to result from shattering during collection or preservation. About 75% of the early stage eggs in our preserved samples also contained broken yolks which could not be accurately measured. To facilitate descriptions, eggs were separated into three stages following Ahlstrom and Ball (1954): early (fertilization to

closure of the blastopore), middle (blastopore closure to tail separation), and late (tail separation to hatching).

Early Stage

During this stage, eggs were distinguishable by measurement of egg and oil globule diameters. The yolk occupied about 81% of the egg diameter. It appeared translucent and yellow-to-amber in color with transmitted, incandescent light. With closure of the blastopore the embryo encompassed about half the circumference of the yolk.

Middle Stage

Faint melanophores began to appear on the dorsal surface of the embryo (Figure 1a). They were widely spaced, appeared randomly distributed, and were easily overlooked at magnifications under 50 ×. No pigment was noted on either the yolk or oil globule. Myomeres (12-22) became visible but were difficult to count with any accuracy. The optic vesicles became clearly visible but lacked pigment. By the end of this stage the number of melanophores increased although they were still present only on the dorsum. In some eggs they began to appear more numerous just behind the head while a few developed on the occiput. As the tail developed free of the yolk material, traces of finfold became visible on the posterior edge of the embryo.

Late Stage

Melanophores enlarged so they became clearly visible (Figure 1b). Some developed along the sides and in some cases a few were noted on the yolk near the embryo. Melanophores along the dorsum commonly migrated into a more or less straight middorsal row extending from the nape to the tip of the tail. As the embryo developed, the portion of this line of pigment posterior to the vent migrated into the dorsal finfold while the lateral melanophores migrated into the ventral finfold (Figure 1c). As this occurred, little pigment remained on the trunk except for the anterior portion of the middorsal row. Numerous small dots persisted on the nape and dorsal surface of the head. Once melanophores had migrated into the finfold they began to coalesce into four distinct spots—two in the dorsal and two in the ventral finfolds; the dorsal pair aligned above the ventral pair. An additional group of melanophores aggregated ventrally near the tip of the notochord (Figure 1d). Much of this pigment spot appeared to be in the finfold but it was always in contact with the trunk and often extended upon it. Some of the small melanophores remaining on the anterior dorsum coalesced and moved into the dorsal finfold approximately midway between the vent and head. In some embryos a portion of the finfold melanophores became dendritic before they coalesced.

The oil globule was located posteriorly in the yolk near the developing vent where it remained through hatching. In some advanced, late stage eggs, one or two melanophores formed on the surface of the oil globule. No additional pigmentation developed on the yolk. Shortly before hatching the embryo encircled the yolk with the tip of the tail almost reaching the snout.

Description of Early Larvae

Two recently hatched larvae measured 1.4 mm NL (notochord length) and were essentially identical to advanced late stage embryos. Three dark spots were present near the margin in the dorsal finfold, two near the margin in the ventral finfold, and one along the ventral body margin near the tip of the notochord. Small melanophores were scattered over the dorsum from the occiput to a point about halfway to the tip of the tail. The eyes remained unpigmented. The oil globule was located at the posterior edge of the yolk sac.

By 2.0 mm NL (Figure 2a) no change in pigmentation had occurred. The yolk was reduced in size by about 50% and the gut and vent more clearly defined.

Specimens 2.0 mm NL were obtained from preserved plankton samples where the finfold and its pigmentation were frequently lost. Between 2.1 and 2.3 mm NL (Figure 2b) the yolk sac was fully resorbed, eye pigmentation developed, and larvae developed many of the characteristics described by Richardson and Joseph (1973) for 2.3-2.5 mm larvae. Melanophores developed along the ventral body margin from the gut to the pronounced spot near the tip of the notochord. As these melanophores developed, most or all of the pigmentation on the dorsum was lost. The distinctive markings in the dorsal and ventral finfolds of yolk-sac larvae remained with the exception of the posterior dorsal spot. This spot was either lost as the caudal band, described by Richardson and

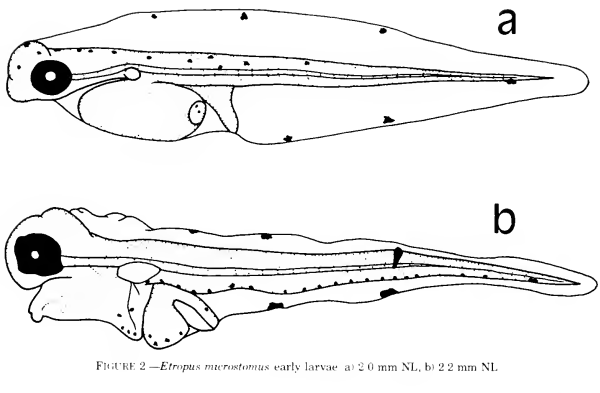


FIGURE 2.—*Etropus microstomus* early larvae: a) 2.0 mm NL, b) 2.2 mm NL.

Joseph, formed or the melanophores migrated ventrally to form all or part of the band. The mid-caudal band was found in larvae as early as 2.1 mm in our collections; it was never observed in larvae still displaying the posterior dorsal finfold spot. The finfold markings appear to have been lost in the 2.5 mm SL (standard length) specimen illustrated by Richardson and Joseph due to finfold mutilation but do appear in their illustrations of 3.5 and 4.5 mm specimens.

The smallest specimen containing pigmentation on the gas bladder in our collections was 2.4 mm. Preopercular spines were first observed at about 2.3 mm. Gas bladder pigmentation and preopercular spines were described by Richardson and Joseph (1973) for their smallest specimen (2.5 mm).

Occurrence

Etropus microstomus eggs were found in our Block Island Sound samples from 11 June until 10 September 1975; sampling was weekly through August, monthly thereafter. Samples taken again on 14 October 1975 did not contain *E. microstomus* eggs. Surface water temperatures during this period ranged from a low of 15.3° C in June to a high of 22.3° C in early August. Larvae were taken from 9 July to 14 October 1975 at which time water temperatures were 15.6° C.

In our weekly 1976 collections, eggs were taken beginning 1 June, larvae beginning 17 June. Both eggs and larvae were found regularly until 26 August when sampling ended. Surface water temperatures averaged 11.9° C on 1 June, 13.2° C on 17 June, and 20.0° C on 26 August.

Similar Species

Prior to formation of the distinctively pigmented embryo in *E. microstomus*, some confusion may occur in separating similar stage eggs of the fourbeard rockling, *Enchelyopus cimbrius*; hakes, *Urophycis* spp.; and butterfish, *Peprilus triacanthus*. According to Scotton et al. (1973), *E. cimbrius* spawns from Nova Scotia to Block Island and *Urophycis* spp. spawn from Nova Scotia to South Carolina, depending upon the species. *Peprilus triacanthus* spawns from Nova Scotia (Scotton et al. 1973) to Chesapeake Bay (Pearson 1941). We regularly collected eggs and larvae of these species in Block Island Sound at the same time that *Etropus microstomus* eggs were taken. Most early and middle stage *E. microstomus* eggs may be distinguished on the basis of their smaller egg and oil globule diameters. Although ranges overlap to some extent (Table 2) mean values for egg and oil globule diameters are fairly distinctive. Only 2% of the 794 eggs we measured contained oil globule diameters ≥ 0.13 mm, the smallest oil

TABLE 2.—Egg and oil globule diameters (millimeters) as reported in the literature for species which might be confused with *Etropus microstomus* eggs. References represent only a portion of those available. Recent literature summaries may be found in Hardy (1978) and Martin and Drewry (1978).

Species	Egg	Oil	Source
Enchelyopus cimbrius	0.65-0.75	0.13-0.15	Battle (1929)
	0.74-0.89 ($\bar{x}$ = 0.82)	0.13-0.20 ($\bar{x}$ = 0.16)	Colton and Marak[1]
Urophycis chuss	0.72-0.76 ($\bar{x}$ = 0.74)	0.15-0.17	Bigelow and Welsh (1925)
	0.62-0.97 ($\bar{x}$ = 0.76)	0.15-0.22 ($\bar{x}$ = 0.19)	Colton and Marak[1]
Urophycis regius	0.67-0.81 ($\bar{x}$ = 0.73)	0.14-0.22 ($\bar{x}$ = 0.18)	Barans and Barans (1972)
Peprilus triacanthus	0.69-0.80 ($\bar{x}$ = 0.75)	0.14-0.22 ($\bar{x}$ = 0.18)	Wheatland (1956)
	0.75-0.79 ($\bar{x}$ = 0.77)	0.17-0.21 ($\bar{x}$ = 0.20)	Colton and Honey (1963)

[1]Colton, J. B., Jr., and R. R. Marak. 1969. Guide for identification of the common planktonic fish eggs and larvae of continental shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Lab. Ref. 69-9, Woods Hole Biol. Lab., 43 p.

globule diameter reported for the other species. Once pigmentation appears on the embryo, distinction is greatly facilitated. *Enchelyopus cimbrius* and *Urophycis* spp. are easily separated by their heavier and more numerous melanophores. Heavy mealonophores are always scattered on the yolk and oil globule of *Urophycis* spp. while *E. cimbrius* have pigmented oil globules and occasionally pigmented yolk. *Peprilus triacanthus* are somewhat more difficult to separate because, like *Etropus microstomus* they have fine melanophores located on the dorsum. However, this pigment generally forms two distinct rows from the eyes to the tail in *P. triacanthus* and does not migrate into the finfold as it does in *E. microstomus*.

Eggs of Gulfstream flounder, *Citharichthys arctifrons*, may resemble *E. microstomus* eggs since the early larvae are quite similar (Richardson and Joseph 1973). Diameters of unfertilized eggs given by Richardson and Joseph ranged from 0.70 to 0.82 mm ($\bar{x}$ = 0.74) which is considerably larger than *E. microstomus*. Presumably water hardening would increase this diameter even further.

Acknowledgments

We are grateful to Masahiro Dojiri for the illustrations.

Literature Cited

AHLSTROM, E. H., AND O. P. BALL.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:209-245.

BARANS, C. A., AND A. C. BARANS.
1972. Eggs and early larval stages of the spotted hake, *Urophycis regius*. Copeia 1972:188-190.

BATTLE, H. I.
1929. Effects of extreme temperatures and salinities on the development of *Enchelyopus cimbrius* (L.). Contrib. Can. Biol. Fish., New Ser. 5:109-192.

BERRIEN, P. L.
1975. A description of Atlantic mackerel, *Scomber scombrus*, eggs and early larvae. Fish. Bull., U.S. 73:186-192.

BIGELOW, H. B., AND W. W. WELSH.
1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(1), 567 p. (Doc. 965.)

COLTON, J. B., JR., AND K. A. HONEY.
1963. The eggs and larval stages of the butterfish, *Peronotus triacanthus*. Copeia 1963:447-450.

HARDY, J. D., JR.
1978. Development of fishes of the Mid-Atlantic Bight. An atlas of egg, larval, and juvenile stages. Vol. II. Anguillidae through Syngnathidae. U.S. Fish. Wildl. Serv., Biol. Serv. Program, 458 p.

MARTIN, F. D., AND G. E. DREWRY.
1978. Development of fishes of the Mid-Atlantic Bight. An atlas of egg, larval, and juvenile stages. Vol. VI. Stromateidae through Ogcocephalidae. U.S. Fish Wildl. Serv., Biol. Serv. Program, 416 p.

PEARSON, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish Wildl. Serv., Fish. Bull. 50:79-102.

RICHARDSON, S. L., AND E. B. JOSEPH.
1973. Larvae and young of western north Atlantic bothid flatfishes *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. Fish. Bull., U.S. 71:735-767.

SCOTTON, L. N., R. E. SMITH, N. S. SMITH, K. S. PRICE, AND D. P. DE SYLVA.
1973. Pictoral guide to the fish larvae of Delaware Bay with information and bibliographies useful for the study of fish larvae. Delaware Bay Rep. Ser. 7, Coll. Mar. Stud., Univ. Del., 206 p.

SMITH, W. G., AND M. P. FAHAY.
1970. Description of eggs and larvae of the summer flounder, *Paralichthys dentatus*. U.S. Fish Wildl. Serv., Res. Rep. 75, 21 p.

WHEATLAND, S. B.
1956. Oceanography of Long Island Sound, 1952-1954. VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanogr. Collect., Yale Univ. 15:234-314.

MICHAEL D. SCHERER
DONALD W. BOURNE

Marine Research, Inc.
141 Falmouth Heights Road
Falmouth, MA 02540

EVIDENCE OF POSTCAPTURE INGESTION BY MIDWATER FISHES IN TRAWL NETS

The ingestion of food items by midwater fishes in trawl nets, if it occurs at appreciable levels, may pose serious bias problems for dietary studies based on stomach content analyses. In a recent discussion of "net feeding," Hopkins and Baird (1977) reviewed the available evidence and found that while it may occur to some degree, net feeding is probably not extensive. In an earlier field study, Hopkins and Baird (1975) used side-by-side nets that provided captured fishes with different levels of exposure to captured zooplankton. On one side the fish were allowed to enter the cod end of the net and mingle with the zooplankton concentrated there. In the adjacent net fishes were excluded from the cod end by an 11 mm mesh bag at its mouth. Their results from 19 intraspecific comparisons of 700 myctophid and gonostomatid fishes showed little significant data that indicated net feeding.

All of the evidence to date, both for and against postcapture ingestion, has been indirect. This is because there was no sure way to determine whether a food item had been ingested in the net. The following study was conducted in order to provide a more direct investigation of stomach content contamination.

Methods

Experiments were conducted by introducing bogus food items into the cod end of a net before launching it, and then examining the stomach contents of captured fishes after recovery. Eleven such hauls were made with Tucker-type midwater trawls in deep water off southern California (Table 1). The nets had a main scoop of 6 mm nylon mesh and a rear section of 0.333 mm plankton netting. The 9 m^2 net utilized an enclosed, bag-type cod end (Baker et al. 1973) on two hauls (10, 11) and a rigid closing cod end (Childress et al. 1978) on three hauls (7, 8, 9). Both of these cod ends are of the flow-through variety and allow the passage of water out the rear. The 2.3 m^2 net had a rigid, nonclosing, 3.7 l plastic jug cod end that restricted flow.

Prior to launching the trawl, approximately 100 ml (or about 3,000 pieces) of artificial prey were placed in the cod end. In all cases, the amount of bogus prey introduced was much less than the eventual catch of similarly sized zooplankton in the cod end. The material consisted of rubber band fragments and bits of filter paper, between 2 and 15 mm in greatest dimension. Their individual volumes ranged between 0.5 and 60 mm^3, which falls within the size range of natural prey items. Upon recovery, the cod end samples were preserved initially in 10% formaldehyde then transferred to 50% isopropanol. In the laboratory, fish stomachs were removed from the body cavity before being opened for examination. Only material from intact stomachs was counted, material found in the mouth and esophagus was not recorded. Data from haul 23 are biased toward larger individuals because the smallest specimens in the catch were not examined. Percent net feeding represents the relative number of individuals of any species which had ingested at least one bogus prey item. It is necessarily a conservative representation because zooplankton from the cod end may also have been ingested after capture but could not be distinguished from naturally ingested prey.

TABLE 1.—Trawling data for the ingestion experiments at Santa Barbara (SB) and San Clemente (SC) Basins, and off Guadalupe Island (GI), Calif.

Haul no	Date 1977	Location	Mouth opening (m^2)	Day/ night	Depth (m)	Duration (min)
1	Apr 12	SB	2.3	N	0-190	60
2	12	SB	2.3	N	0-130	50
3	13	SB	2.3	N	0-150	50
4	13	SB	2.3	D	0-500	95
5	14	SB	2.3	D	0-400	100
6	14	SB	2.3	D	0-590	145
7	Feb 22	SC	9	D	0-425	80
8	22	SC	9	Evening	483-891	180
9	24	SC	9	D	526-634	165
10	Aug 10	GI	9	D	450-480	90
11	13	GI	9	N	0-150	135

Results

A total of 1,211 specimens were examined, representing 15 midwater fish species. Fifty-nine individuals (5% of the total) from 10 species were found with artificial prey in their stomachs (Table 2). Most of the bogus prey ingested (92%) were small (0.5-6 mm^3) and only four fish had swallowed artificial items >12 mm^3. Generally, the average number per stomach was low (Table 2) but a few fish had their stomachs packed with artificial prey. Only 5 of the 59 fishes containing bogus prey had stomachs which were otherwise empty; all others also contained zooplankton, some portion of which may have been ingested in the cod end.

Notable differences in net feeding occurred both interspecifically and intraspecifically. The two

TABLE 2.—Occurrence of bogus prey items in the stomachs of midwater fishes. Sizes are standard lengths in millimeters.

Species	No. of fish	Mean size (range)	Fish that net fed			Mean no. bogus prey	°₀ net fed night:day
			Number	Percent	Mean size		
Bathylagus wesethi	35	50(27-84)	0	—	—	—	—
Leuroglossus stilbius	20	60(45-100)	1	5.0	100	1.0	0:100
Cyclothone acclinidens	64	45(26-57)	1	1.6	56	1.0	—
C. signata	89	20(17-38)	0	—	—	—	—
Poromitra crassiceps	6	44(34-75)	1	16.7	75	3.0	—
Scopelogadus m. bispinosus	13	55(43-69)	0	—	—	—	—
Lampanyctus nitetri	14	77(39-100)	7	50.0	68	3.8	0:50
L. regalis	15	42(35-53)	0	—	—	—	—
Parvilux ingens	11	71(35-172)	0	—	—	—	—
Stenobrachius leucopsarus	138	52(24-82)	32	23.2	61	2.3	5:47
Symbolophorus californiensis	6	48(30-62)	2	33.3	60	3.5	0:67
Triphoturus mexicanus	742	56(19-67)	11	1.5	50	1.2	1.2
Ceratoscopelus townsendi	22	42(33-46)	2	9.1	44	19.5	0:100
Sternoptyx diaphana	20	29(14-37)	1	5.0	37	1.0	0.7
Idiacanthus antrostomus	16	175(63-318)	1	6.3	231	1.0	0:25
Total	1,211		59				

TABLE 3.—Haul by haul comparisons of postcapture ingestion by *Stenobrachius leucopsarus*. Measurements are standard lengths in millimeters.

Item	Nighttime hauls		Daytime hauls		
	1	2	4	5	6
Number of fish examined	48	25	21	26	13
Mean size (range)	46(26-68)	50(30-81)	60(32-79)	53(34-70)	51(36-69)
Number net fed	3	1	12	10	6
Percent net fed	6.3	4.0	57.1	38.5	46.2
Mean size net fed	54	59	64	59	60
Number of fish >51 mm	23	15	19	17	11
Percent fish >51 mm net fed	13.0	6.7	63.2	58.8	54.5
Mean number bogus prey stomach	1.3	1.0	2.0	3.4	1.7
Number of fish net fed/hour	3.0	1.25	7.5	5.9	2.5

most abundant fishes in the collection, myctophids *Stenobrachius leucopsarus* and *Triphoturus mexicanus*, showed a large difference in the percentage of individuals which had ingested the bogus prey items (23.2% vs. 1.5% respectively). In 8 of the 10 species that showed net feeding, larger-than-average individuals were more likely to contain artificial prey than smaller ones.

A haul by haul comparison of data on *S. leucopsarus* (Table 3) shows a greater degree of net feeding in daytime hauls than at night; although the average size of specimens in nighttime hauls is smaller (*t*-test, $P < 0.001$). If we consider only those specimens which were equal to or larger than the smallest individual found with bogus prey in its stomach (51 mm), the trend for greater daytime net feeding still holds. All other species also showed a higher incidence of daytime net feeding (Table 2).

Discussion

The ingestion of bogus prey items by midwater fishes is direct evidence that the contamination of stomach contents can and does occur in the cod ends of midwater trawls. The degree to which it occurs, and thus the seriousness of the bias imparted to dietary studies, is apparently variable. Within a collection of midwater fishes, our data and that of Hopkins and Baird (1975, 1977) indicate that overall the bias may be low. However, the data from the present study showed that important levels of contamination can occur within some species. Hopkins and Baird (1975) based their low estimates of net feeding on intraspecific comparisons of their paired net data. The same data, when examined interspecifically, reveals that in 14 of 19 comparisons (700 fish from 11 species), fishes prevented from reaching the cod end had a lower average number of prey items in their stomachs than fishes which had entered the cod end. The probability of finding no difference in the number of prey items between these samples (i.e., no net feeding) is < 10% (Wilcoxon matched pair signed rank test); thus their data indicating net feeding is significant to at least the 90% level of confidence.

Several factors may be responsible for the observed variations in degree of net feeding. The condition and viability of captured fishes is certainly a key factor; hardy species such as *S. leucopsarus* and *Symbolophorus californiensis* commonly survive capture and arrive at the surface alive and active. The survival of other fishes

(e.g., *T. mexicanus*, *Cyclothone acclinidens*, *C. signata*, *Sternoptyx diaphana*) is usually quite low. Obviously a dead fish cannot swallow cod end material while a stressed but living fish may. The survival factor may have caused some of the differences between our results and those of Hopkins and Baird (1975); off California the survival rate of trawled specimens is relatively high (Childress et al. 1978) while in the Gulf of Mexico it is very low (T. L. Hopkins and R. C. Baird, pers. commun.). Survival rate is probably influenced by haul duration, the depth and temperature range sampled, cod end design, and net construction.

It is also apparent that specimen size can influence the degree of net feeding. It is not clear whether this is due to the greater survival rate of larger individuals or to their larger mouth size. Within the limits of survival rate and size variables, the degree of exposure to prey in the cod end is a function of haul duration, the depth strata sampled, and the amount of time a fish spends in the cod end. Discrete-depth hauls probably decrease the degree of exposure by limiting the number and diversity of prey items while oblique hauls increase exposure. The data also indicate that small prey are more readily ingested in cod ends than large prey. Accordingly, the bias imparted to stomach content analyses by net feeding would be toward the smaller prey items.

Postcapture ingestion is a complex problem and no clear-cut conclusions can be drawn from the available data except that it occurs to a varying degree and that the extent of its occurrence is subject to fish survival, fish size, and exposure. To gain a predictive capability it will be necessary to investigate these factors further.

Acknowledgments

We thank J. L. Cox, J. J. Childress, L. B. Quetin, J. J. Torres, and D. K. Vaughan for their help at sea and in the laboratory. We are grateful to T. L. Hopkins and R. C. Baird for their reviews of the manuscript. The research was supported in part by NSF grants OCE76-02251, OCE78-09018, and OCE76-10407-1. Preliminary and experimental studies were conducted aboard the research vessels *Alpha Helix*, *Velero IV*, and *Ellen B. Scripps*.

Literature Cited

BAKER, A. DEC., M. R. CLARKE, AND M. J. HARRIS
1973. The N.I.O. combination net (RMT 1 + 8) and further developments of rectangular midwater trawls. J. Mar. Biol. Assoc. U.K. 53:167-184.

CHILDRESS, J. J., A. T. BARNES, L. B. QUENTIN, AND B. H. ROBISON.
1978. Thermally protecting cod ends for the recovery of living deep-sea animals. Deep-Sea Res. 25:419-422.

HOPKINS, T. L., AND R. C. BAIRD
1975. Net feeding in mesopelagic fishes. Fish Bull., U.S. 73:908-914.
1977. Aspects of the feeding ecology of oceanic midwater fishes. *In* N. R. Anderson and B. J. Zahuranec (editors), Oceanic sound scattering prediction, p. 325-360. Plenum Press, N.Y.

THOMAS M. LANCRAFT
BRUCE H. ROBISON

Marine Science Institute
University of California
Santa Barbara, CA 93106

INHIBITORY EFFECT OF THE ALGA *PAVLOVA LUTHERII* ON GROWTH OF MUSSEL, *MYTILUS EDULIS*, LARVAE

The culture of bivalve larvae sometimes appears to be more of an art than a science. Many factors can influence the growth and survival of larvae and it is usually difficult to assign a cause to the failure of a particular culture. In one instance we had set up a large experiment with mussel, *Mytilus edulis*, larvae and noticed after 5-8 days that the larvae had ceased to grow in all of our treatments but that they remained alive and active. During this experiment one factor was known to have been changed: Previously we had been feeding the larvae a mixture of the algae *Isochrysis galbana* and *Pavlova lutherii*, while in this experiment only *P. lutherii* was available.

There has been one account in the literature (Fretter and Montgomery 1968) of *P. lutherii* being toxic; yet Bayne (1965) found *P. lutherii* to support normal growth in *M. edulis* larvae. Davis and Guillard (1958) found *P. lutherii* to be as good as *I. galbana* (and about as good as a mixture of the two) when fed to larvae of *Crassostrea virginica* and *Mercenaria mercenaria*. The results of Wilson (1978) show that *P. lutherii* is as satisfactory as other algae as food for *Ostrea edulis* larvae. In order to determine whether our *P. lutherii* cultures were to blame for the lack of growth we observed, we set up an experiment to compare the growth of mussel larvae when fed several diets of algae.

While testing the species of algae, we decided to include different food levels. If *P. lutherii* were toxic, then its effects may increase with concentration of the algae given to the larvae. Another source of toxic substances could be the algal metabolites which accumulate in the algal cultures. In order to test this, we used two different sources of *P. lutherii*, a young culture and an old one. Bayne (1965) had observed a slightly better growth of *M. edulis* larvae when fed *P. lutherii* from a 4-day-old culture compared with those fed a 13-day-old culture.

Methods

Adult mussels were stimulated to spawn by raising the water temperature from an ambient of 15° C to 22°-24° C. The eggs and sperm from five females and seven males were pooled to give a heterogeneous population of larvae. After 2 days the larvae were placed in the various treatment combinations. In the experiment there were five combinations of algae: a) *Isochrysis galbana* alone; b) *I. galbana* plus *Thalassiosira pseudonana* (added after 1 wk); c) *I. galbana* and *P. lutherii* throughout, plus *T. pseudonana* after 1 wk; d) a young culture of *P. lutherii* harvested 4-7 days after innoculation, and e) an old culture of *P. lutherii* harvested 14-20 days after innoculation. In the mixed algae treatments the two or three species were added in equal proportion by cell number.

There were three feeding protocols used. Cell concentrations were increased gradually over the first week of growth, and although the cell concentrations changed in each protocol they will be referred to as "levels" here for simplicity. The food levels used were: 1) 10,000 cells/ml throughout the experiment; 2) 10,000 cells/ml from day 2 to day 4, 15,000 cells/ml from day 4 to day 6, and 20,000 cells/ml for the rest of the experiment; and 3) 50,000 cells/ml from day 2 to day 4, 100,000 cells/ml from day 4 to day 6, and 500,000 cells/ml for the rest of the experiment.

There were 6 replications in 1 l beakers at each of the food type-food level combinations. All beakers were held at 15° C. The initial density of the larvae at day 2 was 20 larvae/ml. All beakers were sampled when the larvae were 16 days old and up to 10 larvae were measured from each beaker.

Results

The main source of variation in the larval lengths at day 16 was due to the food type, with a smaller but significant portion attributable to the food level and the interaction of these two effects (Table 1). The largest source of variation among the types of food was the difference between the larvae fed only *P. lutherii* and those fed the other food types (Figure 1). There was slightly better growth with the young *P. lutherii* as food at the

TABLE 1.—Analysis of variance on size of *Mytilus edulis* larvae as related to food treatment. Analysis performed on mean larval length for 6 replicates per treatment combination.

Source of variation	df	Mean square	F
Food level	2	2 477.2	24.7**
Food type	4	5,952.9	59.35**
Food level × food type	8	307.1	3.06**
Residual	75	100.3	

**P < 0.01

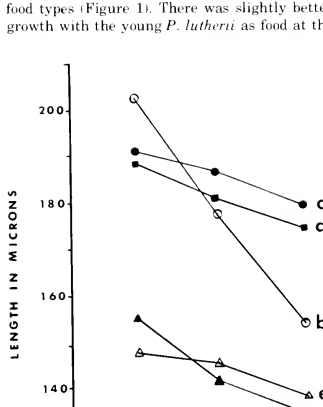


FIGURE 1.—Mean size of mussel larvae at 16 days when grown at three different algal food levels and on five combinations of algal types: a) *Isochrysis galbana* only; b) *I. galbana* and *Thalassiosira pseudonana*; c) *I. galbana*, *T. pseudonana*, and *Pavlova lutheri*; d) young *P. lutheri*; and e) old *P. lutheri*. Means are based on 10 animals from each of 6 replicates at each of the treatment combinations. See text for description of food levels used.

lowest food level compared with the old culture. The interaction of food level and food type was probably in large part due to food type b (*I. galbana* and *T. pseudonana*), which gave the best growth at food level 1 but poor growth at food level 3.

The effect of the food level was to produce higher growth rates at the lower food concentrations. This occurred for all five food types (Figure 1).

Discussion

Contrary to published reports on various bivalve larvae (Guillard 1959; Bayne 1965; Wilson 1978), we have observed poor growth of *M. edulis* larvae when fed only *P. lutherii*. This was true at all three food levels tested and whether the *P. lutherii* culture was young or old. There was no apparent inhibitory effect by the *P. lutherii* on larval growth when fed in combination with the other two algal species. It would appear that the suppression of growth of the larvae when fed only *P. lutherii* was the result of a dietary deficiency. If it were due to toxins in the algal cells, one would expect to see a greater suppression of the growth rate in the larvae at food level 3 when *P. lutherii* was combined with the other algal species.

If the inhibitory effect of *P. lutherii* were primarily due to the accumulation of metabolites in the medium, there should be a more consistent difference between the *P. lutherii* cultures of different age. In fact, there was only a small difference at food level 1. This may indicate that there is some effect of metabolites which were in low enough concentration in the young culture to be diluted at food level 1 but not at the other food levels. Nevertheless, it appears that the main effect of *P. lutherii* is or is equivalent to a dietary deficiency. This could be due to the biochemical compostion of the algal cells such that they are not digested, lack of some essential nutrient, or are not even ingested. The cells are not much bigger than *I. galbana*, especially when fast growing, and there was no evidence of clumping of the cells into large aggregates.

There is some evidence in the data presented by Davis and Guillard (1958) and Bayne (1965) of a suppression of larval growth at high concentration of *P. lutherii*. But to our knowledge there are no reports of suppression of growth in bivalve larvae at lower concentration of *P. lutherii*. This algae has been reported as producing substances toxic to four species of prosobranch larvae (Fretter and Montgomery 1968). Apparently, a toxic substance is emitted by the algae, which accumulates in the algal culture.

The results of the different food levels are not new (Davis and Guillard 1958; Bayne 1965; Rhodes and Landers 1973). The purpose of using different food levels in this experiment was to look for interaction with food type.

At this point we can only speculate as to the reasons for the lack of growth of larvae fed *P. lutherii*. We would not want to generalize and say that all *P. lutherii* could produce the same results. Obviously others have obtained good results with their cultures. (All our algal cultures are grown in the f/2 medium of Guillard (McLachlan 1973), which is commonly used in growing algae for shellfish culture.) One explanation would be that we have inadvertently developed through genetic change a strain of *P. lutherii* which is of inferior quality. Fretter and Montgomery (1968) have suggested that bacteria can metabolize the toxic substance produced by *P. lutherii* and render the algae culture harmless to bivalve larvae. Perhaps the absence of bacteria in our *P. lutherii* cultures, or at least the appropriate bacteria, would explain the discrepancy between our results and others. Unfortunately, we did not check the algal cultures for the presence of bacteria.

The importance of our observations with *P. lutherii* need to be assessed by other workers. The culture conditions of algae will vary from lab to lab and could easily have an influence on the growth of bivalve larvae.

Literature Cited

BAYNE, B. L.
1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1-47.

DAVIS, H. C., AND R. R. GUILLARD
1958. Relative value of ten genera of micro-organisms as food for oyster and clam larvae. U.S. Fish Wildl. Serv., Fish. Bull. 58:293-304.

FRETTER, V., AND M. C. MONTGOMERY.
1968. The treatment of food by prosobranch veligers. J. Mar. Biol. Assoc. U.K. 48:499-520.

GUILLARD, R. R. L.
1959. Further evidence of the destruction of bivalve larvae by bacteria. Biol. Bull. (Woods Hole) 117:258-266.

MCLACHLAN, J.
1973. Growth media—marine. *In* J. R. Stein (editor), Handbook of phycological methods, culture methods and growth measurements, p. 24-51. Camb. Univ. Press, N.Y.

RHODES, E. W., AND W. S. LANDERS
1973. Growth of oyster larvae, *Crassostrea virginica*, of various sizes in different concentrations of the chry-

sophyte *Isochrysis galbana*. Proc. Natl. Shellfish. Assoc. 63:53–59.

WILSON, J. H.

1978. The food value of *Phaeodactylum tricornutum* Bohlin to the larvae of *Ostrea edulis* L. and *Crassostrea gigas* Thunberg. Aquaculture 13:413–423.

G. F. NEWKIRK
D. L. WOOD

Biology Department
Dalhousie University
Halifax, N.S., Canada B3H 4J1

NOAA Technical Reports NMFS published during the first 6 mo of 1979.

Circulars

419. Marine flora and fauna of the northeastern United States. Protozoa: Sarcodina: Amoebea. By Eugene C. Bovee and Thomas K. Sawyer. January 1979, iii + 56 p., 77 fig. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00433-3.

420. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. By James E. Morrow. February 1979, iii + 32 p., 11 plates.

421. Larval development of shallow water barnacles of the Carolinas (Cirripedia: Thoracica) with keys to naupliar stages. By Wilham H. Lang. February 1979, iv + 39 p., 36 fig., 17 tables.

422. A revision of the catsharks, family Scyliorhinidae. By Stewart Springer. April 1979, v + 152 p., 97 fig., 4 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-020-00147-5.

423. Marine flora and fauna of the northeastern United States. Crustacea: Cumacea. By Les Watling. April 1979, iii + 23 p., 35 fig., 1 table. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00446-5.

Special Scientific Report—Fisheries

727. Expendable bathythermograph observations from the NMFS MARAD Ship of Opportunity Program for 1975. By Steven K. Cook, Barclay P. Collins, and Christine S. Carty. January 1979, v + 93 p., 2 fig., 13 tables, 82 app. fig.

728. Vertical sections of semimonthly mean temperature on the San Francisco-Honolulu route, from expendable bathythermograph observations, June 1966-December 1974. By J. F. T. Saur, L. E. Eber, D. R. McLain, and C. E. Dorman. January 1979, iii + 35 p., 4 fig., 1 table, 2 app. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00438-4.

729. References for the identification of marine invertebrates on the southern Atlantic coast of the United States. By Richard E. Dowds. April 1979, iv + 37 p. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00454-6.

730. Surface circulation in the northwestern Gulf of Mexico as deduced from drift bottles. By Robert F. Temple and John A. Martin. May 1979, iii + 13 p., 8 fig., 4 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00456-2.

731. Annotated bibliography and subject index on the shortnose sturgeon, *Acipenser brevirostrum*. By James G. Hoff. April 1979, iii + 16 p. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00452-0.

732. Assessment of the Northwest Atlantic mackerel, *Scomber scombrus*, stock. By Emory D. Anderson. April 1979, iv + 13 p., 9 fig., 15 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00450-3.

733. Possible management procedures for increasing production of sockeye salmon smolts in the Naknek River system, Bristol Bay, Alaska. By Robert J. Ellis and William J. McNeil. April 1979, iii + 9 p., 4 fig., 11 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00451-1.

734. Escape of king crab, *Paralithodes camtschatica*, from derelict pots. By Wilham L. High and Donald D. Worlund. May 1979, iii + 11 p., 5 fig., 6 tables.

Most NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Individual copies of NOAA Technical Reports (in limited numbers) are available free to Federal and State government agencies and may be obtained by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including Zip code.

The **abstract** should not exceed one double-spaced page

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada*. Third Edition, 1970)

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript

Preferably **figures** should be reduced by photography to 5¼ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures) The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper

Do not send original drawings to the Scientific Editor, if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them

Each **table** should start on a separate page. Consistency in headings and format is desirable Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals To avoid confusion with powers, they should be placed to the *left* of numerals

Acknowledgments, if included, are placed at the end of the text

Literature is cited in the text as Lynn and Reid (1968) or (Lynn and Reid 1968) All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations* (*Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, °C (for Celsius), %, ‰ and so forth, should be used Abbreviate units of measure only when used with numerals Periods are only rarely used with abbreviations

We prefer that **measurements** be given in metric units, other equivalent units may be given in parentheses

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper Please triple space above headings We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral, legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Jay C. Quast, Scientific Editor
Fishery Bulletin
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Contents–continued

Notices

DEPARTMENT OF COMMERCE * UNITED STATES OF AMERICA *

Fishery Bulletin

Vol. 77, No. 4

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

Juanita M. Kreps, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881, it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46, the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112. Second-class postage paid at Seattle, WA 98109. Controlled circulation paid to Finance Department, USPS, Washington, DC 20090.

The Director of the Department of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 77, No. 4

(Continued on next page)

Seattle, Washington

1980

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year $12.00 domestic and $15.00 foreign. Cost per single issue $3.00 domestic and $3.75 foreign.

Notes

Vol. 77, No. 3 was published on 30 January 1980.

REVISION OF THE PENAEID SHRIMP GENUS *PENAEOPSIS* (CRUSTACEA: DECAPODA)

ISABEL PEREZ FARFANTE[1]

ABSTRACT

The genus *Penaeopsis*, comprising six species, is defined and its relationships discussed. Five of the species occur in the Indo-West Pacific, *P. balssi*, *P. eduardoi*, *P. challengeri*, *P. jerryi*, and *P. rectacuta*, and one, *P. serrata*, on both sides of the Atlantic. A key for their identification is provided. References, disposition of types, locality records, diagnoses, descriptions, and illustrations for each species are presented. The descriptions, except that of *P. balssi*, are based on material that includes type-specimens. The male of *P. challengeri*, which was not previously known, is described in detail. Intraspecific variation is noted, and distinguishing morphological features as well as affinities are discussed. In addition, geographic and bathymetric ranges are presented, and a graph of depth-temperature relationships of *P. serrata* in four areas within its range is included.

A study of the types of the three species of *Penaeopsis* described by Bate (1881) made obvious not only the need for redescriptions of these specimens, as was pointed out first by Burkenroad (1934a) and most recently by Ivanov and Hassan (1976), but also confirmed the necessity for a revision of the genus. As stated by Perez Farfante (1977b), misidentifications, incomplete descriptions, and lack of detail in some of the illustrations presented by Bate (1881, 1888) have been responsible for much of the persistent confusion in the recognition of the species of *Penaeopsis*. The examination of Bate's types and the study of collections made during the cruises of 26 research vessels have enabled me to: clarify the problems associated with his work; describe two previously unnamed species (Perez Farfante 1977b, 1979), as well as the male of another that had not been known before; prepare detailed accounts of the remaining members of the genus; and determine intraspecific variation. I have also discussed their affinities and delimited their respective geographic and bathymetric distribution. The distributional studies resulted in the restriction of the range of *P. rectacuta* and the considerable extension of that of *P. serrata*, the latter reported by Perez Farfante and Ivanov (1979).

The species of the genus are benthic and, except in the eastern Pacific where none has been recorded, occur in the upper part of the continental and insular slopes of tropical, subtropical, and certain temperate regions of the world. All species have been found in the Indo-West Pacific, except *P. serrata*, which is restricted to the Atlantic, where it is present on both the eastern and western slopes. These shrimps are frequent and often abundant components of the catches made between 250 and 600 m, and two of the species are commercially exploited.

PRESENTATION OF DATA

In the account of the species, most of the terminology used for features of the petasma, thelycum, and appendix masculina follows that proposed by Perez Farfante (1969, 1971). The measurement of rostrum length is the linear distance from apex to orbital margin, that of carapace length (cl) is the distance between orbital margin and the midposterior margin of the carapace, and, finally, that of total length (tl) is the distance from the apex of the rostrum to posterior end of the telson. All measurements are made to the nearest 0.5 mm. The petasmata have been described and depicted unfolded, and the illustrations made from stained specimens.

MATERIAL

Abbreviations of the repositories of the specimens examined during this study follow:

BMNH British Museum (Natural History), London.

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560

Manuscript accepted June 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980

FIU	Department of Biological Sciences, Florida International University, Miami, Fla.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MP	Museum National d'Histoire Naturelle, Paris.
ORI	Oceanographic Research Institute, Durban.
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden.
SAM	South African Museum, Cape Town.
UMML	Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Fla.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
VNIRO	All Union Research Institute of Marine Fisheries and Oceanography, Moscow.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.
ZSI	Zoological Survey of India, Calcutta.

Penaeopsis Bate 1881

Penaeus. Bate 1881:173 [part]. Alcock and Anderson 1899:278. [Not *Penaeus* Fabricius 1798].

Penaeopsis Bate 1881:182 [type-species, *Penaeopsis serratus* Bate 1881, designated by Bouvier 1905a:981]; 1888:273. Bouvier 1905b:747; 1908:3. A. Milne Edwards and Bouvier 1909:220 [part]. De Man 1911:53 [part]. Balss 1925:228. Schmitt 1926:319 [part]. Burkenroad 1934a:48 [part, subgenus *Penaeopsis*]. Kubo 1949:320. Balss 1957:1519 [part]. Burkenroad 1959:285 [Neither *Peneopsis* Faxon 1895, or *Penaeopsis* Yokoya 1941, Barnard 1950]. Gender: feminine. Placed on the Official List of Generic Names in Zoology as Name 1821, International Commission on Zoological Nomenclature 1969, Opinion 864:139.

Parapenaeus Smith 1885:172 [part]. Alcock 1905:519 [part]; 1906:30 [part]. De Man 1911:77 [part]. Balss 1925:228.

Metapenaeus Wood-Mason 1891:271 [part].

Diagnosis.—Body slender, integument glabrous. Rostrum armed only with dorsal teeth; epigastric tooth separated from first rostral tooth by approximately 0.35 length of carapace; two low and sharp adrostral carinae, dorsal one running along bases of teeth. Carapace without longitudinal or transverse sutures; orbital and branchiostegal spines lacking; antennal and hepatic spines moderately long; pterygostomian spine well developed; cervical sulcus well defined, its posterior extremity placed slightly anterior to midlength of carapace, and relatively far ventral to dorsal midline; hepatic sulcus, reaching pterygostomian spine, well marked anteriorly, shallow posterior to hepatic spine; anterior part accompanied by sharp carina; branchiocardiac carina present. Abdomen carinate dorsally from fourth through sixth somites (carina rounded on fourth, keellike on posterior somites, continuous posterolaterally with paired short spines on fourth and fifth somites, and with sharp spine posteriorly); sixth somite bearing interrupted cicatrix on lateral surface, and pair of minute spines posteroventrally. Telson with median sulcus flanked by sharp carinae, and pair of moderately long, fixed lateral spines preceded by two or three pairs of small, movable spines. First article of antennular peduncle bearing long subdistal "parapenaeid spine" on ventromedian margin; antennular flagella with length about 0.75 to almost twice that of carapace; ventral flagellum sexually dimorphic, in male shorter than dorsal and strongly modified, with proximal part forming rigid, flattened, semicircular loop, bearing basal scale and ending distally in usually conspicuous, blunt knob; distal part straight and somewhat compressed. In female, ventral flagellum also bearing basal scale, but straight and longer than dorsal. Mandibular palp two jointed, proximal article short, subtriangular (oriented with base distally), distal article considerably longer than proximal, broadly oval. First maxilla with broad unjointed palp not produced distally. Flagellum of first maxilliped slender, overreaching distal exite of coxa. Third maxilliped lacking basial spine. Basial and ischial spines on first pereopod, always lacking on third. Exopods (small but not vestigial) on all maxillipeds and pereopods. Petasma symmetrical, lacking channeled, hornlike distolateral projections; dorsomedian lobule bearing distal and proximal plates; rib of dorsolateral lobule produced into conspicuous, flattened, proximal process. Appendix masculina small but well developed and relatively heavily sclerotized. Thelycum with well-developed median plate on

sternite XIII, plate on sternite XIV elongate and bearing paired seminal receptacles disposed longitudinally rather than transversely. Pleurobranchia on somites IX-XIII; rudimentary, filamentose arthrobranchia on somite VII, anterior and posterior arthrobranchiae on somites VIII-XII, and only posterior arthrobranchia on somite XIII. Epipod on first maxilliped (if proximal exite of coxa is considered an epipod) and second maxilliped and on first to third pereopods.

In this genus the petasma is structurally very simple, consisting of a plain trough that is neither produced as distal or distolateral hornlike or broad projections, nor bears distal elements associated with the four lobules. The pestasmal lobules are reinforced by plates and ribs: a distal plate and a proximal plate on the dorsomedian lobule, and two longitudinal ribs. One of the longitudinal ribs extends along the dorsolateral lobule and is typically produced proximally as a process the shape of which varies with the species, the other rib forms the ventral costa and occupies the free margin of the ventrolateral lobule. This petasma is similar to that of the genus *Penaeus*, but, in other respects, *Penaeopsis* does not resemble the latter; instead, it is closely related to *Metapenaeopsis* which, surprisingly, exhibits an asymmetrical petasma that is also the most complex among the Penaeoidea.

Small juvenile *Penaeopsis* are armed with an anteriorly directed, sharp spine on sternites XIII and XIV. Both spines disappear in larger males, whereas in females that on sternite XIII is either lost or persists, although considerably reduced, at the apex of the median plate, which, in itself, represents an expansion of the basal portion of the spine. The spine on sternite XIV disappears entirely or becomes incorporated in the median ridge or protuberance of that sternite. As Burkenroad (1934a) has stated, the occurrence of these sternal spines is a larval character present on the postmysis stages of many Penaeidae.

Despite the homogeneity of the few species (six, of which only four were known prior to 1976) currently assigned to the genus *Penaeopsis*, the first three described were assigned to two genera (Bate 1881). Subsequently, various authors have referred Bate's species to four different genera. Schmitt (1926) contributed to our knowledge of the genus when he recognized common superspecific characters in the "small *Penaeopsis serratus*' group." Unfortunately, the characters he chose led him to include within this assemblage two species that are currently recognized as members of the genus *Metapenaeopsis*: *M. coniger* (Wood-Mason 1891) and *M. andamanensis* (Wood-Mason 1891). Schmitt cited the absence of anterior arthrobranchia on somite XIII as one of the characters of the "group," a valid *Penaeopsis* character common to all of the species except those two mentioned above, which he assigned to *Penaeopsis* although he was aware that they possessed such arthrobranchia.

A few years later Burkenroad (1934a) presented an enlightened discussion of two of the four Series—Parapenaeus and Trachypenaeus—into which he (1934b) divided the Penaeinae [= Penaeidae]. His excellent choice of characters for the definition of the genera resulted in very few changes in his classification during the 45 yr that have elapsed since the publication of the two contributions. Among the few alterations that have been made in the taxa recognized by him was the reelevation of *Metapenaeopsis* to generic rank; he had considered *Penaeopsis* and *Metapenaeopsis* to be subgenera of the genus *Penaeopsis*. The members of these two species-groups are closely allied, because both species-groups possess a carapace lacking longitudinal and transverse sutures but bearing pterygostomian spines, two or more well-developed movable spines on the lateral margins of the telson anterior to the fixed pair, and exopods on all maxillipeds and pereopods. However, the two taxa exhibit characters that are now considered to be of generic value, i.e., branchial formula, thelycal features, and basic structure of both the petasma and appendix masculina (for a detailed account of *Metapenaeopsis* see Perez Farfante 1971). These characters were employed by Kubo (1949) in diagnosing the two groups as distinct genera, a revision that is now generally accepted.

Key to Species of *Penaeopsis*

1. Telson bearing three pairs of movable spines 2
   Telson bearing two pairs of movable spines 3

2. Hepatic spine situated at level of antennal spine; branchiocardiac carina long, its anterior extremity close to hepatic sulcus. Thelycum with plate of sternite XIV rounded anterolaterally; median plate of sternite XIII subsemicircular or weakly trilobed ..... *P. jerryi*
   Hepatic spine situated distinctly ventral to level of antennal spine; branchiocardiac carina short, its anterior extremity relatively far from hepatic sulcus. Thelycum with plate of sternite XIV angular anterolaterally; median plate of sternite XIII cordiform ..... *P. rectacuta*
3. Rostrum usually strongly arched, short, in adult reaching at most about midlength of second antennular article. Petasma with proximal process of rib of dorsolateral lobule transversely oval; ventral costa ending distally in broad, roughly semicircular process. Thelycal plate of sternite XIV produced in small lobules and with anterior border straight or, usually, concave on each side of posteromedian projection of sternite XIII; median ridge (sometimes reduced to posterior protuberance) flanked by broad depressions ..... *P. balssi*
   Rostrum not strongly arched, long, in adult overreaching (often considerably) second antennular article. Petasma with proximal process of rib of dorsolateral lobule subrectangular or nearly circular; ventral costa ending distally in spine or subelliptical process. Thelycal plate of sternite XIV weakly to strongly convex on each side of posteromedian projection of sternite XIII, and with neither median ridge nor posterior protuberance flanked by broad depressions 4
4. Petasma with ventral costa produced distally into long spine considerably overreaching level of row of cincinnuli. Thelycum with lateral borders of plate of sternite XIV turning abruptly mesially posterior to midlength, plate bearing short, pedunculate posteromedian protuberance ..... *P. eduardoi*
   Petasma with ventral costa ending distally in blunt, short process or spine not overreaching level of row of cincinnuli. Thelycum with lateral borders of plate of sternite XIV not turning abruptly mesially posterior to midlength, plate bearing long, median ridge or short, subrectangular posteromedian protuberance 5
5. Petasma with ventral costa bearing distolaterally short, flexible projection, and ending distally in rather slender spine, not overreaching level of row of cincinnuli. Thelycum with plate of sternite XIV raised in paired submesial elevations, not produced in lobules anterolaterally, and bearing short, subrectangular posteromedian protuberance sometimes continuous with depressed ridge ..... *P. challengeri*
   Petasma with ventral costa lacking projection, and ending distally in blunt, relatively broad process. Thelycum with plate of sternite XIV raised laterally, produced in lobules anterolaterally and bearing long, ovoid, tear-shaped or subtriangular ridge ..... *P. serrata*

Penaeopsis balssi Ivanov and Hassan 1976

Figures 1-6

Penaeopsis challengeri?. Balss 925:228, fig. 4 [not *Penaeopsis challengeri* De Man 1911].

Penaeopsis serratus. Ramadan 1938:68, fig. 13a-d [not *Penaeus serratus* Bate 1881, or *Penaeopsis serratus* Bate 1881].

?*Penaeopsis rectacuta*. Kensley 1969:154 [not *Penaeus rectacutus* Bate 1881].

Penaeopsis rectacuta. Kensley 1972:20, fig. 8G-I [not *Penaeus rectacutus* Bate 1881].

Penaeopsis serrata. Starobogatov 1972:390, fig. 40. Crosnier and Jouannic 1973:11, pl. 2, fig. 3 [not *Penaeus serratus* Bate 1881, or *Penaeopsis serratus* Bate 1881].

Penaeopsis balssi Ivanov and Hassan 1976:1, fig. 1-2 [holotype, ♀, Zool. Mus. Acad. Sci. U.S.S.R. Leningrad, 1/62552; type-locality, off southern Mozambique, 25°26′ S (not 23°26′ S as stated in original description, Boris G. Ivanov[2]), 33°31′ E, 410 m, *Van Gogh* stn 264]. Perez Farfante 1977b:173.

Material.

KENYA—2 ♀, BMNH, off mouth of Tana

[2]Boris G. Ivanov, All Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow, pers. commun. 1979.

River, Kipini, staff Institute of Oceanographic Sciences. 3♀, BMNH, off Formosa Bay, 290 m, 15 February 1975, staff Institute of Oceanographic Sciences. 1♂ 1♀, USNM, off Ras Ngomeni, 300-310 m, 12 December 1975, *Professor Mesyatsev.* 4♀, BMNH, off Kenya, 15 February 1975, staff Institute of Oceanographic Sciences.

TANZANIA—3♀, BMNH, Pemba Channel, 329 m [in Sewell 1935], 14 January 1934, John Murray Expedition stn 110. 1♀, BMNH, Pemba Channel, 439 m, 12 January 1934, John Murray Expedition stn 107. 11♂ 17♀, BMNH NW of Zanzibar I, 280 m, 11 January 1934, John Murray Expedition stn 105A. 2♂ 2♀, RMNH, off Kunduchi, 20 km N of Dar es Salaam, 370-400 m, July 1974, C. Sankarankutty.

MOZAMBIQUE—4♀, USNM, Monte Belo, 270 m, 28 October 1975, E. Sorensen.

SOUTH AFRICA—4♂, USNM, 1♀, ORI, off Zululand, Natal, 280 m, A. J. de Freitas. 3♂ 11♀, SAM-USNM, off Natal, 454-280 m, 25 May 1975, *Meiring Naude* stn SM15.

Diagnosis.—Rostrum arched (usually strongly so) and short, reaching at most midlength of second antennular article. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing strong mesial crest; proximal process of rib of dorsolateral lobule suboval and directed mesially; ventral costa ending distally in roughly semicircular process. Thelycal plate of sternite XIV with anterior border usually concave on each side of posteromedian projection of sternite XIII and distinctly slanting posterolaterally; median ridge broadest and highest posteriorly, usually gently tapering anteriorly (sometimes reduced to posterior protuberance), and flanked by deep, broad depressions; median plate of sternite XIII subtriangular to orbicular.

Description.—Rostrum (Figure 1) usually markedly arcuate (always strongly so in young), deep basally, and short, in adult reaching at most midlength of second antennular article, its length ranging from about 0.35 to 0.45 that of carapace. Rostral plus epigastric teeth 9-13; rostral teeth evenly spaced and close together along entire margin, second rostral tooth, occasionally third, located in line with orbital margin. Postrostral carina extending posteriorly for short distance beyond epigastric tooth, ending at level of dorsal extremity of cervical sulcus; small dorsal tubercle (occasionally indistinct) located near posterior margin of carapace. Antennal spine slender, sharp, and followed by short but well-defined carina; hepatic spine about as long as, and positioned ventral to but close to level of, antennal spine. Anteroventral angle of carapace (ventral membrane excluded) moderately to broadly obtuse (Figure 2*A*). Cervical carina sharp, accompanying sulcus well marked; hepatic carina descending obliquely in arc anteroventrally from below hepatic spine, then continuing in almost straight line to apex of pterygostomian spine; hepatic sulcus barely distinct posteriorly; branchiocardiac carina strong to almost indistinct, extending posterodorsally in arc, occasionally in sigmoidal curve, from behind hepatic sulcus to rather near posterior margin of carapace.

Mandible, first maxilla, and first maxilliped as illustrated (Figure 3 *A-C*).

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 as long as second in former and 1.45 in latter; prosartema falling conspicuously short of distal margin of eye, but its long setae reaching that far; stylocerite ending in small spine, length about 0.4 that of first article; distolateral spine long, slender, and sharp, reaching base of distal

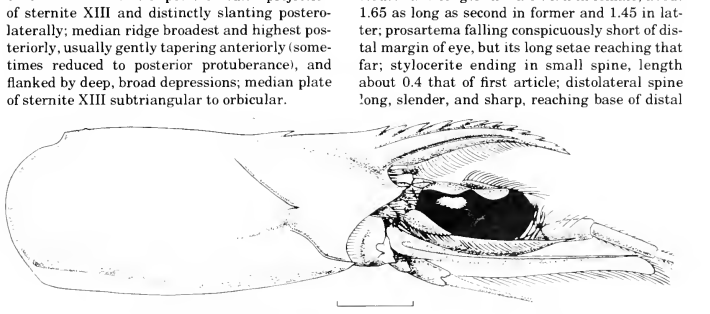


FIGURE 1.—*Penaeopsis balssi*, ♀ 21.5 mm cl, Formosa Bay, Kenya. Cephalothorax, lateral view. Scale = 5 mm.

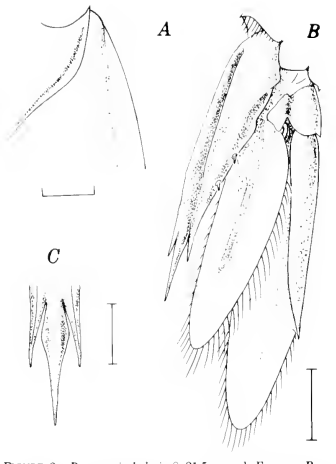


FIGURE 2.—*Penaeopsis balssi*, ♀ 21.5 mm cl. Formosa Bay, Kenya. *A*, Anteroventral part of carapace. *B*, ♂ 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam, Tanzania. Telson and right uropod, lateral view. *C*, Same specimen, tip of telson, dorsal view. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

0.3 of second article. Flagella in both male and female similar to those of *P. rectacuta* (see p. 743).

Scaphocerite falling short of, or slightly overreaching, distal end of antennular peduncle; lateral rib ending in sharp spine not quite reaching terminal margin of lamella. Antennal flagellum incomplete in specimens studied.

Third maxilliped extending at least to base of second antennular article and at most to distal 0.4 length of third; ratio of dactyl/propodus 0.75-0.80.

First pereopod extending to distal end of carpocerite or exceeding it by length of dactyl. Second pereopod surpassing carpocerite at least by dactyl and at most by propodus and 0.2 length of carpus (also reaching between distal 0.3 of first antennular article and about midlength of second). Third pereopod reaching at least to midlength of second article and at most to near end of peduncle. Fourth pereopod overreaching carpocerite by 0.8 length of dactyl or by as much as length of dactyl and propodus. Fifth pereopod extending to distal 0.2 of first article or as far as distal 0.3 of second. Order of pereopods in terms of their maximum anterior extensions: first (shortest), fourth, second, fifth, and third. Third maxilliped falling slightly short of third pereopod.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing almost indistinct, interrupted cicatrix on lateral surface. Telson (Figure 2*B*) armed with two pairs of small, movable spines; pair of fixed spines long, extending about midlength of terminal portion (Figure 2*C*); terminal portion hastate, convex dorsally, its length about 7 times basal width. Mesial ramus of uropod overreaching apex of telson by as much as 0.15 its own length; lateral ramus exceeding mesial one by as much as 0.3 its own length.

Petasma (Figure 4*A*, *B*) with dorsomedian lobule produced in relatively broad distomedian projection, bearing elongate distal plate and subtriangular proximal plate raised mesially in strong crest; rib of dorsolateral lobule terminat-

FIGURE 3.—*Penaeopsis balssi*, ♀ 38.5 mm cl, off Natal, South Africa. *A*, Mandible. *B*, First maxilla. *C*, First maxilliped (all from left side). Scale = 5 mm.

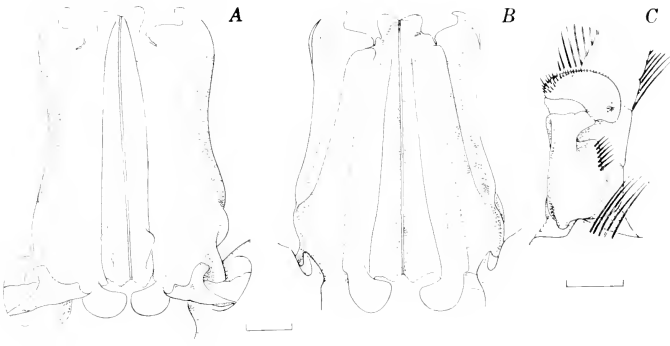


FIGURE 4.—*Penaeopsis balssi*, ♂ 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam. *A*, Petasma, dorsal view. *B*, Ventral view *C*, Right appendix masculina, dorsal view. Scales = 1 mm.

ing proximally in flattened, mesially directed suboval process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part broad (extending beyond level of tip of ventral costa) and slightly reflexed inwardly; distal part of ventral costa curving dorsomesially and ending in conspicuous, subsemicircular process (free from, though closely appressed to, margin of dorsolateral lobule) reaching about level of cincinnuli.

Appendix masculina (Figure 4*C*) transversely oval, about twice as broad as long, dorsally convex but for lateral depression, and bearing mesial patch of long setae continuing as increasingly narrower band of shorter setae along distal margin.

Thelycum (Figure 5) with anterior border of plate of sternite XIV posterolaterally inclined, plate produced into paired rather elongate, small lobules flanking posteromedian projection of sternite XIII, almost flat to distinctly convex ventrolaterally, and abruptly slanting dorsomesially toward deep, usually broad, submedian depressions flanking median ridge; latter broad and most prominent basally, tapering and becoming low anteriorly, sometimes reduced to short basal protuberance; lateral portions of sternite XIV densely studded with long setae, row of similar ones extending along anterior border of thoracic ridge, and others forming patch at base of median

FIGURE 5.—*Penaeopsis balssi*, ♀ 21 mm cl, off Formosa Bay, Kenya, Thelycum ventral view. Scale = 1 mm.

ridge. Median plate of sternite XIII subtriangular to orbicular, densely studded with long setae radiating from naked central depression; posteromedian projection broad, subrectangular, with

posterior margin straight or emarginate. Sternite XII armed with posteromedian subconical tooth (apex slightly displaced anteriorly and sometimes produced in slender spine) and bearing narrow median carina; oblique pair of ridges extending posterolaterally from base of tooth.

Spermatophore similar to that of *P. rectacuta* (see p. 746).

Maximum lengths.—Males 30 mm cl, 128 mm tl; females 37 mm cl, 150 mm tl.

Geographic and bathymetric ranges.—Indian Ocean, off the coast of Africa (Figure 6), from Somalia to Natal, South Africa, and also off Madagascar, at depths between 280 and 977 m (northernmost record and maximum depth from Balss 1925). The records of this species, as well as those of *P. jerryi*, from Madagascar are not included in Figure 6, because Crosnier and Jouannic (1973) reported the occurrence of these shrimps and their bathymetric ranges in the surrounding waters, but did not cite the localities at which they have been found.

Affinities.—*Penaeopsis balssi* can be distinguished readily from other members of the genus by the usually strongly arcuate and short rostrum, which in adults does not surpass midlength of the second antennular article; in the other species it is straight, slightly sinuous or only somewhat arched, and overreaches the second article or often even the peduncle. The structure of the genitalia in *P. balssi* is closer to that of *P. rectacuta* than to those of its other congeners. In the petasma of *P. balssi*, however, the rather flexible, distolateral part of the ventrolateral lobule is broad, and the ventral costa terminates apically in a broad, nearly rounded process, whereas in that of *P. rectacuta* the distolateral part is relatively narrow, and the ventral costa terminates in a much narrower process. Furthermore, the proximal process of the dorsolateral lobule is suboval and directed mesially in *P. balssi*, whereas in *P. rectacuta* it is nearly circular and extends proximally. The thelycum in *P. balssi* has the plate of sternite XIV flat to strongly convex laterally instead of slanting directly from the border as it does in *P. rectacuta*, and its median ridge is more prominent caudally than in the latter species. These two shrimps differ also by the anteroventral angle of the carapace, about 90° in the latter and obtuse in *P. balssi*.

Variation.—In this species the rostrum is usually strongly arched, but in occasional specimens it is only sightly so; the number of rostral teeth ranges from 8 to 12, and although in most specimens the second tooth is situated opposite the orbital margin, in some, the third tooth occupies this position so that two teeth, instead of one, are on the carapace. As in *P. rectacuta*, the scaphocerite falls short of, reaches, or overreaches the end of the antennular peduncle. In males the distomedian projections of the petasma may be asymmetrical (Ivanov and Hassan 1976), and in some their free margin is scalloped; also the rounded distolateral portion of the ventrolateral lobule occasionally is conspicuously expanded distally. In females, the thelycal plate of sternite XIV varies from nearly flat to strongly convex laterally, and the median ridge may extend to, or end before reaching, the posteromedian projection of the median plate of sternite XIII; the latter plate may be subtriangular, cordiform, or orbicular, and its projection has the caudal margin either straight or shallowly emarginate; also, the posteromedian tooth of sternite XII, often low conical, may be produced into a rather long apical spine directed anteriorly.

Remarks.—According to Boris G. Ivanov (see footnote 2) the coordinates provided by Ivanov and Hassan (1976) for *Van Gogh* stn 34, where two female and two male paratypes were obtained, were incorrect, that the latitude should have been cited as 25°23′ S instead of 23°23′ S.

Ramadan (1938) illustrated the thelyca of an adult and two juveniles in different stages of development. In the juveniles, the submesial depressions are represented by paired pits, and the median plate of sternite XIII is well defined and produced into a sharp, slender, apical spine. This latter feature is not included in Ramadan's illustrations but was observed by me during the examination of the juveniles available to Ramadan, which range in size from 8 to 12 mm cl.

Penaeopsis challengeri De Man 1911

Figures 6-10

Penaeus serratus Bate 1881:182 [lectotype, by present action, ♀, BMNH 1978.323; type-locality, off Matuku, Fiji Is., 19°09′35″ S. 179°41′50″ E, 315 fathoms (576 m), *Challenger* stn 173]; 1888:268 [part], pl. 37,

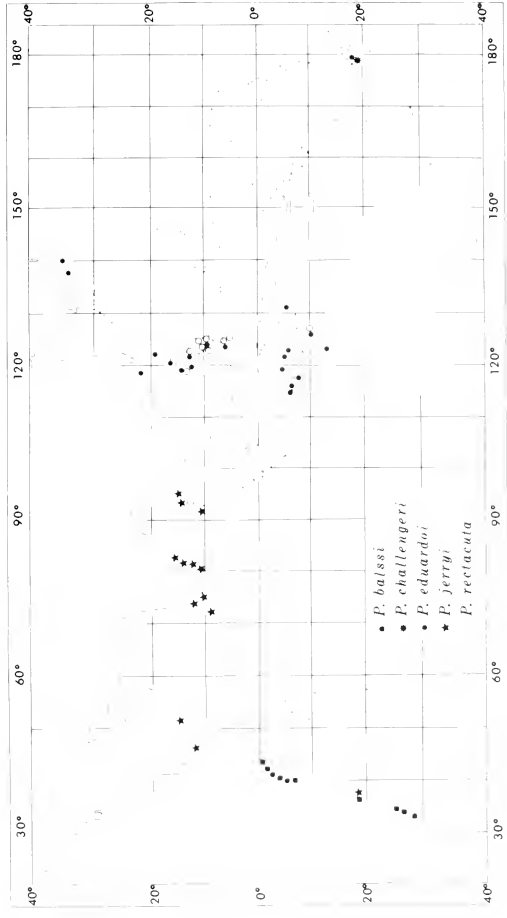


FIGURE 6.—Ranges of *Penaeopsis balssi*, *P. challengeri*, *P. eduardoi*, *P. jerryi*, and *P. rectacuta* based on published records and specimens personally examined

fig. 1, 1a-b, 1'", 1z, 1br. Alcock and Anderson 1899:278. A Milne Edwards and Bouvier 1909:225.

Penaeus (Metapenaeus) serratus. Alcock and Anderson 1894:145.

Parapeneus serratus. Alcock 1905:520; 1906:52.

Penaeopsis challengeri De Man 1911:76 [part, replacement name only; not female from Siboga Expedition stn 253, which belongs to *P. eduardoi*]. Schmitt 1926:325. Ivanov and Hassan 1976:4. Perez Farfante 1977b:173; 1979:208.

Penaeopsis (Penaeopsis) serratus. Burkenroad 1934a:8. Anderson and Lindner 1945:309.

Penaeopsis serratus. Kubo 1949:322.

Penaeopsis serrata. Burukovsky 1974:31.

Not *Penaeopsis serratus* Bate 1881.

Material.

Bate's syntypic series—Lectotype. Paralectotypes:

Fiji Islands—1♂ 3♀, BMNH 1978.324, from type-locality (1♂ from syntypic series assigned to *P. eduardoi* by Perez Farfante 1977b).

Diagnosis.—Rostrum slightly arched. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa bearing flexible distolateral projection and ending distally in moderately long spine, not reaching level of cincinnuli. Thelycal plate of sternite XIV with anterior border strongly arched on each side of posteromedian projection of sternite XIII, raised in submesial elevations, and bearing posteromedian subrectangular protuberance (sometimes continuous with depressed ridge) armed with median tooth anteriorly.

Description.—Rostrum (Figure 7) slightly arched in adult, considerably so in young, and deep basally. Rostral plus epigastric teeth 12 (12 or 13 according to Bate 1888) in single specimen available (male) with rostrum unbroken, second rostral tooth situated in line with orbital margin, rostral teeth close together except for more anterior ones. Postrostral carina extending posteriorly for short distance beyond epigastric tooth, ending at about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine larger than, and positioned distinctly ventral to, antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 8*A*). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sharp, slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina very conspicuous, sinuous, and long, extending from short distance behind posterior end of hepatic sulcus posterodorsally almost to margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.5 times as long as second in former and 1.3 times in latter; prosartema extending to distal margin of first article; distolateral spine slender and sharp, reaching as far as proximal 0.4 of second article; stylocerite ending in small spine, length about 0.4 that of first article. Antennular flagella similar to those of *P. rectacuta.*

Scaphocerite almost reaching or slightly sur-

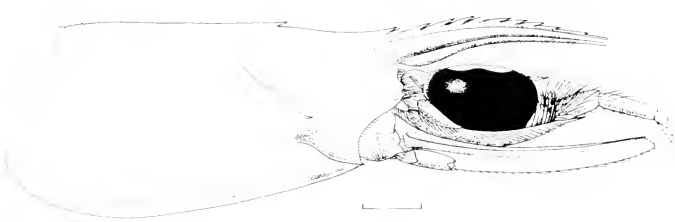


FIGURE 7.—*Penaeopsis challengeri,* lectotype ♀ 24.5 mm cl, off Matuku, Fiji Islands. Cephalothorax, lateral view. Scale = 5 mm.

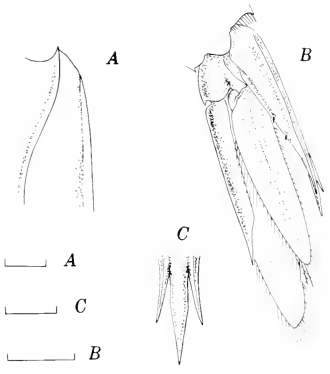


FIGURE 8.—*Penaeopsis challengeri*, lectotype. *A*, Anteroventral part of carapace. *B*, Telson and right uropod, lateral view. *C*, Tip of telson, dorsal view. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

passing distal end of antennular peduncle; lateral rib ending in sharp spine falling short of distal margin of lamella. Antennal flagellum incomplete in available specimens.

Third maxilliped reaching between distal 0.4 of second article and proximal 0.3 of third; ratio of dactyl/propodus about 0.65 in males and 0.75 in females.

First pereopod surpassing carpocerite by half to entire length of dactyl, armed with distomesial spine on basis and ischium. Second pereopod overreaching carpocerite by length of propodus and 0.2 that of carpus (also reaching distal end of first antennular article), with basis and ischium unarmed. Fourth pereopod overreaching carpocerite by length of dactyl and 0.2 that of propodus. Remaining pereopods broken in specimens studied.

Abdomen with sixth somite elongate, about 1.7 times as long as maximum height, bearing barely distinct cicatrix on lateral surface. Telson (Figure 8*B*) with lateral margins armed with two pairs of small movable spines; pair of fixed spines (Figure 8*C*) long, extending as far as base of distal third of terminal portion; terminal portion hastate, distinctly convex dorsally, its length about 5 times basal width. Mesial ramus of uropod slightly overreaching apex of telson (Bate 1888) or overreaching it by as much as 0.2 of its own length, and lateral ramus, in turn, surpassing mesial by as much as 0.3 of its own length.

Petasma (Figure 9*A*, *B*) with dorsomedian lobule produced into well-defined distomedian projection, and bearing small distal plate and

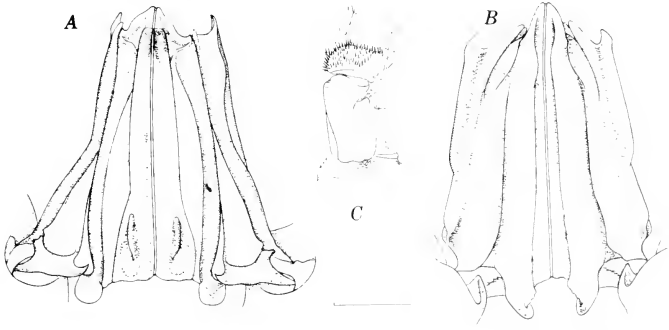


FIGURE 9.—*Penaeopsis challengeri*, ♂ 19 mm cl, off Matuku, Fiji Islands. *A*, Petasma, dorsal view. *B*, Ventral view of same. *C*, Right appendix masculina, dorsal view. Scale = 1 mm.

much larger proximal one, latter raised mesially in conspicuous crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule bearing flexible, roughly triangular, subterminal projection distolaterally; ventral costa continuing beyond projection, curving gently dorsomesially, and forming moderately long blunt spine (free from, although closely appressed to, margin of dorsolateral lobule), not reaching level of row of cincinnuli.

Appendix masculina (Figure 9C) transversely oval (considerably broader than long), strongly convex dorsally, and with about two-thirds of dorsal surface covered with short setae.

Thelycum (Figure 10*A*, *B*) with anterior border of plate of sternite XIV strongly arched (delimiting broad lobes) on each side of posteromedian projection of sternite XIII, and bearing long setae, latter also present along lateral borders; plate raised in paired submesial elevations separated anteriorly by deep depression, sometimes interrupted by low median ridge, and bearing posteromedian, strong, subrectangular protuberance armed with anterior, compressed tooth. Median plate of sternite XIII roughly pentagonal, setose, bearing central depression continous with median groove reaching, or almost reaching, apex; posteromedian projection short, with posterior margin entire. Sternite XII armed with small subconical, posteromedian tooth and oblique paired ridges across posterior border.

Maximum lengths.—Only male available, a juvenile 14 mm cl, 65 mm tl; lectotypic female, 24 mm cl, 114 mm tl.

Geographic and bathymetric ranges.—Known only from the type-locality, off Matuku, Fiji Islands, (lat. 19°09′35″ S, long. 179°41′50″ E), 576 m, *Challenger* stn 173 (Figure 6).

Affinities.—The affinities of *P. challengeri* and *P. balssi* are evident in the rostrum, which in both is arched (although considerably more so in the latter) and deep basally, and in the telsonic armature, which consists of two pairs of movable spines in addition to the fixed pair. *Penaeopsis challengeri*, however, differs strikingly from *P. balssi*, as well as from its other congeners, in the unique structure of the external genitalia. In males of *P. challengeri* the ventrolateral lobule of the petasma bears a flexible, roughly triangular process which does not extend beyond the level of the tip of the ventral costa, and the latter ends distally in a spine similar to, but shorter than, that of *P. eduardoi*. The proximal process of the rib of the dorsolateral lobule is subcircular in *P. challengeri* like that in *P. eduardoi* and *P. rectacuta*, but different from the transversely oval one in *P. balssi*. In females of *P. challengeri* the plate of sternite XIV is produced in paired, broad anterior lobes, is raised ventrally in a pair of longitudinal, submesial elevations, and bears a subrectangular posteromedian protuberance sometimes continuing anteriorly as a weak, depressed ridge. In the other species the plate, if produced, forms only small anterior lobes, is flat or (in *P. balssi*) raised in lateral, rather than submesial,

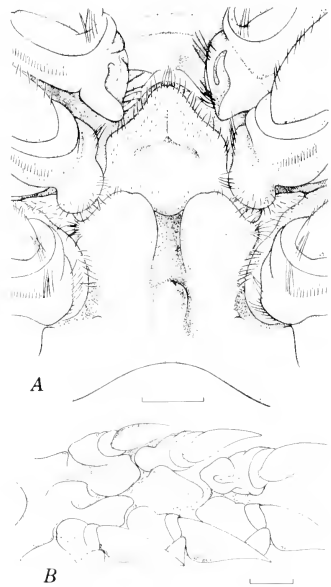


FIGURE 10.—*Penaeopsis challengeri*. *A*, ♀ 22 mm cl, off Matuku, Fiji Islands. Thelycum, ventral view. *B*, Lectotype. Thelycum, ventrolateral view (hairs not shown). Scales = 1 mm.

elevations, and the posteromedian protuberance is caudally peduncuIate in *P. eduardoi* (in the other species a strong median ridge instead of a protuberance is usually present). Finally, in *P. challengeri* the median plate of sternite XIII is subpentagonal instead of semicircular or cordiform and exhibits a central depression which continues anteriorly as a median groove.

Remarks.–As Pérez Farfante (1977b) pointed out, Bate (1888) illustrated the petasma of a male of his *Penaeus serratus* [= *Penaeopsis challengeri*] that actually belongs to a different species, *Penaeopsis eduardoi*. This male together with nine females and at least one other male were taken of Matuku, Fiji Islands, at *Challenger* stn 173. Five of these females were identified by Bate as *Penaeus rectacutus* [they are actually, at least the three that are now in the BMNH, *Penaeopsis eduardoi*], the other four females are syntypes of his *Penaeus serratus*, and the male must be assumed to be a member of the syntypic series. It is beyond question that the male depicted by Bate as *P. serratus* is a specimen of *Penaeopsis eduardoi*: the dorsomedian projections of the petasma are obsolete and each ventral costa is produced in a long spine extending considerably farther distodorsally than that in *Penaeus serratus*. The probability that Bate also examined the syntypic second male (which is *P. serratus*, 65 mm tl) is indicated by his statement "Length . . . of the largest male 76 mm"; this clearly indicates that he had at least one other male in addition to the "largest" one. The smaller male was in the jar with the three females of "*Penaeus rectacutus*" [= *Penaeopsis eduardoi*], but Bate mentioned no male of this species whereas he referred to males of *Penaeus serratus;* consequently, it seems most likely that the small male *P. serratus* was mistakingly placed with the three females of the former species. In regard to the number of male specimens recognized by Bate as "*Penaeus serratus*," it should be mentioned that Alcock and Anderson (1899) stated that "there are two *Challenger* specimens [of *P. serratus*] from Fiji in the Indian Museum" and it is possible that one of them is a male that was examined by Bate.

Inasmuch as the type-material of *P. serratus* Bate included a second species, *Penaeopsis eduardoi*, and a holotype was not designated, it is desirable to select one specimen as the lectotype to associate the name with the species to which it is applied. Although Bate (1888:269) mentioned the "type" of *Penaeus serratus*, there is no indication as to which specimen he was referring; however, he stated that some specimens taken off the Fiji Islands "were placed under *Penaeus rectacutus* because the thelycum corresponds with that species rather than with the type of this [*Penaeus serratus*]." His statement leaves no doubt that it was a female to which he was referring. Because the first specimen specifically cited by him (p. 268) was the "largest female, 114 mm" [24 mm cl], I have selected it as the lectotype of *Penaeus serratus* Bate 1881. This specimen has been assigned BMNH 1978.323.

The very young specimen (a female) taken in the Torres Strait, at *Challenger* stn 184, which Bate (1888) recorded as "*Penaeus serratus*," is actually a member of the genus *Metapenaeopsis*, *M. sinuosa* Dall 1957, or a closely related species.

In the last 45 yr various authors (Burkenroad 1934a; Kubo 1949; Ivanov and Hassan 1976) have pointed out the difficulty in defining the specific characters of "*Penaeus serratus*." The uncertainty was due to Bate's (1881) imprecise original diagnosis and the inadequate, although rather elaborate, description, accompanied by figures lacking detail (e.g., a sketchy one of the thelycum and incomplete representations of the telson which is depicted as lacking movable spines), that was subsequently presented by him (1888). I have studied part of the type-series and offer a new description and illustrations of those specimens, including the only available description of the petasma.

Penaeopsis challengeri, like all of its congeners except *P. rectacuta* and *P. jerryi*, possesses only two pairs of movable spines on the telson. This character was noted by Bate (1888); however, in discussing the relationships of *P. eduardoi* with other members of *Penaeopsis*, I (1977b) erroneously stated that *P. challengeri* exhibits three pairs of movable telsonic spines. The specimens examined by me at the time were the four female syntypes in only one of which the telson is entire, but it had been bent and torn in such a way that its sharp edge projected laterally in what appeared to be a pair of minute movable spines. My confirmation of Bate's observation on the spination of the telson has been based on a reexamination of the just mentioned female, and a study of the male which, although caught together with the four female syntypes of "*Penaeus serratus*," was not explicitly cited by him.

Alcock and Anderson (1899) concluded that "*P.*

serratus" [= *P. challengeri*] lacks an epipod on somite XII (third pereopod), whereas *P. rectacuta* has one. This observation is in error; not only both of these species possess such an epipod, but also its presence is typical of all members of the genus.

Penaeopsis eduardoi Pérez Farfante 1977

Figures 6, 11-14

Penaeus rectacutus. Bate 1888:266 [part], pl. 36, fig. 2z. ? Villaluz and Arriola 1938:38, pl. 3, fig. 3.

Penaeus serratus. Bate 1888:268 [part], pl. 37, fig. 1", 1q.

Parapenaeus rectacutus. De Man 1911:82; 1913, pl. 8, fig. 26a-c. Yokoya 1933:9.

Penaeopsis rectactus. Kubo 1949:322, fig. 1H; 8J; 19C; 23A-B; 36K-L; 47J; 58P; 76A, F; 78K; 118 A-E, [?F], G; 119.

Penaeopsis challengeri. De Man 1911:76 [part, ♀ from Siboga-Expedition stn 253]. Ivanov and Hassan 1976:4.

Penaeopsis rectacutus. Burukovsky 1974:31, fig. 37a-c.

Penaeopsis eduardoi Pérez Farfante 1977b:172, fig. 1-4 [holotype, ♀, USNM 168298; type-locality, Balayan Bay, Luzon I., Philippines, 13°41′00″ N, 120°47′05″ E, 366 m, *Albatross* stn 5116]. Pérez Farfante 1979:208.

Not *Penaeus rectacutus* Bate 1881, or *Penaeus serratus* Bate 1881, or *Penaeopsis challengeri* De Man 1911.

Material.—For list of records see Perez Farfante 1977b. Additional records are:

PHILIPPINES—1♂, USNM, W of Cabo Engaño, N Luzon, 410 m, 12 November 1908, *Albatross* stn 5325. 3♀, USNM, W of San Fernando Pt, Luzon, 315 m, 10 May 1909, *Albatross* stn 5440. 9♂ 8♀, USNM, Balayan Bay, Luzon, 366 m, 20 January 1908, *Albatross* stn 5116. 1♀, VNIRO, Burias Pass, Sibuyan Sea, 400 m, 1 June 1973, *Lira* haul 71. 1♂, USNM, off Calapan, Mindoro I, 198 m, 2 February 1908, *Albatross* stn 5121. 2♂ 1♀, USNM, Macajalar Bay, Mindanao, 479 m, 5 August 1909, *Albatross* stn 5506.

INDONESIA—1♀, USNM, off Tanakeke I, Flores Sea, 386 m, 21 December 1909, *Albatross* stn 5662. 1♀, VNIRO, S of Roti I, Timor Sea, 400 m, 1 June 1973, *Lira*, O. A. Petrov. 1♂ 2♀, VNIRO, S of Timor I, Timor Sea, 320-355 m, 5 May 1973, *Lira*, O. A. Petrov.

Diagnosis.—Rostrum straight or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule lacking mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa lacking distolateral projection and ending distally in long spine extending beyond level of row of cincinnuli. Thelycal plate of sternite XIV with anterior border weakly to distinctly arched on each side of posteromedian projection of sternite XIII and strongly sloping posterolaterally; lateral borders turning mesially behind midlength, then posteriorly; short posteromedian protuberance caudally pedunculate.

Description.—Rostrum (Figure 11) horizontal or somewhat upturned, straight or slightly sinuous (strongly arched in young), and long, reaching at least midlength of third antennular article and often overreaching peduncle, its length ranging from about 0.7 to 0.9 that of carapace. Rostral

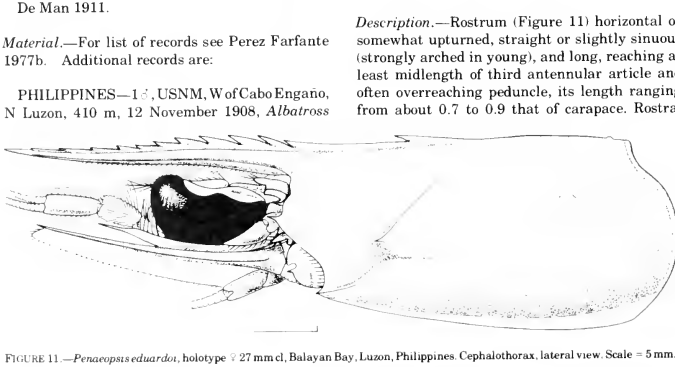


FIGURE 11.—*Penaeopsis eduardoi*, holotype ♀ 27 mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5 mm.

plus epigastric teeth 8-15, basal rostral teeth close together, ultimate 3 or 4 usually relatively widely spaced; first rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth, ending at about posterior 0.4 length of carapace, beyond level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 12A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of ptergostomian spine), hepatic sulcus well marked along carina, very shallow posteriorly. Branchiocardiac carina, extending well behind hepatic sulcus posterodorsally to near margin of carapace, indistinct in many large individuals.

Antennular peduncle with length equivalent to about 0.65 that of carapace, third article stouter and longer in male than in female, about 1.50 as long as second in former and 1.25 in latter; prosartema not quite reaching distal margin of first article; distolateral spine long, slender, and sharp, reaching between basal 0.65 and distal margin of second article; stylocerite ending in small spine, length about 0.4 that of first article. Flagella similar to those of *P. rectacuta*, but ventral flagellum in male with less conspicuous knob at junction between semicircular proximal part and straight distal part.

Scaphocerite extending to, or barely surpassing, antennular peduncle; lateral rib ending in sharp spine ending slightly short of distal margin of lamella. Antennal flagellum broken in specimens examined, but not <2.5 as long as body.

Third maxilliped of male extending as far as distal 0.35 of third antennular article, that of female to distal margin; ratio of dactyl/propodus about 0.70 in male and 0.75 in female.

First pereopod extending to about distal end of carpocerite. Second pereopod overreaching carpocerite by length of dactyl or by almost entire propodus (i.e., reaching at least distal 0.4, at most 0.1, of first antennular article). Third pereopod of male reaching between proximal 0.35 and distal end of second article, that of female, between midlength and distal end of third article. Fourth pereopod extending to distal end of carpocerite or surpassing it by length of dactyl. Fifth pereopod reaching at least midlength of second article or slightly overreaching third. Order of pereopods in terms of their maximum anterior extensions: first, fourth, second, third, and fifth (or fifth, and third). Third maxilliped reaching about as far as fifth pereopod.

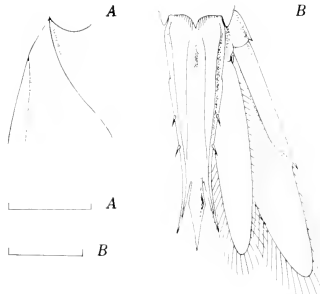


FIGURE 12.—*Penaeopsis eduardoi*, holotype. *A*, Anteroventral part of carapace. *B*, Telson and right uropod, dorsal view. Scales = 5 mm.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather strong, usually interrupted cicatrix on lateral surface. Telson (Figure 12*B*) with lateral margins armed with two pairs of small, movable spines; pair of fixed spines very long, in young reaching level of apex of telson; terminal portion hastate, its length 6-7 times basal width. Mesial ramus of uropod reaching, or slightly overreaching, apex of telson; lateral ramus surpassing mesial one by almost 0.2 of its own length.

Petasma (Figure 13*A*, *B*) with distomedian projection virtually obsolete, distal plate relatively broad, and proximal plate flush with surrounding membranous portion, lacking mesial crest. Rib of dorsolateral lobule terminating proximally in subcircular process. Ventral costa with distolateral portion situated marginally (where bent inward), curving rather gently at about 120° and continuing in long spine distodorsally beyond row of cincinnuli.

Appendix masculina (Figure 13*C*) transversely oval, broader than long, width 1.35-1.60 length, strongly convex dorsally, and bearing short setae around entire margin.

Thelycum (Figure 14) with anterior border of

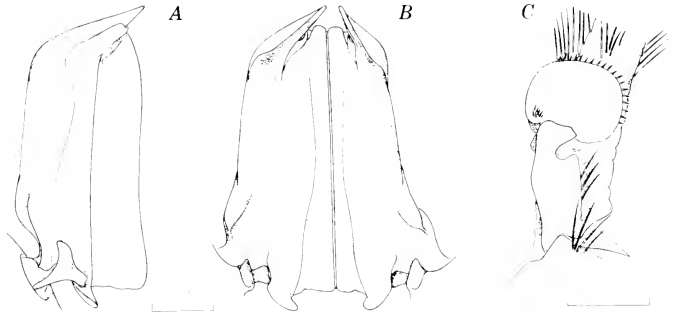


FIGURE 13.—*Penaeopsis eduardoi*, ♂ 16.5 mm cl, off Matuku, Fiji Islands. *A*, Petasma, lateral view of left half. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales = 1 mm

FIGURE 14.—*Penaeopsis eduardoi*, holotype Thelycum, ventral view. Scale = 1 mm.

plate of sternite XIV faintly to distinctly convex on each side of posteromedian projection of sternite XIII, and conspicuously sloping posterolaterally; lateral borders sharply turning mesially behind midlength then posteriorly before joining posterior thoracic ridge; plate densely setose anteriorly, strongly slanting dorsomesially toward deep anteromedian portion, and armed with short, caudally pedunculate posteromedian protuberance. Median plate of sternite XIII semicircular to subcordiform (with blunt apex), flat, covered with setae; posteromedian projection caudally bifurcate. Sternite XII bearing posteromedian, semiconical, broad (rather than compressed) tooth; oblique pair of strong, sharp ridges extending posterolaterally from base of tooth.

Maximum lengths.—Males 26 mm cl, about 114 mm tl; females 34 mm cl, about 130 mm tl.

Geographic and bathymetric ranges.—*Penaeopsis eduardoi* has been found off the Fiji Islands and from Japan through the Philippines and Indonesia to the Timor Sea (Figure 6), in depths between 289 and 570 m.

Previously, Pérez Farfante (1977b) noted that the range of this species extends to the "southwestern part of the Bay of Bengal." In their treatment of "*Metapenaeus rectacutus*" [= *P. jer-*

Maximum lengths.—160 mm tl (Crosnier and Jouannic 1973). Largest specimens examined by me: males 23 mm cl, about 107 mm tl; females 33 mm cl, about 138 mm tl.

Geographic and bathymetric ranges.—Indian Ocean (Figure 6), from the Bay of Bengal (Andaman Sea; off Madras) through the Arabian Sea (off Cochin) to the Gulf Aden (off Berbera) and south to off Mozambique and Madagascar. It has been found at depths between 183 and 677 m.

Affinities.—*Penaeopsis jerryi* differs from the closely related *P. rectacuta*, from the South China Sea, Philippines, and Indonesia, mainly by the position of the hepatic spine, the length of the branchiocardiac carina, and features of the thelycum.

In *P. rectacuta* the hepatic spine is located at a level distinctly ventral to, instead of about the same level as, that of the antennal spine, and the branchiocardiac carina ends farther from the hepatic sulcus than it does in *P. jerryi*.

The petasmata of the two species, although similar, differ in that the rib of the dorsolateral lobule in *P. rectacuta* is straight distally and terminates proximally in a subcircular process, whereas in *P. jerryi* the rib sometimes turns laterally and often ends in a semicircular process.

In *P. rectacuta* the thelycal plate of sternite XIV is usually roughly trapezoidal, with the anterior border almost straight on each side of the posteromedian projection of sternite XIII, and the anterolateral corners forming angles, whereas in *P. jerryi* this plate is roughly elliptical with the anterior border arcuate and the anterolateral and posterolateral corners arched. Finally, in *P. jerryi* the median plate of sternite XIII is subsemicircular [e.g., in females illustrated by Alcock (1906, pl. 6: fig. 19a) and by Ivanov and Hassan (1976, fig. 3) as well as in most of those examined by me], or occasionally weakly trilobed as in the specimen figured by Ramadan (1938, fig. 12b). In a few females I have studied, the plate, although almost semicircular, is produced into a minute anteromedian spine, its general shape thus being quite different from the cordiform median plate of *P. rectacuta*.

In occasional specimens of *P. jerryi*, the basis of the second pair of pereopods is armed with a distomesial spine (Alcock 1901a), a feature that has not been observed in the other species. Also, as pointed out by Ramadan (1938) and confirmed by my observation, some individuals bear less than the tree typical pairs of movable spines on the telson (one or two pairs) and I found one with the spination asymmetrical.

Remarks.—On the basis of the scant information provided by Balss (1925) it has not been possible for me to determine the identity of the two females he recorded as *"Parapenaeus rectacutus"* from the Nicobar Islands, Bay of Bengal. According to him, the telson bears two pairs of movable spines, a characteristic of three of the five Indo-West Pacific members of the genus—*Penaeopsis balssi*, *P. challengeri*, and *P. eduardoi*. In the same work, however, he identified specimens belonging to *P. balssi*, which were taken off east Africa, as *"?Penaeopsis challengeri"*; consequently, it seems very unlikely that the two females belong to *P. balssi*. It also seems improbable that they are members of *P. challengeri* or *P. eduardoi* because these species are not known to occur in the Indian Ocean. Balss added that in his specimens the second pair of pereopods is armed with spines; such have been observed only in occasional individuals of *P. jerryi*; but three, not two pairs of movable telsonic spines are characteristic of this shrimp typically. Balss' specimens, however, may prove to be atypical *P. jerryi* because this shrimp is the only species of the genus that has been recorded from the area.

Commercial importance.—Survey fishing off the west coast of India at depths between 175 and 375 m (George 1966, 1969; Jones 1967; Longhurst 1971) demonstrated the presence of *P. jerryi* in sufficient numbers for possible commercial exploitation of this shrimp. Crosnier and Jouannic (1973) noted that this species eventually will become commercially fished off Madagascar.

Penaeopsis rectacuta (Bate 1881)

Figures 6, 20-27

Penaeus rectacutus Bate 1881:180 [♀ holotype, BNMH; type-locality, between Bohol and Cebu, Philippines, 10°14′ N, 123°54′ E, 95 fathoms (174 m), *Challenger* stn 209]; 1888:266 [part], pl. 36, fig. 2, 2′, 2 p [fig. 2z = *P. eduardoi*]. Estampador 1937:493. Domantay 1956:363. Pérez Farfante 1977b:172.

Parapeneus rectacutus. Alcock 1905:520 [part, references only].

Penaeopsis (Penaeopsis) rectacutus. Burkenroad 1934a:5 Anderson and Lindner 1945:309.

Penaeopsis rectacuta. Hall 1962:18, fig. 89, 89a, 89b. Holthuis and Rosa 1965:3 [part]. Starobogatov 1972, pl. 5, fig. 39a-b (figures, but not key). Pérez Farfante 1977b:180; 1979:208.

Common names: needle shrimp; camarón aguja; crevette aiguille.

Material.

PHILIPPINES—Luzon: 5♂ 10♀, USNM, SW of Nasugbu, 247 m, 15 January 1908, *Albatross* stn 5110. 1♀, USNM, Balayan Bay, 324 m, 17 January 1908, *Albatross* stn 5112. 1♂, USNM, Balayan Bay, 366 m, 20 January 1908, *Albatross* stn 5116. 1♀, USNM, off Malabrigo Pt., 198 m, 2 February 1908, *Albatross* stn 5121. 2♂ 1♀, USNM, Tabayas Bay, 274 m, 24 February 1909, *Albatross* stn 5372. 3♀, USNM, Tabayas Bay, 348 m, 2 March 1909, *Albatross* stn 5374. 2♀, USNM, Albay Gulf, 368 m, 8 June 1909 *Albatross* stn 5459.

Leyte: 2♀, USNM, off Palompon, 344 m, 16 March 1909, *Albatross* stn 5402. 10♂ 13♀, USNM, off Palompon, 333 m, 16 March 1909, *Albatross* stn 5403.

Camotes Is: 2♂ 1♀, USNM, Off Pacijan, 291 m, 18 March 1909, *Albatross* stn 5408. 1♀, USNM, off Pacijan, 346 m, 18 March 1909 *Albatross* stn 5409.

Between Bohol and Cebu (Bohol Strait): Holotype. 1♂, USNM, 274 m, 15 March 1909, *Albatross* stn 5416. 4♂ 3♀, USNM, 265 m, 23 March 1909, *Albatross* stn 5411. 3♂ 9♀, USNM, 296 m, 23 March 1909, *Albatross* stn 5412. 2♀, USNM, 291 m, 25 March 1909, *Albatross* stn 5418. 3♀, USNM, 320 m, 25 March 1909, *Albatross* stn 5419. 1♂ 15♀, USNM, 318 m, 9 April 1908, *Albatross* stn 5197.

Mindanao: 1♂ 1♀, USNM, off Tagolo Pt, 401 m, 20 August 1909, *Albatross* tn 5541. 3♂ 8♀, USNM, off Tagolo Pt, 366 m, 9 August 1909, *Albatross* stn 5518. 1♂ 1♀, USNM, off Tagolo Pt, 320 m, 9 August 1909, *Albatross* stn 5516. 4♂ 5♀, USNM, NE Tagolo Pt, 320 m, 9 August 1909, *Albatross* stn 5517. 1♂ 2♀, USNM, E of Illana Bay, 289 m, 22 May 1908, *Albatross* stn 5256. 5♀, USNM, Gulf of Davao, 247 m, 18 May 1908, *Albatross* stn 5247.

INDONESIA—2♂ 8♀, BMNH, off Sarawak, Borneo, 198 m, 8 December 1955, *Manihini* stn C5-19. 2♂ (1♀ tentatively assigned), VNIRO. SE Timor I, Timor Sea, 320-355 m, 5 May 1963, *Lira*, O. A. Petrov.

Diagnosis.—Rostrum usually straight, sometimes slightly arched or sinuous, and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located ventral to level of antennal spine; branchiocardiac carina with anterior end relatively far from hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border transverse or slightly inclined posterolaterally, straight or somewhat sinuous and with anterolateral corners almost forming right angles; median ridge broadest and most salient posteriorly, usually flasklike or gently tapering anteriorly; median plate of sternite XIII cordiform, with acute apex.

Description.—Rostrum (Figure 20) almost horizontal, usually straight, sometimes slightly arched or sinuous in adult (straight or barely arcuate in young), falling short of or overreaching distal margin of antennular peduncle, its length ranging from about 0.7 to 0.8 that of carapace. Rostral plus epigastric teeth 11-18 (usually 11-14), second rostral tooth (occasionally third) located in line with orbital margin, basal teeth close together, those toward apex variously spaced, and extending almost to end of rostrum but occasionally only to base of distal 0.25. Postrostral carina low, although well defined, behind epigastric tooth, ending just behind dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine slightly larger than, and situated ventral to level of, antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 21*B*). Antennal carina almost indistinct; cervical carina sharp, accompanying sulcus well marked; hepatic carina broadly sigmoid, descending obliquely anteroventrally from below hepatic spine, then turning almost anteriorly in slightly concave line to apex of pterygostomian spine; branchiocardiac carina well marked, with anterior extremity not nearly reaching posterior end of hepatic sulcus and ex-

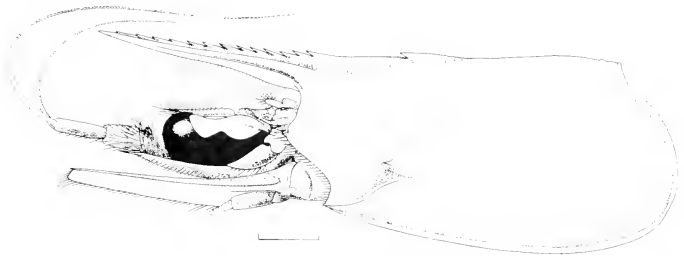


FIGURE 20.—*Penaeopsis rectacuta*, ♀ 27 mm cl, Albay Gulf, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5 mm.

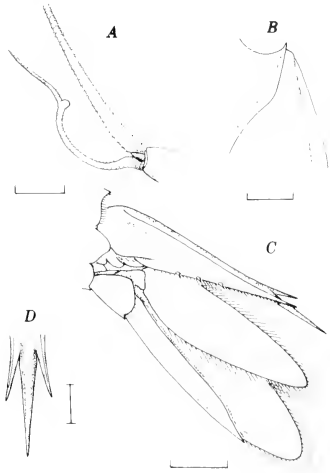


FIGURE 21.—*Penaeopsis rectacuta*. *A*, ♂ 25 mm cl, Balayan Bay, Luzon, Philippines, right flagella (mesial view). *B*, ♀ 27 mm cl, Albay Gulf, Luzon, Philippines, anteroventral part of carapace. *C*, ♀ 28.5 mm cl, Gulf of Davao, Mindanao, telson and left uropod, lateral view. *D*, Same specimen, tip of telson, dorsal view. Scales: *A*, *B*, *D* = 2 mm; *C* = 5 mm.

tending posterodorsally to rather near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 times as long as second in former and 1.40 times in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching between proximal 0.3 and, at least, midlength of second article; stylocerite ending in small spine, length about 0.4 that of first article. In both sexes dorsal flagellum not evenly tapering, its stout proximal part suddenly narrowing into filiform distal part; but in male, dorsal flagellum longer than ventral, its length about 1.7 that of carapace, whereas in female, dorsal flagellum shorter than ventral, about as long as carapace. Ventral flagellum in male (Figure 21*A*) with strong knob at junction between semicircular proximal part and straight distal part; in female, ventral flagellum straight, tapering to filiform distal part. (Shape of both flagella in male and female characteristic of all species of genus.)

Scaphocerite falling short of to surpassing distal end of antennular peduncle, reaching at most as far as base of distal fourth of thickening of dorsal flagellum; lateral rib ending in slender spine, not quite reaching distal margin of lamella. Antennal flagellum broken in shrimp examined.

Third maxilliped extending at least to basal 0.2 of second antennular article and at most to midlength of third; ratio of dactyl/propodus about 0.65 in males and 0.70 in females.

First pereopod exceeding carpocerite by tip of dactyl or by as much as length of propodus. Second pereopod surpassing carpocerite at least by length of propodus and at most by propodus and 0.3 length of carpus (i.e., reaching between base of

second article and proximal 0.2 of third). Third pereopod of male overreaching antennular peduncle by as much as length of dactyl, that of female, by propodus. Fourth pereopod surpassing carpocerite by length of dactyl or by a maximum of dactyl and propodus. Fifth pereopod exceeding antennular peduncle by dactyl or by latter plus 0.4 length of propodus. Order of pereopods in terms of their maximum extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second, and fifth almost as far as (occasionally farther than) third.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather prominent interrupted cicatrix on lateral surface. Telson (Figure 21*C*) with lateral margins bearing three pairs of short movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 21*D*) with length 6-8 times basal width, flasklike in shape, its lateral margins convex or forming widely obtuse angles anteriorly, converging posteriorly, and with dorsal surface subplane. Mesial ramus of uropod reaching apex of telson or overreaching it by as much as 0.20 of its own length; lateral ramus overreaching mesial by about 0.25 of its own length.

Petasma (Figure 22*A*, *B*) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in low, sometimes sharp crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule with distolateral portion broadly rounded, bearing distally rather flexible and translucent marginal region, strongly reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially at about right angle, and ending in short, relatively narrow process (free from, though closely appressed to, margin of dorsolateral lobule) reaching approximately to level of cincinnuli.

Appendix masculina (Figure 22*C*) considerably broader than long (width 1.7-2.0 length), roughly kidney-shaped; band of relatively long setae extending around free margin, broadening and forming patch mesially, or setae covering more than half of dorsal surface.

Thelycum (Figures 23; 24*A*, *B*) with anterior border of plate of sternite XIV transverse or slightly inclined posterolaterally, almost straight or somewhat sinuous on each side of posteromedian projection of sternite XIII, and forming almost right angle with lateral borders. Plate (produced anteriorly in paired small submesial lobules), densely setose laterally, strongly slanting dorsomesially toward deep, usually narrow, submedian depressions; median ridge of variable length, broadening and much higher posteriorly, usually appearing flask-shaped, its bulbous portion cov-

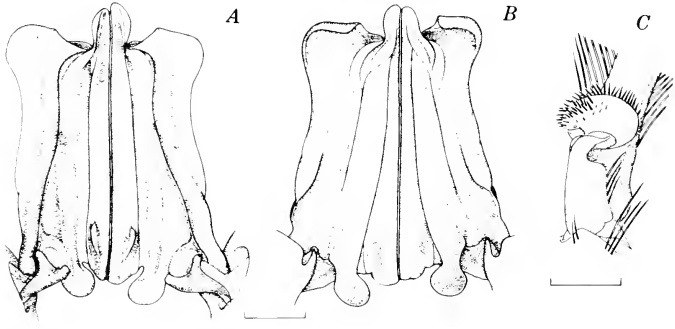


FIGURE 22.—*Penaeopsis rectacuta*, ♂ 17.5 mm cl, Singapore. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scale = 1 mm.

ryi], Alcock and Anderson (1894) stated (in the account of the deep sea Crustacea collected in the Bay of Bengal and Laccadive Sea by the *Investigator* during the seasons 1891-92 and 1893-94) that they had little hesitation in identifying the females with Bate's *"Penaeus rectacutus,"* but that the males "appear to agree in every detail . . .with Spence Bate's figures and descriptions of *Penaeus serratus*." Because the male *"Penaeus serratus"* figured by Bate is a member of *Penaeopsis eduardoi*, I assumed that the males available to them belonged to the latter species. On the basis of their statement that "*M. rectacutus*" was common in the Bay of Bengal between 100 and 280 fm (183 and 357 m) and my noting the fact that the stations established by the *Investigator* during the years and within the depth limits cited above were all located in the southwestern part of the Bay of Bengal, I was led to the conclusion that *P. eduardoi* had been found in the latter area. Further studies, together with the fact that no specimen of *P. eduardoi* has been reported west of the Strait of Malacca, have inclined me to believe that Alcock and Anderson probably misidentified the males of *"Metapenaeus rectacutus"* [= *Penaeopsis jerryi*] as *"Penaeus serratus"* [= *Penaeopsis eduardoi*]. It should be added that the specimens of "*M. rectacutus*" examined by the later authors are no longer extant (G. Ramakrishna[3]).

Affinities.—*Penaeopsis eduardoi* differs from *P. rectacuta* and *P. jerryi* in possessing two pairs of movable spines on the telson, a character it shares with two other Indo-West Pacific species, *P. challengeri* and *P. balssi*, as well as with the amphi-Atlantic *P. serrata*. *Penaeopsis eduardoi*, however, can be distinguished from all its congeners by features of the petasma and thelycum. It is the only species in which the distomedian projections of the petasma are obsolete, the proximal plate lacks mesial crest, and the ventral costa is produced in a long, distal spine extending beyond the row of cincinnuli. The thelycum, in turn, is unique in that the plate of sternite XIV exhibits a caudally pedunculate posteromedian protuberance, whereas in all the other species the latter is represented by a ridge or protuberance which is broad caudally or lacks a peduncle. Furthermore, sternite XII is armed with an elongate, broad basally, semiconical, anteriorly directed tooth, which in the other members of *Penaeopsis* is indistinct or either laterally compressed, or short, subconical and directed ventrally or anteroventrally.

Variation.—Discussed by Perez Farfante 1977b.

Penaeopsis jerryi Pérez Farfante 1979

Figures 6, 15-19

Metapenaeus rectacutus. Wood-Mason 1891:274. Alcock 1901b:50. Alcock and Anderson 1894:145.

Peneus rectacutus. Alcock 1898:73.

Penaeus rectacutus. Alcock and Anderson 1899:278.

Peneus (Parapeneus) rectacutus. Alcock 1901a:17 Alcock and McArdle 1901, pl. 49, fig. 5.

Parapeneus rectacutus. Alcock 1902:268, fig. 62; 1905:520 [part]; 1906:33, pl. 6, fig. 19, 19a-b. Kemp and Sewell 1912:16. ?Balss 1925:228.

Parapenaeus rectacutus. Schmitt 1926:319.

Penaeopsis rectacutus. Schmitt 1926:321. Ramadan 1938:67, fig. 12a-b. Sewell 1955:202. Kurian 1964:216.

Penaeopsis rectacuta. Holthuis and Rosa 1965:3 [part]. George 1966:342. Jones 1967:1337; 1969:747. George 1969:27. Longhurst 1971:224. Starobogatov 1972:390 [key, but not figures]. Crosnier and Jouannic 1973:12, pl. 3, fig. 3. Ivanov and Hassan 1976:5, fig. 3.

Penaeopsis jerryi Pérez Farfante 1979:208, fig. 1-4 [holotype, ♀, BNMH 1978:325; type-locality: off Berbera, Somalia, Gulf of Aden, 10°29′48″ N, 45°01′48″ E, John Murray Expedition stn 16].

Not *Penaeus rectacutus* Bate 1881.

Material.

Holotype. Paratypes:

YEMEN—2♂ 2♀, USNM 171430, off Saihut (15°10′ N, 50°58′ E), 240-239 m, 16 May 1971, A. D. Druzhinin.

SOMALIA—20♂ 49♀, BMNH 1978.326, collected with holotype.

INDIA—2♂ 2♀, USNM 171431, off Cochin, summer 1978, Staff of the Department of Marine Science, University of Cochin. 1♀, USNM 42755, off False Divi Pt (15°56′50″N, 81°30′30″E), 439-505 m, 24 December 1890, *Investigator* stn

[3]G. Ramakrishna, Superintending Zoologist, Zoological Survey of India, pers. commun. 20 March 1978.

120. 2♂ 1♀, ZSI 2589-95/10, N of North Andaman I (14°13′ N, 93°40′ E), 677-766 m, 8 April 1898, *Investigator* stn 235.

Diagnosis.—Rostrum straight or sinuous (occasionally convex basally, straight anteriorly), and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located at about same level as that of antennal spine; branchiocardiac carina with anterior end very close to hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian protuberance of sternite XIII and strongly inclined posterolaterally; anterolateral and posterolateral corners of plate arched; median ridge broadest and most salient posteriorly, often gradually tapering anteriorly, sometimes reduced to posterior tubercle; median plate of sternite XIII subsemicircular to trilobed.

Description.—Rostrum (Figures 15, 16) almost horizontal, straight or slightly sinuous (occasionally convex basally, straight anteriorly), falling short of to overreaching distal margin of antennular peduncle, its length 0.8-0.9 that of carapace. Rostral plus epigastric teeth 12-16 (usually 12-14), second (occasionally first) rostral tooth situated in line with orbital margin, basal teeth close together, those toward apex more widely spaced, and extending almost to tip of rostrum, but sometimes only to base of anterior 0.2. Postrostral carina extending posteriorly to about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine moderately long; antennal carina short but prominent. Hepatic spine slightly larger than, and situated at about same level as (rather than ventral to), antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 17*A*). Cervical carina sharp, accompanying sulcus well marked; hepatic carina slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina strong, with anterior extremity almost reaching posterior end of hepatic sulcus and extending posteriorly to near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in mature male than in

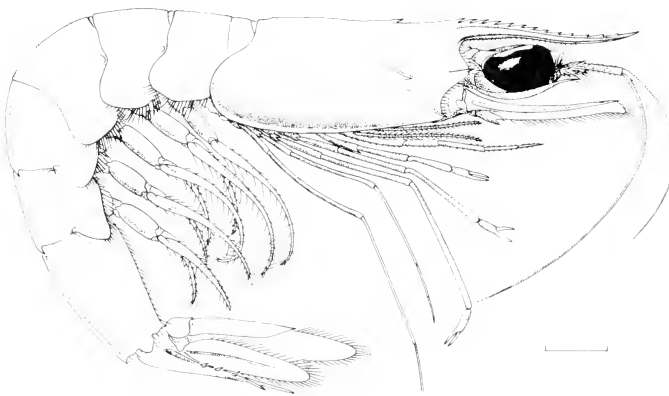


FIGURE 15.—*Penaeopsis jerryi*, ♀ 17.5 mm cl, off Berbera, Gulf of Aden, Somalia. Lateral view. Scale = 5 mm.

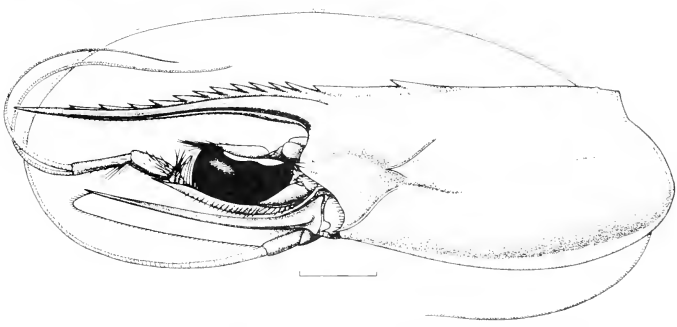


FIGURE 16.—*Penaeopsis jerryi, holotype* ♀ 20.5 mm cl, off Berbera, Gulf of Aden, Somalia. Cephalothorax, lateral view. Scale = 5 mm.

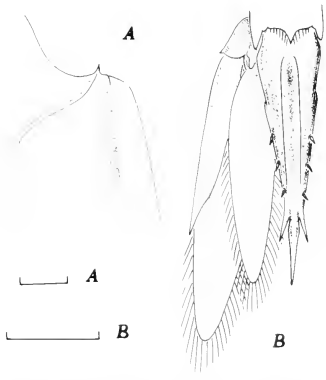


FIGURE 17.—*Penaeopsis jerryi*, holotype. *A*, Anteroventral part of carapace. *B*, Telson and left uropod, dorsal view. Scales: *A* = 2 mm, *B* = 5 mm.

female, about 1.6 times as long as second in former and 1.4 in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching about midlength of second article. Flagella similar to those of *P. rectacuta*.

Scaphocerite falling short of to overreaching distal end of antennular peduncle; lateral rib ending in slender spine, falling slightly short of margin of lamella. Antennal flagellum more than twice the length of the animal (Kurian 1964).

Third maxilliped and pereopods in most specimens too poorly preserved to allow observations on their maximum anterior extensions.

Abdomen with sixth somite elongate, about 1.7 times height, bearing long, strong, interrupted cicatrix on lateral surface; cicatrix also on fifth and fourth somites. Telson (Figure 17*B*) with lateral margins bearing three pairs of small, movable spines (occasionally only one or two pairs, rarely with different numbers of spines on margins); fixed spines variable in length, reaching at most base of distal third of terminal portion; terminal portion with length about 6-7 times basal width, narrowly hastate or with lateral margins basally rounded, and dorsal surface moderately convex. Mesial ramus of uropod falling short of to overreaching apex of telson by as much as 0.2 of its own length; lateral ramus overreaching mesial ramus by about 0.2 of its own length.

Petasma (Figure 18*A*, *B*) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in blunt crest; rib of dorsolateral lobule with distal part straight or turning laterally, and terminating proximally in semicircular or subcircular process. Ventrolateral lobule bearing

distally rather flexible and translucent marginal region, reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially and ending in short, relatively narrow process reaching approximately to level of cincinnuli.

Appendix masculina (Figure 18*C*) considerably broader than long (width about 1.7 length), roughly oval; band of setae extending around free margin, broadening and forming patch mesially.

Thelycum (Figure 19) with plate of sternite XIV roughly subelliptical in outline, its anterior border strongly arcuate and inclined posterolaterally, and anterolateral and posterolateral corners arched, plate sloping toward submedian depressions of variable length, and bearing long marginal setae; median ridge broadest and most prominent posteriorly, tapering anteriorly, sometimes reduced to posterior tubercle. Posterior thoracic ridge narrow and projecting anteroventrally at base of median ridge, fringed anteriorly with closely set setae. Median plate of sternite XIII subsemicircular to roughly trilobed, sometimes with minute anteromedian spine, and covered with setae except for central depression; posteromedian projection broad, with posterior margin entire or very shallowly emarginate. Sternite XII bearing posteromedian, subconical tooth with apex directed anteroventrally; oblique pairs of sharp ridges extending posterolaterally from base of tooth.

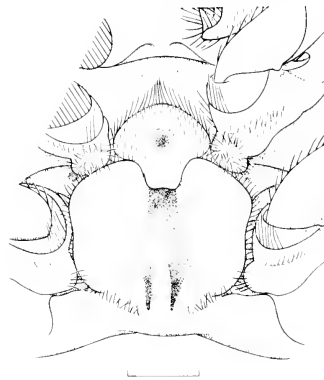


FIGURE 19.—*Penaeopsis jerryi*, holotype. Thelycum ventral view. Scale = 1 mm.

Spermatophore bearing mesial element which in impregnated females lies exposed on the thelycum.

Color.—Red (Wood-Mason 1891), or dark brown with reddish tint (Kurian 1964).

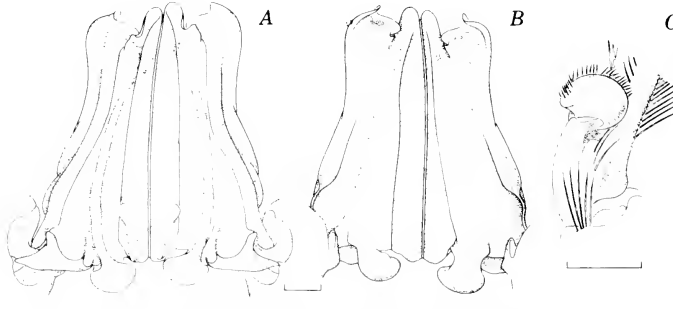


FIGURE 18.—*Penaeopsis jerryi*, ♀ 19 mm cl, of Berbera, Gulf of Aden, Somalia. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Paratype ♀ 21 mm cl, off Cochin, India, right appendix masculina, dorsal view. Scales = 1 mm.

Parapeneus paradoxus. Boone 1927:79 (part; not *Neopenaeopsis paradoxus* Bouvier 1905b = *Peneus longirostris* Lucas 1846).

Penaeopsis (Penaeopsis) megalops. Burkenroad 1934a:12, fig. 1. Anderson and Lindner 1945:309. Springer and Bullis 1956:9.

Peneopsis megalops. Bullis 1956:10. Bullis and Rathjen 1959:18.

Penaeopsis serrata. Holthuis and Rosa 1965:4. Longhurst 1971:220. Ivanov and Hassan 1976:4. Pérez Farfante 1977a:297; 1977b:180. Pérez Farfante and Ivanov 1979:204. Perez Farfante 1979:208. Wenner and Boesch 1979:110.

Common names: megalops shrimp; camarón megalops; crevette megalops.

Material.

UNITED STATES—New Jersey: 1♀, USNM, E of Barnegat, 275-290 m, 12 August 1972, *Gosnold* cruise 197, stn 111.

North Carolina: 3♀, USNM, off Back Bay, 331 m, 23 July 1969, *Oregon II* stn 10659. 11♂ 8♀, USNM, SE of Cape Lookout, 366 m, 10 June 1962, *Silver Bay* stn 4160. 11♂ 7♀, USNM, off Carolina Beach, 412 m, 16 November 1956, *Combat* stn 178. 27♂ 37♀, USNM, SE of Cape Fear, 459 m, 16 November 1956, *Combat* stn 179.

South Carolina: 2♂ 8♀, USNM, off Charleston, 366 m, 28 May 1949, *Albatross III* stn 1922. 1♂ 1♀, USNM, off Port Royal Sound, 366 m, 23 January 1972, *Oregon II* stn 11734.

Georgia: 1♀, USNM, off Ossawa, 183 m, 21 January 1972, *Oregon II* stn 11719. 1♂ 1♀, USNM, off Ossawa, 238 m, 21 January 1972, *Oregon II* stn 11720.

Florida: 2♂ 6♀, USNM, off St Augustine, 329 m, 20 January 1972, *Silver Bay* stn 3677. 2♀, USNM, off Flagler Beach, 338 m, 3 February 1962, *Silver Bay* stn 3728. 2♂ 2♀, UMML, off Delray Beach, 549 m, 13 September 1966, *Gerda* stn 806. 1♂ 3♀, FIU, NW of Cayo Sal Bank, 366 m, 14 May 1978, *Bellow* stn 5 #3. 10♂ 8♀, USNM, SW of Marquesas Keys 402-269 m, 2 February 1968, *Gerda* stn 969. 6♂ 7♀, USNM, S of Dry Tortugas, 366 m, 10 July 1955, *Oregon* stn 1330. 15♂ 21♀, UMML, S of Dry Tortugas, 329-366 m, 28 April 1969, *Gerda* stn 1096. 30♂ 28♀, USNM, S of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 7♂ 38♀, USNM, 31 July 1930, stn 37-38; 3♂ 20♀, USNM, 402-433 m, 31 July 1930, stn 38-30; 8♂ 13♀, USNM, 366-430 m, 8 July 1931, stn 21-31; 28♂ 113♀, USNM, 256-329 m, 31 July 1931, stn 37-30; 2♂, USNM, 256-360 m, 30 July 1932, stn 67-32; all from the Tortugas area, W. L. Schmitt. 9♂ 15♀, USNM, NW of Dry Tortugas, 366 m, 10 June 1959, *Silver Bay* stn 1201. 7♂ 2♀, USNM, S of St George I, 366 m, 21 August 1970, *Oregon II* stn 11180. 15♀, USNM, S of Gulf Beach, 274 m, 16 June 1964, *Oregon* stn 4946.

Alabama: 9♂ 21♀, USNM, off Mobile Bay, 320 m, 27 April 1951, *Oregon* stn 314.

Louisana (all from Mississippi Delta area): 14♂ 55♀, USNM, 274 m, 23 October 1962, *Oregon* stn 4002. 9♂ 15♀, USNM, 732 m, 3 June 1959, *Silver Bay* stn 1181. 1♂ 3♀, USNM, 366 m, 31 January 1955, *Oregon* stn 1238.

Texas: 10♀, USNM, off Galveston, 476 m, 13 March 1969, *Oregon II* stn 10616. 3♂ 16♀, USNM, off Galveston, 457-549 m, 16 April 1952, *Oregon* stn 542. 32♂ 38♀, USNM, off Padre I, 366 m, 28 November 1950, *Oregon* stn 162. 3♂ 8♀, USNM, off Padre I, 430 m, 28 November 1950, *Oregon* stn 163. 1♀, USNM, off Port Isabel, 457-476 m, 5 August 1969, *Western Gulf* stn 37.

MEXICO (GULF OF MEXICO)—Tamaulipas: 1♂ 1♀, USNM, off Los Lavaderos, 558 m, 2 June 1970, *Oregon II* stn 10953. 3♂ 2♀, USNM, SW of Soto la Marina, 329 m, 1 June 1970, *Oregon II* stn 10951.

Veracruz: 2♀, USNM, off Tecolutla, 375 m, 4 June 1970, *Oregon II* stn 10958. 2♀, USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, *Oregon II* stn 10960.

Tabasco: 1♀, USNM, W of Laguna del Carmen, 430 m, 6 June 1970, *Oregon II* stn 10963.

Campeche: 1♀, USNM, off Punta Frontera, 366 m, 15 May 1954, *Oregon* stn 1054.

Yucatan; 46♂ 78♀, USNM, Yucatan Channel, 377 m, 19 June 1952, *Oregon* stn 590.

BAHAMA ISLANDS—1♀, USNM, NW of Matanilla Reef, 567 m, 17 July 1965, *Gerda* stn 664. 2♂ 6♀, USNM, W of Grand Bahama I, 494-531 m, 13 June 1969, *Gerda* stn 1125. 9♂ 3♀, USNM, Santaren Channel, 508 m, 22 June 1967, *Gerda* stn 817.

CUBA—30♂ 36♀, USNM, NE of Las Villas 516 m, 27 June 1970, *Pillsbury* stn 1171. 67♂ 24♀, USNM, off Las Villas, 512 m, 16 July 1955, *Oregon* stn 1342. 34♂ 37♀, USNM, off Archipiélago de Sabana, 466 m, 16 December 1969, *Oregon II* stn 10863. 2♂ 7♀, MCZ, Bahia de Cochinos, 274-311 m, 25 February 1938, *Atlantis* stn 2963B. 3♂ 2♀, MCZ, Bahia de Cochinos, 402-

503 m, 25 February 1938, *Atlantis* stn 2963D.

JAMAICA—6♂ 4♀, USNM, off Great Pedro Bluff, 530 m, 16 May 1962, *Oregon* stn 3552. 1♂ 3♀, USNM, off Great Pedro Bluff, 311 m, 16 May 1962, *Oregon* stn 3549.

DOMINICAN REPUBLIC—10♂ 5♀, USNM, off Puerto Plata, 421-549 m, 15 October 1963, *Silver Bay* stn 5166. 2♀, USNM, off El Macao, 549 m, 17 October 1963, *Silver Bay* stn 5181.

VIRGIN ISLANDS—2♂ 2♀, USNM, N of Virgin Is, 165-915 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 102. 1♀, USNM, off Charlotte Amalie, 402 m, 26 September 1959, *Oregon* stn 2606.

PUERTO RICO—1♀, USNM, N of Culebra I, 366-732 m, 26 February 1933, Johnson-Smithsonian Deep Sea Expedition stn 81. 2♂ 6♀, USNM, off San Juan, 256-293 m, 25 September 1959, *Oregon* stn 2603. 4♂, USNM, NE of Puerto Rico, 183-549 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 100. 2♂ 2♀, USNM, off Añasco, 549 m, 6 October 1959, *Oregon* stn 2652.

LESSER ANTILLES—7♀, USNM, NW of Dog I, 628 m, 6 December 1969, *Oregon II* stn 10835. 1♀, USNM, W of Anguilla, 658 m, 7 December 1969, *Oregon II* stn 10837. 29♂ 14♀, USNM, E of Saba, 549-585 m, 18 May 1967, *Oregon* stn 6695. 13♂ 17♀, USNM, E of St Christopher, 578 m, 8 December 1969, *Oregon II* stn 10842. 13♂ 9♀, UMML, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, *Pillsbury* stn 936. 25♂ 17♀, USNM, off Dominica, 503 m, 4 March 1966, *Oregon* stn 5926. 13♂ 14♀, USNM, E of Dominica, 649 m, 5 March 1966, *Oregon* stn 5929. 2♂ 4♀, UMML, SE of Pointe du Cap, St Lucia, 274-567 m, 7 July 1969, *Pillsbury* stn 891. 3♂ 2♀, USNM, E of Georgetown, St Vincent, 348-466 m, 6 July 1969, *Pillsbury* stn 877. 1♂ 1♀, MCZ 7200, + 1♀, MP, syntypes of *Penaeopsis serratus* Bate, off Barbados, 399 m, 5 March 1879, *Blake* stn 275. 11♂ 5♀, USNM, S of Bonaire, 393 m, 27 September 1963, *Oregon* stn 4405. 1♀, USNM, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 2♀, syntypes of *Parapenaeus megalops* Smith, USNM 7262, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125.

WESTERN CARIBBEAN—20♂ 16♀, USNM, Arrowsmith Bank, 225-250 m, 14 March 1958, *Pillsbury* stn 587. 18♂ 5♀, USNM, NW of Rosalind Bank, 274 m, 7 June 1962, *Oregon* stn 3628. 23♀, USNM, NW of Rosalind Bank, 366 m, 23 August 1957, *Oregon* stn 1883. 8♂ 83♀, USNM, W of Quita Sueño Bank, 450-576 m, 31 January 1971, *Pillsbury* stn 1355. 1♂ 5♀, USNM, W of I de Providencia, 457 m, 21 November 1968, *Oregon II* stn 10200. 7♂ 4♀, USNM, W of I de San Andrés, 457 m, 23 May 1962, *Oregon* stn 3572.

MEXICO (CARIBBEAN SEA)—Quintana Roo: 1♀, RMNH, SE of I Mujeres, 567-570 m, 23 May 1967, *Pillsbury* stn 585. 1♂, USNM, W of I de Cozumel, 439-463 m, 16 March 1968, *Pillsbury* stn 600. 26♂ 34♀, USNM, W of I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BRITISH HONDURAS—92♀, USNM, NE of Stann Creek, 219-311 m, 10 June 1962, *Oregon* stn 3637. 25♂ 11♀, YPM, N of Glover Reef, 669 m, 20 April 1925, *Pawnee* stn 35. 9♂ 32♀, YPM, N of Glover Reef, 885 m, 20 April 1925, *Pawnee* stn 36.

NICARAGUA—2♀, USNM, NE of Is del Maiz, 549-585, 23 May 1962, *Oregon* stn 3576.

PANAMA—1♀, USNM, off Bocas del Toro, 512 m, 25 May 1962, *Oregon* stn 3583. 1♂ 2♀, USNM, Golfo de los Mosquitos, 457 m, 31 May 1962, *Oregon* stn 3599. 3♀, USNM, NE of Belén, 439 m, 30 May 1962, *Oregon* stn 3592.

COLOMBIA—5♂ 1♀, syntypes of *Parapenaeus megalops* Smith 1885, USNM 7263, Golfo de Urabá, 283 m, 23 March 1884, *Albatross* stn 2143. 1♀, UMML, SW of I de Barú, 135-130 m, 14 July 1966, *Pillsbury* stn 375. 19♀, USNM, off I de Barú, 366 m, 25 May 1964, *Oregon* stn 4882. 12♀, USNM, W of Cartagena, 170-150 m, 1 August 1968, *Pillsbury* stn 797. 1♀, USNM, off Cabo de la Aguja, 176-165 m, 31 July 1968, *Pillsbury* stn 785. 3♂ 2♀, USNM, W of Cabo de la Vela, 357 m, 20 November 1970, *Oregon II* stn 11289.

VENEZUELA—7♂ 7♀, UMML, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 23♂ 6♀, USNM, off Is Los Testigos, 366-439 m, 24 September 1964, *Oregon* stn 5037. 5♂ 2♀, USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, *Oregon* stn 1981.

TRINIDAD-TOBAGO—1♀, USNM, NE of Charlotteville, 165-183 m, 21 September 1964, *Oregon* stn 5021.

GUYANA—3♂ 3♀, USNM, NE of Berbice R, 366 m, 6 November 1957, *Oregon* stn 2004.

FRENCH GUIANA—1♂ 14♀, USNM, N of Roche Brigandin, 457 m, 10 November 1957, *Oregon* stn 2028.

BRASIL—2♂ 2♀, USNM, SE of Rio Grande do Sul, 345-260 m, 19 January 1967, *Akademic Knipovich*.

MOROCCO—2♀, RMNH, off Rabat, 300-600 m, 12 May 1971, Cadiz trawlers, RMNH Expedition. 2♀, RMNH, Casablanca, 28 June 1951, C. Maurin.

WESTERN SAHARA—1♂ 3, VNIRO-USNM, N of Boca Grande, 640-600 m, 11 May 1965, R. N. Burukovsky. 1♂ 3♀, VNIRO-USNM, off Villa Bens, 420-380 m, 11 May 1965, R. N. Burukovsky. 2♂ 2♀, MP 304, syntypes of *Artemesia talismani* Bouvier 1905, off Guerguerat, 410 m, 9 July 1883, *Talisman* stn 72.

Diagnosis.—Rostrum straight, basally arcuate or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two (rarely three) pairs of movable spines. Petasma with proximal plate of dorsomedian lobule thickened mesially but lacking mesial crest; proximal process of rib of dorsolateral lobule subrectangular; ventral costa ending distally in relatively broad, inwardly excavate process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian projection of sternite XIII, and anterolateral extremities uniquely produced into lobules of variable lengths; median ridge usually ovoid or tear-shaped; median plate of sternite XIII subsemicircular to roughly pentagonal with depression extending across entire width.

Description.—Rostrum (Figures 28, 29) almost horizontal or somewhat upturned, variable in shape, straight, or basally arcuate or sinuous (strongly arched in young, Figure 30), and long, reaching between midlength of third article of antennular peduncle and proximal fourth of thickened portion of dorsal flagellum, its length rang-

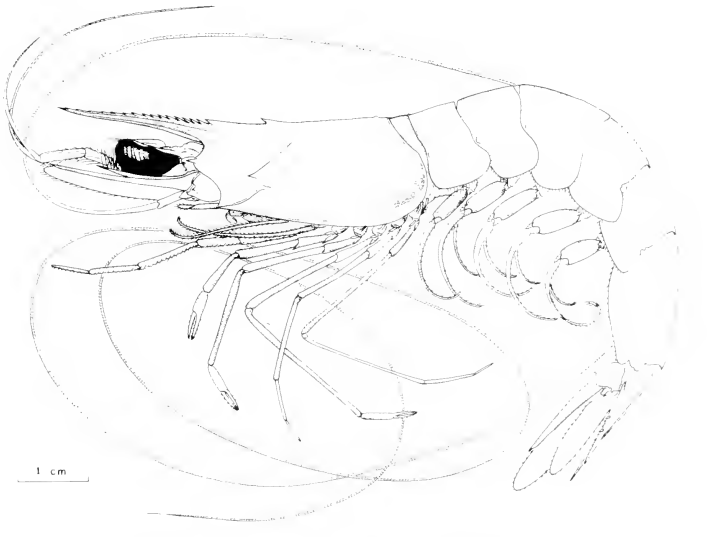


FIGURE 28.—*Penaeopsis serrata*, ♀ 27 mm cl, W of Puerto Rico. Lateral view. Scale = 10 mm.

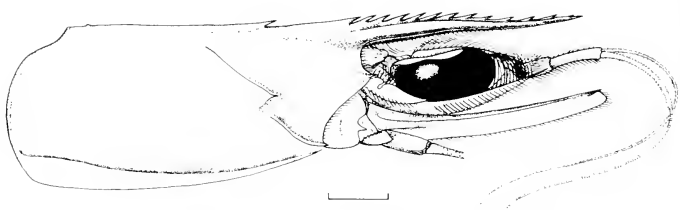


FIGURE 29.—*Penaeopsis serrata*, ♀ 27 mm cl, Golfo de los Mosquitos, Panama. Cephalothorax, lateral view. Scale = 5 mm.

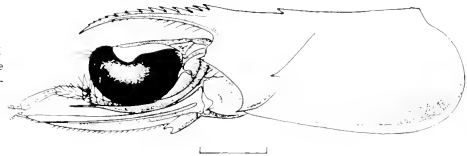


FIGURE 30.—*Penaeopsis serrata*, ♀ juvenile 9.5 mm cl, Northwest Providence Channel, Bahamas. Cephalothorax lateral view. Scale = 3 mm.

ing from about 0.65 to 0.85 that of carapace. Rostral plus epigastric teeth 10-19 (rarely <13 or >16), basal rostral teeth close together, those toward apex variously spaced; second or first (latter usually in young) rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth ending at about level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 31*A*). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of pterygostomian spine), hepatic sulcus well marked along carina, shallow posteriorly. Branchiocardiac carina very weak, extending posterodorsally to near margin of carapace.

Antennular peduncle with length equivalent to about 0.70 that of carapace, third article sexually dimorphic, slightly longer and considerably stouter in males than in females, about 1.4 times as long as second in former and 1.2 times in latter; prosartema reaching, or almost reaching, distomesial margin of eye; distolateral spine long, slender, and sharp, reaching between midlength and distal fourth of second article; stylocerite ending in small spine, about 0.4 as long as first article. In male, ventral flagellum shorter (even when forcibly straightened) than dorsal, with inconspicuous knob at junction between proximal and distal parts; dorsal flagellum 1.5-1.8 times as long as carapace. In female, ventral flagellum (tapering to filiform distal part) longer than dorsal, 1.5-1.7 times as long as carapace; dorsal flagellum 0.8-1.0 times as long.

Scaphocerite falling slightly short of to somewhat overreaching antennular peduncle; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, about 3 times tl of shrimp (based on measurements made by me on freshly collected specimens during a Caribbean Sea cruise of *Oregon II* in 1969).

Third maxilliped extending at least to basal 0.4 of second antennular article and at most to distal end of third; ratio of dactyl/propodus about 0.75 in males and 0.85 in females.

First pereopod reaching distal end of carpocerite or overreaching it by as much as 0.8 length of propodus. Second pereopod surpassing carpocerite by at least length of propodus and by as much as that of propodus and half length of carpus (i.e., reaching between base of second antennular article and midlength of third). Third pereopod

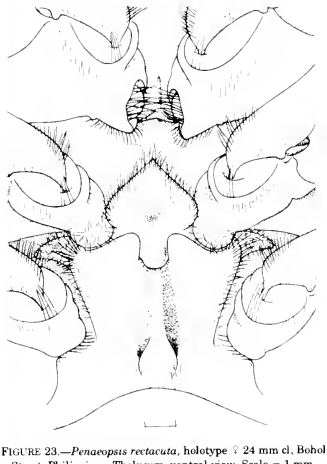


FIGURE 23.—*Penaeopsis rectacuta*, holotype ♀ 24 mm cl, Bohol Strait, Philippines. Thelycum, ventral view. Scale = 1 mm.

ered with setae. Posterior thoracic ridge fringed anteriorly with closely set setae. Median plate of sternite XIII cordiform (with acute apex), covered with setae except for central depression (occasionally prolonged across entire width of plate); posteromedian projection subrectangular or subelliptical, with posterior margin entire or, occasionally, shallowly emarginate. Sternite XII bearing posteromedian, often laterally compressed tooth of variable size, sometimes produced in apical spine; oblique pair of sharp ridges extending posterolaterally from base of tooth.

Thelycum in young females (9-11 mm cl) with median plate of sternite XIII produced anteriorly in long, slender spine, and posteromedian projection consisting of only minute knob; plate of sternite XIV bearing short median ridge also produced anteriorly in long, slender spine, latter indistinct in females 13 mm cl.

The female holotype, 26 mm cl, is in poor condition, with many parts missing; however, except for the rostrum, which is almost entirely lost, the carapace is well preserved as are the antennular peduncle, most of the abdomen, and the thelycum. The following characters of the carapace may be readily observed: the second rostral tooth is situated opposite the orbital margin, while the

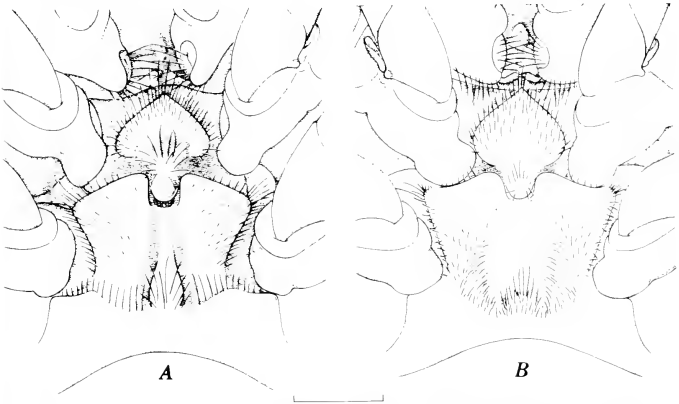


FIGURE 24.—*Penaeopsis rectacuta*. *A*, ♀ 25.5 mm cl, off Tagolo Point, Mindanao, Philippines. *B*, ♀ 24 mm cl, Tabayas Bay vicinity of Marinduque Island, Philippines. Thelyca, ventral view (setae omitted on the legs). Scale = 2 mm.

epigastric tooth is found at the anterior 0.35 of the carapace, and the hepatic spine lies conspicuously ventral to the antennal spine; the postrostral carina extends along anterior 0.55 of the carapace, ending just posterior to the cervical sulcus; and the anteroventral corner forms an angle of about 90°. The antennular peduncle is 0.75 as long as the carapace, the third article is 1.35 times the length of the second, and the stylocerite is 0.4 that of the first article. The scaphocerite falls slightly short of the end of the antennular peduncle, and the terminal spine of the lateral rib does not reach the distal margin of the lamella. The low, sharp middorsal keel of the abdomen extends from the fourth to the sixth somites, and the length of the latter is 1.7 times its maximum height. The thelycum is depicted in Figure 23.

In this species each spermatophore bears a conspicuous, somewhat rigid element which in impregnated females lies over the plate of sternite XIV (Figure 25). The paired elements, which project from the mesial extremity of the sperm sacs enclosed in the seminal receptacles, are joined along their mesial margins and form a roughly circular scale covering a large part of the plate. A similar spermatophore is also found in *P. balssi*, *P. eduardoi*, and *P. jerryi*, the other three Indo-West Pacific species in which I have observed impregnated females.

Maximum lengths.—Males 25 mm cl, about 110 mm tl; females 31 mm cl, about 135 mm tl.

Geographic and bathymetric ranges.—Indo-West Pacific (Figure 6) from the Philippines (Bate 1881) and Timor Sea to the south China Sea (north of Borneo, Hall 1962). It has been found at depths between 174 and 401 m.

Affinities.—Two features of the carapace distinguish *P. rectacuta* from the closely allied, western Indo-West Pacific *P. jerryi*: 1) the position of the hepatic spine, which in the former is situated distinctly ventral to the antennal spine whereas it occurs at about the same level in *P. jerryi*, and 2) the length of the branchiocardiac carina which is relatively short in *P. rectacuta* (its anterior extremity situated well behind the posterior end of the hepatic sulcus) and is long in *P. jerryi* (its anterior extremity located quite near the posterior end of the sulcus). In addition, the thelycum of *P. rectacuta* has the anterior border of the plate of sternite XIV almost straight or slightly sinuous and forms an angle with the lateral border, whereas in *P. jerryi* it is strongly convex and continuous through a broad arc with the lateral border. Furthermore, the median plate of sternite XIII is cordiform and rather elongate in *P. rectacuta* and subsemicircular, or occasionally trilobed in *P. jerryi*.

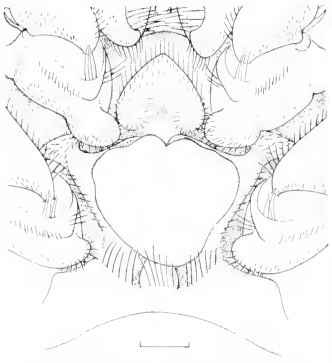


FIGURE 25.—*Penaeopsis rectacuta*, ♀ 25.5 mm cl, vicinity of western Bohol, Philippines. Compound spermatophore attached to female. Scale = 1 mm.

Variation.—This shrimp exhibits a rather large number of morphological variations. In the adult the rostrum may be straight, slightly convex or sinuous, and the number of rostral teeth ranges from 10 to 17. The scaphocerite falls short of, reaches as far as or extends beyond, the antennular peduncle. In the females, the anterior border of the plate of sternite XIV (Figure 24*A*, *B*) varies from transverse to slightly inclined posterolaterally, the median ridge may be short or extend to the posteromedian projection of sternite XIII, and the submedian depressions that flank the ridge, although most often narrow, may be broad. Furthermore, the setation of the plate, usually extending over the lateral portions, sometimes is absent anteriorly and lacking posteriorly or vice versa. The median plate of sternite XIII usually bears a central depression, but occasionally the latter extends across the entire width of the plate, and the caudal margin of the posteromedian pro-

jection, which is straight in most specimens, sometimes exhibits a shallow emargination. Finally, the tooth on sternite XII may vary considerably in size and shape; although usually compressed, it may be subconical or infrequently strongly produced in an apical spine. Sometimes the entire range of variation of certain characters is represented within a single lot. Among the 16 specimens collected at *Albatross* stn 5197, off western Bohol, Philippines, the number of rostral teeth ranges from 11 to 17 and in several lots females, in which the posteromedian projection of sternite XIII is straight caudally were found together with others bearing a slightly emarginate one. These variations, thus, are intraspecific, not even associated with local populations.

A discussion of the features that separate this species from *P. eduardoi* was presented by Pérez Farfante (1977b). As noted by Hall (1962), typical *P. rectacuta* possesses longer pereopods than do specimens reported by De Man (1911) as "*Parapenaeus rectacutus*," which actually are *Penaeopsis eduardoi*. In *P. rectacuta*, however, the third maxilliped is slightly shorter than that of *P. eduardoi*.

Remarks.—The specimens from off Borneo recorded by Hall (1962) as *P. rectacuta* were in my opinion, correctly identified. The suggestion by Ivanov and Hassan (1976) that they might belong to *P. balssi*—under the synonymy of which the authors, "with some hesitation," included the record preceded by a question mark—is not justified. I have found that the petasmata of these specimens are typical and the thelyca vary but slightly from that of the holotype. The only obvious difference is that in the females, the median ridge of the plate of sternite XIV, although broadest posteriorly, is not flasklike. Also, this plate is rather densely setose laterally, as indicated by Ivanov and Hassan, and the transverse thoracic ridge bears a row of setae across the anterior border which is lacking in the holotype; it is probable that in the latter the setae have been lost, as have almost the entire rostrum, telson, and at least part of the appendages during or after capture.

Pérez Farfante (1978) described three specimens found in the waters of the Philippines having gonopores on the coxae of the fifth pair of pereopods and both male and female genitalia. The petasma, appendix masculina, and thelycum of the three exhibit unique features, but in most respects these shrimp are markedly similar to members of *P. rectacuta*. It was concluded that they are probably anomalus intersexes of this species. Recently, Boris G. Ivanov of VNIRO, kindly made available to me three specimens (two males and one female; Figures 26*A*-*C*; 27)

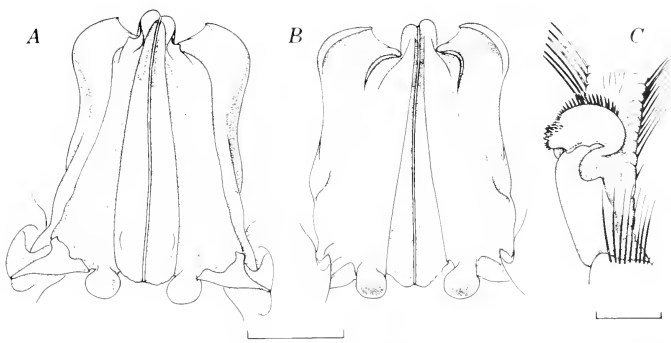


FIGURE 26.—*Penaeopsis rectacuta*, ♂ 21 mm cl, S of Timor Island, Timor Sea. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales: *A*, *B* = 2 mm; *C* = 1 mm.

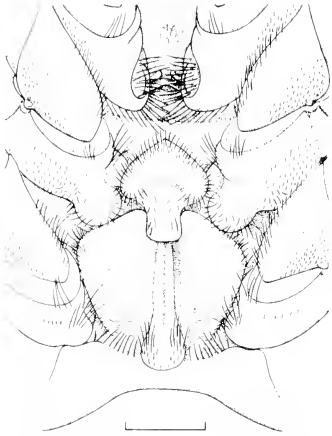


FIGURE 27.—*?Penaeopsis rectacuta*, ♀ 31 mm cl, S of Timor Island, Timor Sea. Thelycum, ventral view. Scale = 2 mm.

collected in the Timor Sea by O. A. Petrov during a cruise of the RV *Lira*. There is little doubt in my mind that the males are members of *P. rectacuta*. The female, except for the thelycum, also possesses features typical of *P. rectacuta*. In the thelycum the anterior border of the plate of sternite XIV is considerably more inclined posterolaterally than in typical females. The anterior part of the median ridge is uniquely divided by a groove, and the bulbous posterior part is larger and overlaps the thoracic ridge. Finally, the posteromedian projection of sternite XIII is considerably larger than in any specimen of *P. rectacuta* examined by me. A bopyrid isopod was found in the branchial chamber of this specimen; it might have been responsible for these peculiar features of the female genitalia.

Commercial importance.—Although no estimates of the economic importance of this species have been recorded, it has been cited among the commercially exploited shrimps of the Philippines by Domantay (1956), and as of economic value throughout its range by Holthuis and Rosa (1965).

Penaeopsis serrata Bate 1881

Figures 28-38

Penaeopsis serrata Bate 1881:183 [syntypes by implication, 1♂ 1♀, MCZ 7200, 1♀, MP; type-locality, off Barbados, "Gulf of Mexico," *Blake* stn 275, 218 fathoms (399 m)]. Bouvier 1905a:981; 1908:5. A. Milne Edwards and Bouvier 1909:221, pl. 4, fig. 1-4. De Man 1911:53. Balss 1925:229. Schmitt 1926:320. Boone 1927:80 [part]. Maurin 1952:91; 1961:530; 1962:210; 1963:1. Burkenroad 1963:172. Maurin 1965:116; 1968a:33; 1968b:479, fig. 3 *P. s.* Lagardère 1971:33, fig. 39-42. [Placed on the Official List of Specific Names in Zoology as Name No. 2276, International Commission on Zoological Nomenclature 1969, Opinion 864:141].

Parapenaeus megalops Smith 1885:172 [syntypes, 2♀, USNM 7262, S of Curaçao, 11°43′ N, 69°09′30″ W, 208 fathoms (380 m), *Albatross* stn 2125. 5♂ 1♀, USNM 7263, Golfo de Urabá, 9°30′45″ N, 76°25′30″ W, 155 fathoms (283 m), *Albatross* stn 2143]. Rathbun 1901:102. Bouvier 1908:7. A. Milne Edwards and Bouvier 1909:225. Hay and Shore 1918:379, pl. 25, fig. 8. Schmitt 1926:319.

Parapeneus megalops. Faxon 1896:163. Alcock 1905:520; 1906:52.

Artemesia talismani Bouvier 1905a:982 [syntypes, 2♂ 2♀, MP 304, off Guerguerat, Western Sahara, 25°41′ N, 15°56′ W (of Greenwich; 18°16′ W of Paris on label accompanying specimens), 410 m, 9 July 1883, *Talisman* stn 72; type-locality, "côtes du Maroc et du Sahara"]; 1908:7. A. Milne Edwards and Bouvier 1909:225.

Penaeopsis serratus var. *antillensis* A. Milne Edwards and Bouvier 1909:226, pl. 3, fig. 10, pl. 4, fig. 5 [holotype, ♂, MCZ 7201; type-locality, off St. Kitts, 208 fathoms (380 m) 1978-79, *Blake* stn 148]. De Man 1911:53.

Penaeopsis megalops. De Man 1911:53. Schmitt 1926:320. Burkenroad 1936:139. Kubo 1949:321. Voss 1955:8, fig. 19. Burkenroad 1963:172. Bullis and Thompson 1965:5. Joyce and Eldred 1966:26. Anderson and Bullis 1970:116. Roberts and Pequegnat 1970:49. Pequegnat and Roberts 1971:8. Longhurst 1971:237. Perez Farfante 1971:4. Crosnier and Forest 1973:305. Burukovsky 1974:31.

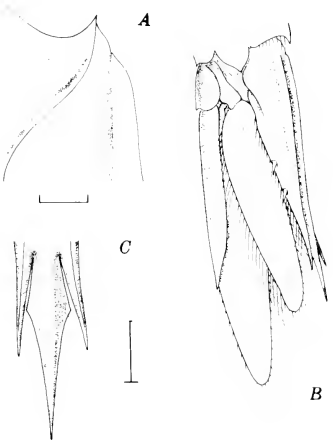


FIGURE 31.—*Penaeopsis serrata*, ♀ 29.5 mm cl, Dry Tortugas Islands, Fla. *A*, Anteroventral part of carapace. *B*, Telson and left uropod. *C*, Tip of telson. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

attaining distal end of antennular peduncle or overreaching it by as much as length of propodus. Fourth pereopod surpassing carpocerite by tip of dactyl or by maximum of dactyl plus about one-half length of propodus. Fifth pereopod extending at least to midlength of second antennular article and at most to distal end of third. Order of pereopods in terms of their maximum anterior extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second. Third maxilliped reaching about as far as fifth pereopod.

Abdomen with sixth somite elongate, about 1.8 times maximum height, bearing faint, interrupted cicatrix on lateral surface. Telson (Figure 31*B*) with lateral margins armed with two (rarely three) pairs of short, slender movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 31*C*) with length 6-9 times basal width, spear shaped and with dorsal surface convex. Mesial ramus of uropod almost reaching or surpassing apex of telson by as much as 0.15 of its own length; lateral ramus overreaching mesial ramus by 0.25-0.30 of its own length.

Petasma (Figure 32*A*, *B*) with dorsomedian lobule produced in well-defined distomedian projection, bearing narrow distal plate and broader proximal plate thickened mesially, but not form-

FIGURE 32.—*Penaeopsis serrata*, ♂ 22 mm cl, Golfo de los Mosquitos, Panama. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. *D*, Mesial view. Scales = 1 mm.

ing crest; rib of dorsolateral lobule terminating proximally in flattened subrectangular process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part narrow and turned inwardly; ventral costa curving abruptly dorsomesially and ending in relatively broad process (with interior surface excavate) reaching approximately to level of cincinnuli; costa bearing ventral (inner) row of setae along attached margin.

Appendix masculina (Figure 32*C*, *D*) considerably broader than long (width 1.7 to almost twice length), subelliptical, convex mesially, flat laterally, and bearing mesial patch of setae.

Petasmal endopods becoming joined in male 12 mm cl. Armature of sternites XIII and XIV in very small juvenile male (discussed on p. 723) illustrated in Figure 33.

Thelycum (Figure 34) with anterior border of plate of sternite XIV slightly to strongly inclined posterolaterally, broadly arched on each side of posteromedian projection of sternite XIII; plate of sternite XIV with anterolateral extremities produced laterally into lobules of variable lengths, and lateral portions setose and raised (ventrally), slanting dorsomesially toward corresponding, narrow, submedian depression; median ridge usually ovoid or tear-shaped, sometimes subtriangular, greatly raised except for short, low, anterior part abutting projection of sternite XIII, and naked posteriorly; posterior thoracic ridge also lacking setae. Median plate of sternite XIII broad, subsemicircular, cordiform or roughly pentagonal, with transverse depression across its entire width, bearing or lacking minute anteromedian spine, and covered with densely set setae anteriorly; posteromedian projection strongly developed, broad, with posterior margin slightly emarginate to deeply bifid and studded with numerous posteriorly pointed setae. Sternite XII bearing posteromedian subconical tooth, its apex pointed ventrally or anteroventrally; oblique pair of ridges extending posterolaterally from base of tooth.

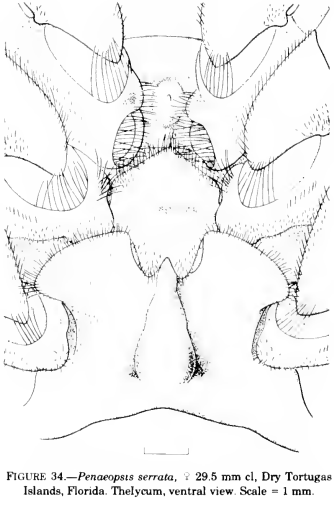


FIGURE 34.—*Penaeopsis serrata*, ♀ 29.5 mm cl, Dry Tortugas Islands, Florida. Thelycum, ventral view. Scale = 1 mm.

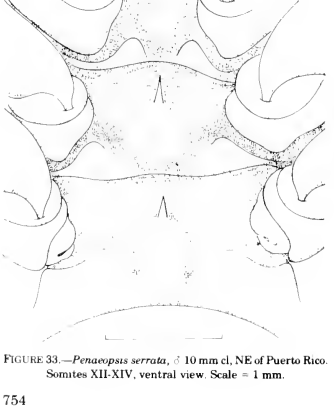


FIGURE 33.—*Penaeopsis serrata*, ♂ 10 mm cl, NE of Puerto Rico. Somites XII-XIV, ventral view. Scale = 1 mm.

Seminal receptacles (Figure 35*A*, *B*) consisting of paired bilobed membranous sacs, derived from invaginations of sternite XIV. Submedian sac large, extending posteriorly to rather near caudal margin of sternite XIV, other smaller one extending laterally; both diverging from broad an-

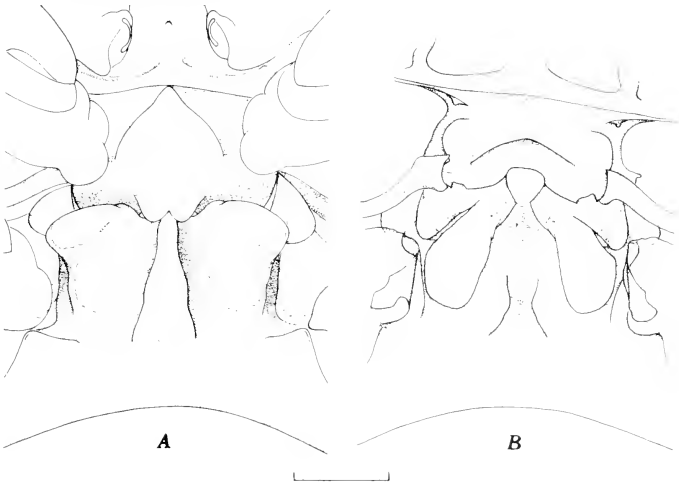


FIGURE 35.—*Penaeopsis serrata*, ♀ 30 mm cl, N of Thunder Knoll, off Honduras. Sperm receptacles. *A*, Ventral view. *B*, Dorsal view (specimen stained). Scale = 2 mm.

teromedian sinus. Receptacles opening through long, paired slits located between sternites XIII and XIV, and separated by narrow, shallow, anteromedian portion of sternite XIV.

Stages in development of thelycum: in female 8 mm cl (Figure 36*A*), plate of sternite XIV bearing median ridge produced anteriorly in long, sharp spine not quite reaching sternite XIII; anterolateral portions ventrally convex, covering invaginations (seminal receptacles) from slitlike openings along anterior margin of plate. Sternite XIII with small triangular median plate produced in long, sharp anteromedian spine reaching margin of sternite XII. Sternite XII bearing minute, sharp posteromedian tooth and pair of ridges extending posterolaterally from base of tooth (tooth and ridges changing little except increasing in size to facies in adult).

In female 9.5 mm cl (Figure 36*B*), plate of sternite XIV with spine proportionately smaller than that in few preceding instars, farther removed from sternite XIII; anterolateral portions with openings of seminal receptacles enlarged and still exposed. Sternite XIII with spine on median plate distinctly overreaching sternite XII.

In female 10.5 mm cl (Figure 36*C*), plate of sternite XIV with median ridge virtually reaching sternite XIII and bearing no more than rudiment of spine; anterolateral portions overlapping sternite XIII mesially, obscuring openings of sperm receptacles, and frequently produced laterally in short lobules, continuous with well-defined, exposed hoods. Median plate of sternite XIII with spine still slightly overreaching sternite XII.

In female 12.5 mm cl (Figure 36*D*), plate of sternite XIV with elongate trapezoidal (usually becoming tear-shaped with increasing size) median ridge, reaching sternite XIII; basal part of ridge with strong median elevation; anterolateral portions broadly overlapping sternite XIII and bearing prominent lobules partly obscuring hoods. Median plate of sternite XIII considerably broadened, its anteromedian spine minute and far removed from sternite XII; plate produced in

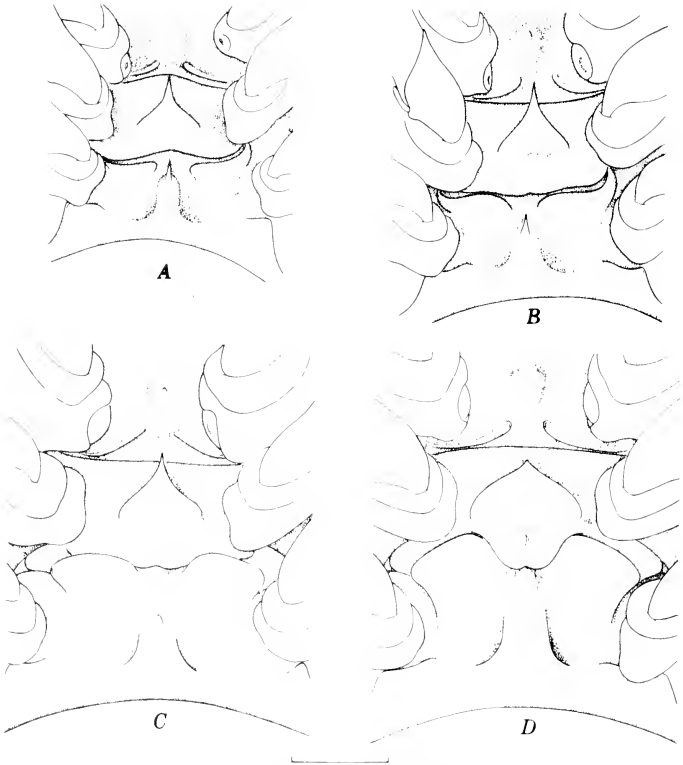


FIGURE 36.—*Penaeopsis serrata*. Stages of development of thelycum in juvenile females. *A*, 8 mm cl; *B*, 9.5 mm cl; *C*, 10.5 mm cl; *D*, 12.5 mm cl. All from W of Cartagena, Columbia. Scale = 1 mm.

broad posteromedian projection markedly overlapping sternite XIV.

In *P. serrata* the spermatophore does not bear the mesially attached element which in impregnated females of *P. balssi*, *P. eduardoi*, *P. jerryi*, and *P. rectacuta* (i.e., all the Indo-West Pacific species except *P. challengeri* of which I have not examined females carrying spermatophores) lies exposed on the thelycum. Because of the absence of this element, impregnated females of the former species are not readily recognized. The presence of a certain accessory structure in the sper-

matophore of one species of a genus and its absence in others is not unique in *Penaeopsis*; for in the family Penaeidae a similar phenomenon occurs even within the species of a subgenus. In the genus *Penaeus*, for instance, of the eight species of the American subgenus *Farfantepenaeus* Burukovsky 1972, only one, *Penaeus (F.) brevirostris* Kingsley 1878, exhibits a large, fleshy structure attached to the sperm sac which in impregnated females entirely covers the plate of sternite XIV, much like the comparable accessory element of the spermatophores of *P. rectacuta* and *P. eduardoi*. The spermatophores of the remaining seven species of *Farfantepenaeus* lack such a membranous structure.

Color.—This is one of the most beautifully colored shrimp I have seen. The following description is based on observations of a large number of freshly collected specimens obtained during the 1969 cruise of the *Oregon II* in the Caribbean (from Puerto Rico to Antigua).

Body varying from translucent light pink (sometimes with salmon hue) to deep reddish pink, interrupted by an iridescent violet to purple subelliptical patch on gastric region and various other white, deep red, violet or purple markings (lines, bands, patches, dots) on other areas. In many individuals, rostrum with numerous red chromatophores and red tip. Carapace bearing small patch of red chromatophores at base of antennal spine; anterior cardiac region with narrow, deep violet arc or transverse band running ventrally and followed by median, reddish purple subrectangular area. Some coloration continuing laterally in short posterior band, then broadening abruptly on branchiostegites, extending ventrally to margin of carapace and anteriorly to hepatic sulcus; subrectangular area flanked by white band running anteriorly to hepatic region; posterior portion of carapace white. In other individuals entire branchiostegites of highly iridescent, deep reddish pink or reddish purple. Abdominal somites with transverse reddish to purple band along posterior margin of terga; band often divided by narrow white stripe extending along dorsal midline; anterodorsal extremities of pleura bearing brilliant red or purple spot forming striking paired rows; pleura of first five somites marked by reddish to purple marginal line; bearing larger median spot and, occasionally, narrow angular stripe extending from anterodorsal spot on pleuron to median spot of same color as line; sixth somite bordered only posteriorly by line of same color as that on margin of pleura of preceding somites. Telson with paired ribs and lateral margins reddish to purple, sometimes also fixed spines and line joining their bases similarly colored. Ocular peduncle white with red stripe along margin of cornea; basal article bearing large, brilliant red or deep purple circle. Antennular peduncle highly iridescent pink proximally becoming increasingly reddish distally; distal and sometimes lateral margins of articles red or purple; flagella pink or reddish, fading distally; frequently ventral flagellum white and dorsal reddish. Antennal flagella pink. Pereopods of lighter shade than body, but lateral surfaces usually darker and strongly iridescent. Bases of pleopods white, light pink, or violet with posterolateral surfaces iridescent with deep pink or violet hues; endopods and exopods translucent, and bearing reddish or purplish spot proximally. Uropods with lateral portion of protopod of darker shade than mesial; rami usually of same or lighter color than body but deeper proximally.

Maximum lengths.—Males 120 mm tl; female 150 mm tl (Maurin 1952). Largest specimens examined by me: males 24 mm cl, 112 mm tl; females 34.5 mm cl, 135 mm tl.

Geographic and bathymetric ranges (Figure 37).—Western Atlantic: from east of Barnegat, N.J., south of Martha's Vineyard, Mass. (lat. 40°00′ N, long. 70°47′ W, coordinates from Haedrich et al. 1975, *Gosnold* cruise 197, stn 111), through the Gulf of Mexico and the Caribbean south to French Guiana (lat. 7°11′ N, long. 52°58′ W). Also found at a disjunct locality, off Rio Grande do Sul (lat. 32°45′24″S, long. 50°24′00″W). The record from off Barnegat, which represents the most northerly point at which this shrimp has been found, and that off Rio Grande do Sul, marking the southernmost record of the occurrence of the species, were both reported by Perez Farfante and Ivanov (1979).

Eastern Atlantic: from south of Cabo San Vicente, Portugal, to off Cadiz, Spain (Maurin 1961, 1965) and off the northwest coast of Africa to Tamzak ("Tamxat") (lat. 17°26′ N, long. 16°03′ W), Mauritania (Maurin 1968b).

In the western Atlantic, *Penaeopsis serrata* frequents depths between 183 and about 750 m (records of its presence in shallower water are almost certainly erroneous), with maximum concentrations occurring from 300 to 450 m. In the eastern

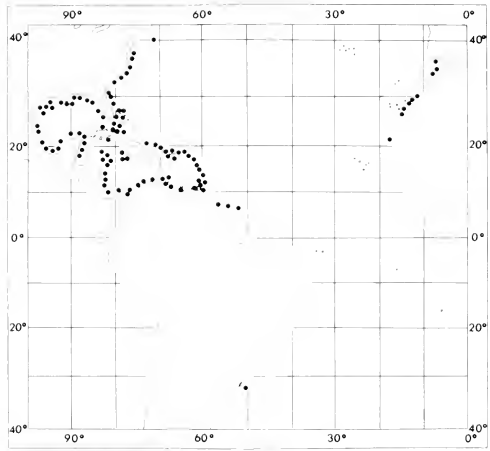


FIGURE 37.—Range of *Penaeopsis serrata* based on published records and specimens personally examined

Atlantic it has been reported between 120 (Lagardère 1971) and 700 m (Maurin 1961).

The temperature-depth relationship for *P. serrata* is presented in Figure 38. In three areas, two in the Gulf of Mexico and one in the southern part of the Caribbean (off Venezuela), this shrimp shows similar ranges of temperature and depth. In the northeast Gulf, however, the range is apparently more extensive, the animals having penetrated shallower and warmer as well as deeper and colder waters. According to the available data, the population off the southeast coast of the United States occurs within the shallower range depths occupied by other populations, but at lower temperatures. Actually, in that area the shrimp is not restricted to the depths presented in the graph,

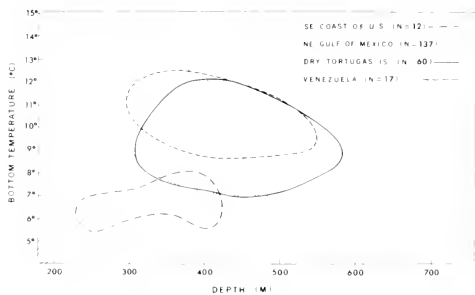


FIGURE 38.—Depth-temperature relationships for *Penaeopsis serrata* in four western Atlantic areas (data obtained from *Oregon* and *Oregon II* Station Lists).

because in at least one locality (for which temperature data are lacking) it has been found at about 550 m (see "Material" herein), i.e., only 150 m above the maximum depth at which it has been taken in the northeast Gulf. Because the temperature-depth distribution of the population off the southeast coast of the United States is based on only 12 records, one may only point out the unusual conditions existing in this segment of the range of *P. serrata*. According to my observations, the specimens of that population exhibit no morphological differences from those of other localities throughout the broad range of the species, but Harvey R. Bullis Jr.[4] stated that the specimens, observed by him immediately after capture, had a different coloration from those caught elsewhere. Furthermore, Bullis and Rathjen (1959) found that off the southeast coast of the United States *P. serrata* was most abundant at slightly greater depths than *Pleoticus robustus* (Smith 1885), whereas in all other areas megalops was not abundant where it occurs with, or at shallower depths than, *P. robustus*.

Variation.—This species, like most members of the genus, exhibits a large number of characters that are highly variable. Among them, the rostrum, strongly arched in the young, may be straight, arcuate only basally or sinuous in the adult, and horizontal or upturned; the number of rostral teeth ranges from 10 to 19. The scaphocerite may fall short of or surpass the distal end of the antennular peduncle, and the mesial ramus of the uropod may not reach the apex of telson or may extend beyond it by as much as 0.15 of its own length. The thelycal features, especially, show a wide range of variation: the anterior border of the plate of sternite XIV, usually strongly arched on each side of the posteromedian projection of sternite XIII, sometimes is moderately or only slightly so; and the anterolateral lobules of that plate although generally strongly developed are sometimes quite short. The median plate of sternite XIII varies in shape (from subsemicircular to roughly pentagonal), while the posteromedian projection, although always broad, may range from slightly emarginate to deeply bifid. The entire range of variations in some of the characters cited have been observed in animals from the same locality.

[4]Harvey R. Bullis, Jr., formerly Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. December 1978.

At least in the western Atlantic populations, there are also differences in the relative extension of the third maxilliped and pereopods. I have noticed that in the populations of the Caribbean and Atlantic coast of South America they extend distally slightly farther than they do in northern populations. In the former populations the range extension of these appendages falls within the upper half of the limits cited herein and in the northern ones within the lower half. Because most of the few specimens available to me from the eastern Atlantic are poorly preserved, I have been unable to arrive at definite conclusions as to the relative length of the appendages in the populations occurring in that region.

Affinities.—*Penaeopsis serrata*, the only Atlantic member of the genus, differs from its congeners in that the branchiocardiac carina and interrupted cicatrix on the sixth abdominal somite are very weak, and the knob at the distal end of the semicircular part of the ventral antennular flagellum in the male is rather inconspicuous. More strikingly, it differs from its allies in a number of features of the external genitalia, as pointed out below. It appears to be closer to *P. rectacuta* than to any of the other species. They share long rostra which tend to possess a large number of teeth (up to 18 in *P. serrata* and 17 in *P. rectacuta*), and the second tooth is located at the level of the orbital margin. In both, the hepatic spine is situated ventral to the level of the antennal spine, and the branchiocardiac carina does not approach closely the hepatic sulcus. The petasmata are also rather similar and the telson of *P. serrata* is sometimes, although rarely, armed with three pairs of movable spines as is typical of that of *P. rectacuta*.

The thelyca exhibit the most obvious differences between the two species. In *P. serrata* the plate of sternite XIV is uniquely produced into laterally directed lobules, bears an entirely naked and much stronger median ridge (usually subovoid instead of flasklike as it is generally in *P. rectacuta*), and the posterior thoracic ridge lacks setae across its anterior border. Furthermore, in *P. serrata* the median plate of sternite XIII, although variable in shape, is generally semicircular or roughly pentagonal, whereas in *P. rectacuta* it is cordiform. The posteromedian projection of sternite XIII is also broader and emarginate (often deeply) rather than entire as it usually is in *P. rectacuta*. The males of these species can also be distinguished by the proximal plate of the dorsomedian lobule of the

petasma which in *P. serrata*, although thickened mesially, does not form a sharp crest as it does in *P. rectacuta*; by the proximal plate of the dorsolateral lobule subrectangular in the former and nearly circular in the latter; and by the apical process of the ventral costa which is conspicuously broader in *P. serrata* than in *P. rectacuta*.

Remarks.—With reference to the types of this species, both Bate (1881) and A. Milne Edwards considered the account of *P. serratus* included in the A. Milne Edwards' manuscript—later published jointly by A. Milne Edwards and Bouvier (1909)—to constitute the original description; therefore, it seems reasonable to me that the syntypes of this species, from Barbados, designated by A. Milne Edwards and Bouvier are, by implication, also those of Bate. Furthermore, Bate (1881:180) stated that "I have not had an opportunity of examining the branchial apparatus to feel quite certain that the genus [*Penaeopsis*] is a good determination," thereby indicating that he had not examined any specimens of *P. serrata*.

Commercial importance.—Extensive explorations in the Gulf of Mexico, the Caribbean, and along the northern coast of South America by the U.S. Government vessels *Oregon* and *Oregon II* demonstrated the occurrence of megalops in many areas on the upper slope of the continental and insular shelves. It is common in many localities, and, on the basis of collections made by the RV *Alaminos*, Roberts and Pequegnat (1970) stated that this shrimp "is the most abundant penaeid caught by the *Alaminos* in the Gulf, and it appears to be most abundant in the De Soto Canyon around 200 fathoms [366 m] and, secondarily, off the Rio Grande in 150 fathoms [274 m]." Even though it is frequently taken while trawling for the royal red shrimp, *Pleoticus robustus* (Smith 1885), Harvey R. Bullis, Jr. (see footnote 4) has informed me that no serious effort was made during the cruises of the *Oregon* and *Oregon II* to assess the commercial potential of *P. serrata*. The reason for lack of interest in investigating possibilities for commercial exploitations was the small size of this shrimp—according to Bullis, the average count of megalops tails would have been in the range of 60-100/lb (132-220/kg). In the eastern Atlantic this species constitutes a part of the commercial catches: Maurin (1952) cited it as one of the shrimps commercially fished off Morocco at depths >200 m; I have examined two females sorted by L. B. Holthuis from commercial catches made by a Cadiz trawler off Rabat, Morocco; and Holthuis and Rosa (1965) listed it among the shrimps of economic value in the "Southeast Atlantic Area."

ACKNOWLEDGMENTS

This study has been made possible through the generous cooperation of many colleagues on four continents who made available to me invaluable collections. In addition, some of them provided facilities for me to work at their respective institutions. I am deeply indebted to Anthony A. Fincham and Raymond W. Ingle (BMNH), Jacques Forest (MP), and Lipke B. Holthuis (RMNH) for placing at my disposal critical specimens and providing working space and encouragement. I am also grateful to the following individuals for making additional material available to me: Alan Crosnier, Office de la Recherche Scientifique et Technique Outre Mer, Paris; Antonio J. de Freitas (ORI); Richard L. Haedrich, Woods Hole Oceanographic Institution, Woods Hole, Mass.; Willard D. Hartman (YPM); Boris G. Ivanov (VNIRO); Brian Kensley (formerly SAM); Herbert W. Levi (MCZ); Patsy A. McLaughlin (FIU); G. Ramakrishna (ZSI); P. Subramanian, Center of Advanced Study in Marine Biology, Parangipettai; Krishna Kant Tiwari (ZSI); and Gilbert L. Voss (UMML).

Thanks are due Harvey R. Bullis, Jr., formerly of the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, Fla., for the graph of the depth-temperature relationship and for his cooperation through the many years during which he, in charge of the *Oregon* and *Oregon II*, preserved and made available to me extensive collections of penaeoids from catches of those U.S. Government vessels.

I am also indebted to my colleagues Horton H. Hobbs, Jr. of the Smithsonian Institution for his invaluable advice and critical comments during the preparation of this work, and Fenner A. Chace, Jr. and Raymond B. Manning, both of the Smithsonian Institution, for the review of the manuscript and helpful suggestions.

An important contribution to this study was the cooperation of María M. Dieguez, who rendered the detailed illustrations and assisted me in the preparation of the lists of material. Finally, I am grateful to Arleen S. McClain and Virginia R. Thomas for typing the manuscript.

LITERATURE CITED

ALCOCK, A. W.

1898. A summary of the deep-sea zoological work of the Royal Indian Marine Survey ship *Investigator* from 1884 to 1897. Sci. Mem. Med. Off. Army India 11:45-93.

1901a. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine Survey ship Investigator. Indian Mus., Calcutta, 286 p.

1901b. Zoological gleanings from the Royal Indian Marine Survey ship *Investigator*. Sci. Mem. Off. Army India 12:35-76.

1902. A naturalist in Indian Seas or, four years with the Royal Indian Marine Survey ship 'Investigator'. John Murray, Lond., 328 p.

1905. A revision of the "genus" *Peneus*, with diagnoses of some new species and varieties. Ann. Mag. Nat. Hist., Ser. 7, 16:508-532.

1906. Fasciculus I. The prawns of the *Peneus* group. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part III. Macrura. Indian Mus., Calcutta, 55 p.

ALCOCK, A. W., AND A. R. ANDERSON.

1894. Natural history notes from H. M. Indian Marine Survey steamer *Investugator*, Commander, C. F. Oldham, R.N., commanding. Series II, No. 14. An account of a recent collection of deep sea Crustacea from the Bay of Bengal and Laccadive Sea. J. Asiat. Soc. Bengal 63(Part II, 3):141-185.

1899. Natural history notes from H. M. Royal Indian Marine Survey ship *Investigator*, Commander T. H. Heming, R.N., commanding. Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897-98. Ann. Mag. Nat. Hist., Ser. 7, 3:1-27, 278-292.

ALCOCK, A. W., AND A. F. MCARDLE.

1901. Illustrations of the zoology of the Royal Indian Marine Survey ship *Investigator*, under the command of Commander T. H. Heming, R.N., Crustacea. Part IX, plates 49-55. Off. Supt. Gov. Print. India, Calcutta.

ANDERSON, W. W., AND H. R. BULLIS, JR.

1970. Searching the shrimp beds by sub. Sea Front. 16:112-119.

ANDERSON, W. W., AND M. J. LINDNER.

1945. A provisional key to the shrimps of the family Penaeidae with especial reference to American forms. Trans. Am. Fish. Soc. 73:284-319.

BALSS, H.

1925. Macrura der Deutschen Tiefsee-Expedition, 2. Natantia, A. Wiss. Ergeb. Dtsch. Tiefsee-Exped. *Valdwia* 20:217-315.

1957. Decapoda. VIII. Systematik. *In* H. G. Bronn, Klassen and Ordnungen des Tierreichs. 5, sect. 1, book 7:1505-1672.

BARNARD, K. H.

1950. Descriptive catalogue of South African decapod Crustacea. Ann. S. Afr. Mus. 38:1-837.

BATE, C. S.

1881. On the Penaeidea. Ann. Mag. Nat. Hist., Ser. 5, 8:169-196.

1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873-76. Rep. Sci. Res. Voy. H.M.S. Challenger 1873-76, Zool. 24, 942 p.

BOONE, L.

1927. Scientific results of the first oceanographic expedition of the "Pawnee" 1925. Crustacea from tropical east American seas. Bull. Bingham Oceanogr. Collect., Yale Univ. 1(2), 147 p.

BOUVIER, E. L.

1905a. Sur les Peneides et les Stenopides recueillis par les expeditions françaises et monegasques dans l'Atlantique oriental. C. R. Acad. Sci., Paris 140:980-983.

1905b. Sur les macroures nageurs (abstraction faite des Carides), recueillis par les expeditions americaines du *Hassler* et du *Blake*. C. R. Acad. Sci., Paris 141:746-749.

1908. Quelques observations systématiques sur la sous-famille des Penaeinae Alcock. Bull. Inst. Océanogr. (Monaco) 119, 10 p.

BULLIS, H. R., JR.

1956. Preliminary results of deep-water exploration for shrimp in the Gulf of Mexico by the M/V *Oregon* (1950-1956). Commer. Fish. Rev. 18(12):1-12.

BULLIS, H. R., JR, AND W. F. RATHJEN.

1959. Shrimp explorations off southeastern coast of the United States (1956-1958). Commer. Fish. Rev. 21(6):1-20.

BULLIS, H. R., JR, AND J. R. THOMPSON.

1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican* made during 1956-1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

BURKENROAD, M. D.

1934a. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection, with a revision of *Penaeopsis* and descriptions of two new genera and eleven new American species. Bull. Bingham Oceanogr. Collect., Yale Univ. 4(7), 109 p.

1934b. The Penaeidea of Louisiana with a discussion of their world relationships. Bull. Am. Mus. Nat. Hist. 68:61-143.

1936. The Aristeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. Bull. Bingham Oceanogr. Collect., Yale Univ. 5(2), 151 p.

1959. Addenda et Corrigenda au Memoire XXV. Penaeidae par Martin D. Burkenroad (pages 67-92). *In* Mission Robert Ph. Dollfus en Egypte (decembre 1927 - mars 1929), *S. S. "Al Sayad."* Resultats scientifiques, 3e Partie [contributions] (XXIII-XXXIV), p. 285. Centre National de la Recherche Scientifique, Paris.

1963. Comments on the petition concerning peneid names (Crustacea Decapoda) (Z. N. (S.) 962). Bull. Zool. Nomencl. 20:169-174.

BURUKOVSKY, R. N.

1972. Some problems of the systematics and distribution of the shrimps of the genus *Penaeus*. [In Russ.] Fisheries Research in the Atlantic Ocean. Tr. Atl. Nauch.-Issled. Inst. Rybn. Khoz. Okeanogr. 42:3-21. (Translated by Israel Program Sci. Transl., TT72-50101.)

1974. Keys to the shrimps, spiny lobsters and homarids. [In Russ.] Moscow: Pishchevaia promyshlennost, "Food Industry," 126 p.

CROSNIER, A., AND J. FOREST.

1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune Tropicale Tome XIX. O.R.S.T.O.M. (Off. Rech. Sci. Tech. Outre-Mer), Paris, 409 p.

CROSNIER, A., AND C. JOUANNIC.

1973. Note d'information sur les prospections de la pente

continentale malgache effectuées par le N. O. Vauban - Bathymetrie - Sedimentologie - Pêche au chalut. O.R.S.T.O.M. Centre Nosy-Be Doc. Sci. 42, 18 p.

DOMANTAY, J. S.
1956. Prawn fisheries of the Philippines. Indo-Pac. Fish. Counc. Proc. 6:362-366.

ESTAMPADOR, E. P.
1937. A check list of Philippine crustacean decapods. Philipp. J. Sci. 62:465-559.

FABRICIUS, J. C.
1798. Supplementum entomologiae systematicae. Hafniae, 572 p.

FAXON, W.
1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XV. The stalk-eyed Crustacea. Mem. Mus. Comp. Zool. Harv. Coll. 18, 292 p.
1896. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, 1877 to 1880, by the U.S. Coast Survey steamer "Blake," Lieut. Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XXXVII. Supplementary notes on the Crustacea. Bull. Mus. Comp. Zool. Harv. Coll. 30:153-166.

GEORGE, M. J.
1966. On a collection of penaeid prawns from the offshore waters of the south-west coast of India. *In* Symposium on Crustacea, p. 337-346. Mar. Biol. Assoc. India, Symp. Ser. 2.
1969. Prawn fisheries of India. II Systematics-taxonomic considerations and general distribution. Cent. Mar. Fish. Res. Inst., Bull. 14:5-48.

HAEDRICH, R. L., G. T. ROWE, AND P. T. POLLONI
1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.

HALL, D. N. F.
1962. Observations on the taxonomy and biology of some Indo-West-Pacific Penaeidae (Crustacea, Decapoda). Colon. Off., Lond. Fish. Publ. 17, 229 p.

HAY, W. P., AND C. A. SHORE
1918. The decapod crustaceans of Beaufort, N.C., and the surrounding region. Bull. [U.S.] Bur. Fish. 35:369-475.

HOLTHUIS, L. B., AND H. ROSA, JR.
1965. List of species of shrimps and prawns of economic value. FAO Fish. Tech. Pap. 52, 21 p.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE.
1969. Penaeid generic names (Crustacea, Decapoda): addition of twenty-eight to the Official List. Opinion 864. Bull. Zool. Nomencl. 25:138-147.

IVANOV, B. G., AND A. M. HASSAN.
1976. Penaeid shrimps (Decapoda, Penaeidae) collected off east Africa by the fishing vessel "Van Gogh", 2. Deep-water shrimps of the genera *Penaeopsis* and *Parapenaeus* with description of *Penaeopsis balssi* sp. nov. Crustaceana 31:1-10.

JONES, S.
1967. The crustacean fishery resources of India. *In* Symposium on Crustacea, p. 1328-1340. Mar. Biol. Assoc. India, Symp. Ser. 2.
1969. The prawn fishery resources of India. FAO Fish. Rep. 57:735-747.

JOYCE, E. A., JR., AND B. ELDRED.
1966. The Florida shrimping industry. Fla. State Board Conserv., Educ. Ser. 15, 47 p.

KEMP, S., AND R. B. S. SEWELL.
1912. II. Notes on Decapoda in the Indian Museum. III. The species obtained by R.I.M.S.S. 'Investigator' during the survey season 1910-11. Rec. Indian Mus. 7:15-32.

KENSLEY, B. F.
1969. Decapod Crustacea from the south-west Indian Ocean. Ann. S. Afr. Mus. 52:149-181.
1972. Shrimps and prawns of southern Africa. South Afr. Mus., Cape Town, 65 p.

KINGSLEY, J. S.
1878. Notes on the North American Caridea in the museum of Peabody Academy of Science at Salem, Mass. Proc. Acad. Nat. Sci. Phila. 30:89-98.

KUBO, I.
1949. Studies on penaeids of Japanese and its adjacent waters. J. Tokyo Coll. Fish. 36(1), 467 p.

KURIAN, C. V.
1964. On the occurrence of the deep-water prawn *Penaeopsis rectacutus* (Spence Bate) off the Kerla coast. Curr. Sci. (Bangalore) 33:216-217.

LAGARDERE, J. P.
1971. Les crevettes des côtes du Maroc. Trav. Inst. Sci. Cherifien Fac. Sci., Ser. Zool. 36:1-140.

LONGHURST, A. R.
1971. Crustacean resources. *In* J. A. Gulland (editor), The fish resources of the ocean, p. 206-255. FAO, Rome.

LUCAS, H.
1846. Crustaces, Arachnides, Myriapodes et Hexapodes. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sciences physiques. Zoologie 1. Hist. Nat. Anim. Articulés Part 1:1-403.

MAN, J. G. DE.
1911. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga-Exped. Monogr. 39*a*, 131 p.
1913. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga-Exped. Monogr. 39*a*, Part 1 (Suppl.), 10 pl.

MAURIN, C.
1952. Crustacés. Note préliminaire sur les crevettes des côtes du Maroc. Cons. Perm. Int. Explor. Mer, Ann. Biol. 8:91-92.
1961. Répartition des crevettes profondes sur les côtes sud du bassin occidental de la Méditerranée et dans la région atlantique ibéro-marocaine. Comm. Int. Explor. Sci. Mer Medit. Rapp. P.-V. Reun. 16:529-532.
1962. Etude des fonds chalutables de la Mediterranee occidentale (ecologie et pêche). Resultats des campagnes de navires oceanographiques "President-Theodore-Tissier" 1957 à 1960 et "Thalassa" 1960 et 1961. Rev. Trav. Inst. Pêches Marit. 26:163-218.
1963. Les crevettes capturées par la "Thalassa" au large des côtes du Rio de Oro et de Mauritanie. Ecologie et pêche. Cons. Int. Explor. Mer, Comm. Mollusques Crustacés No. 48, 2 (unnumbered) + 3 p.
1965. Les crevettes profondes de la région atlantique ibéro-marocaine: répartition bathymetrique et geo-

graphique, importance économique. Comm. Int. Explor. Sci. Mer Médit. Rapp. P.-V. Reun. 156:116-119.

1968a. Ecologie ichthylogique des fonds chalutables atlantiques (de la baie ibero-marocaine à la Mauritanie) et de la Mediterranée occidentale. Rev. Trav. Inst. Pêches Marit. 32:1-147.

1968b. Les Crustacés captures par la "Thalassa" au large des côtes nord-ouest africaines. Rev. Roum. Biol., Ser. Zool. 13:479-493.

MILNE EDWARDS, A., AND E. L. BOUVIER.

1909. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey steamer "Blake," Lieut. Com. C. D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XLIV. Les Penéides et Stenopides. Mem. Mus. Comp. Zool. Harv. Coll. 27:177-274.

PEQUEGNAT, W. E., AND T. W. ROBERTS.

1971. Decapod shrimps of the family Penaeidae. *In* W. E. Pequegnat, L. H. Pequegnat, R. W. Firth, Jr., B. M. James, and T. W. Roberts (editors), Gulf of Mexico deep-sea fauna Decapoda and Euphausiacea, p. 8-9. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 20.

PEREZ FARFANTE, I.

1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

1971. Western Atlantic shrimps of the genus *Metapenaeopsis* (Crustacea, Decapoda, Penaeidae), with descriptions of three new species. Smithson. Contrib. Zool. 79, 37 p.

1977a. American solenocerid shrimps of the genera *Hymenopenaeus, Haliporoides, Pleoticus, Hadropenaeus* new genus, and *Mesopenaeus* new genus. Fish. Bull., U.S. 75:261-346.

1977b. *Penaeopsis eduardoi*, a new species of shrimp (Crustacea: Penaeidae) from the Indo-West Pacific. Proc. Biol. Soc. Wash. 90:172-182.

1978. Intersex anomalies in shrimp of the genus *Penaeopsis* (Crustacea: Penaeidae). Fish. Bull., U.S. 76:687-691.

1979. *Penaeopsis jerryi*, new species from the Indian Ocean (Crustacea: Penaeoidea). Proc. Biol. Soc. Wash. 92:208-215.

PEREZ FARFANTE, I., AND B. G. IVANOV.

1979. Range extension of *Penaeopsis serrata* (Crustacea: Penaeoidea) to off New Jersey and Rio Grande do Sul. Proc. Biol. Soc. Wash. 92:204-207.

RAMADAN, M. M.

1938. Crustacea: Penaeidae. John Murray Exped. 1933-34. Sci. Rep. 5:35-76.

RATHBUN, M. J.

1901. The Brachyura and Macrura of Porto Rico. [Preprint] U.S. Fish Comm. Bull. 1900 [1902], 20(2):1-127, [Preprint index] 129-137, 2 pl.

ROBERTS, T. W., AND W. E. PEQUEGNAT.

1970. Deep-water decapod shrimps of the family Penaeidae. *In* W. E. Pequegnat and F. A. Chace, Jr. (editors), Contributions on the biology of the Gulf of Mexico, p. 21-57. Tex. A & M Univ. Oceanogr. Stud. 1.

SCHMITT, W. L.

1926. Report on the Crustacea Macrura (families Peneidae, Campylonotidae and Pandalidae) obtained by the F.I.S. "Endeavour" in Australian seas. With notes on the species of *"Penaeus"* described by Haswell and contained, in part, in the collections of the Macleay Museum, at the University of Sidney. Biological results of the Fishing Experiments carried on by the F.I.S. "Endeavour" 1909-14. Commonw. Aust. Dep. Trade Customs 5, Part 6:311-381.

SEWELL, R. B. S.

1935. Introduction and list of stations. Br. Mus. Nat. Hist., John Murray Exped., 1933-34. Sci. Rep. 1(1):1-41.

1955. A study of the sea coast of southern Arabia. Proc. Linn. Soc. Lond. 165:188-210.

SMITH, S. I.

1885. On some genera and species of Penaeidae, mostly from recent dredgings of the United States Fish Commission. Proc. U.S. Natl. Mus. 8:170-190.

SPRINGER, S., AND H. R. BULLIS, JR.

1956. Collections by the *Oregon* in the Gulf Mexico. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.

STAROBOGATOV, Y. I.

1972. Penaeidae (Crustacea Decapoda) of the Tonking Gulf. [In Russ.] Akad. Nauk. SSSR, Zool. Inst. Issled. Fauny More) 10(18):359-415.

VILLALUZ, D. K., AND F. J. ARRIOLA.

1938. Five other known species of *Penaeus* in the Philippines. Philipp. J. Sci. 66:35-41.

VOSS, G. L.

1955. A key to the commercial and potentially commercial shrimp of the family Penaeidae of the western North Atlantic and the Gulf of Mexico. Fla. State Board Conserv., Tech. Ser. 14, 22 p.

WENNER, E. L, AND D. F. BOESCH.

1979. Distribution patterns of epibenthic decapod Crustacea along the shelf-slope coenocline, middle Atlantic bight, U.S.A. Bull. Biol. Soc. Wash. 3:106-133.

WOOD-MASON, J.

1891. Phylum Appendiculata. Branch Arthropoda. Class Crustacea. *In* J. Wood-Mason and A. Alcock (editors), Natural history notes from H. M. Indian Marine Survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding. - *Series II, No. 1.* On the results of deep-sea dredging during the season 1890-91. Ann. Mag. Nat. Hist., Ser. 6, 8:269-286.

YOKOYA, Y.

1933. On the distribution of decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S. S. *Söyö-Maru*, during the year 1923-30. J. Coll. Agric., Tokyo Imp. Univ. 12:1-226.

1941. On the classification of penaeid shrimps by the structural features of the appendix masculina. J. Coll. Agric., Tokyo Imp. Univ. 15:45-68.

LIKELIHOOD METHODS FOR THE VON BERTALANFFY GROWTH CURVE

DANIEL K. KIMURA[1]

ABSTRACT

Likelihood methods for the von Bertalanffy growth curve are examined under the assumption of independent, normally distributed errors. The following are examined: determining the best method of estimation, relationships between methods of estimation, failure of assumptions, constructing confidence regions, and applying likelihood ratio tests. An example is presented illustrating many of the methods discussed in theory.

The paper may be viewed as an application of classic nonlinear least squares methods to the von Bertalanffy curve. As such, the concepts discussed are generally applicable and the paper may serve as an introduction to nonlinear least squares.

Since the application of the von Bertalanffy (1938) growth curve by Beverton and Holt (1957) to the yield per recruit problem, this curve has been widely used in fisheries biology. The original curve has been generalized (Richards 1959; Chapman 1961). However, this paper will not deal with the more general Chapman-Richards growth curve. Nor will it deal with the biological motivation for these curves which have been discussed by the cited authors. Instead, I confine my study to the classic von Bertalanffy curve and examine what appears to be reasonable methods for the statistical treatment of data.

THE MODEL AND ITS MAXIMUM LIKELIHOOD ESTIMATES

I assume that age-length data are available on some species, and that the relationship between age and length can be adequately described by the von Bertalanffy growth curve. Using the usual notation, the length of the uth individual of age t_u is assumed to be

$$\begin{aligned} l_u &= l_\infty(1-\exp(-K(t_u-t_0))) + \epsilon_u \\ &= \mu(l_\infty, K, t_0, t_u) + \epsilon_u \\ &= \mu(t_u) + \epsilon_u \end{aligned}$$

where l_∞ is asymptotic length, K a constant describing how rapidly this length is achieved, t_0 the hypothetical age at length zero, and the ϵ_u's independent $N(0,\sigma^2)$ random variables.

For this model, parameters can best be estimated using the method of maximum likelihood. The principal reasons why maximum likelihood estimates are desirable are that under very general conditions (much more general than described here) they are consistent (converge in probability to the correct value), asymptotically normal, and asymptotically attain (except under unusual circumstances) the smallest possible variance. It will not be necessary to expand on these properties because they are among the most important results in statistics, and are discussed to some extent in virtually every book on mathematical statistics.

Letting $S(l_\infty,K,t_0) = \Sigma_u(l_u-\mu(l_\infty,K,t_0,t_u))^2$, the likelihood function can be written as

$$\begin{aligned} &\mathcal{L}(l_\infty, K, t_0, \sigma^2) \\ &\quad = (2\pi\sigma^2)^{-N/2} \exp(-S(l_\infty, K, t_0)/2\sigma^2) \end{aligned} \quad (1)$$

where N is the number of observations. Since for any given value of σ^2, say σ_0^2, $\mathcal{L}(l_\infty,K,t_0,\sigma_0^2)$ is maximized when $S(l_\infty,K,t_0)$ is minimized, it follows that the maximum likelihood (ML) estimates of (l_∞,K,t_0), say $(\hat{l}_\infty,\hat{K},\hat{t}_0)$, are the least squares (LS) estimates. These estimates shall be referred to as ML or LS depending on the property which is being emphasized.

The ML estimate of σ^2 is obtained in the usual way by first taking the log likelihood, calculating the partial derivative with respect to σ^2, and setting this result equal to zero

$$\begin{aligned} &\log(\mathcal{L}(l_\infty, K, t_0, \sigma^2)) \\ &\quad = -(N/2)\log(2\pi\sigma^2) - S(l_\infty, K, t_0)/2\sigma^2 \end{aligned}$$

[1]Washington Department of Fisheries, Olympia, WA 98504.

Manuscript accepted July 1979.
FISHERY BULLETIN VOL. 77, NO. 4, 1980

$$\frac{\partial \log(\mathcal{L}(l_\infty, K, t_0, \sigma^2))}{\partial \sigma^2}$$

$$= -N/2\sigma^2 + S(l_\infty, K, t_0)/2(\sigma^2)^2 = 0$$

$$\hat{\sigma}^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/N .$$

Thus the problem of ML estimation for the von Bertalanffy curve reduces to finding LS estimates of (l_∞, K, t_0). Note that this is a general property of the normal error model, since no special properties of the von Bertalanffy curve have been used.

The normal equations for finding ML estimates are obtained by taking the partial derivative of $S(l_\infty, K, t_0)$ with respect to the unknown parameters and setting the results equal to zero (i.e., $\partial S/\partial l_\infty = 0$; $\partial S/\partial K = 0$; $\partial S/\partial t_0 = 0$). Because these equations do not allow a simple solution, the graphical Ford-Walford method (Ricker 1975; actually the regression of l_{t+1} on l_t) has been widely used. The Ford-Walford plot, in addition to a plot of average length at age, should be adequate for determining the age range following the von Bertalanffy curve.

For the von Bertalanffy curve, proper ML estimates can only be found using iterative algorithms. A number of authors (Stevens 1951; Tomlinson and Abramson 1961; Allen 1966) have suggested specialized algorithms. Although these algorithms may have advantages when computers are not available, the easiest way to obtain ML estimates is to use any of the general purpose nonlinear LS computer programs available in BMD (Dixon 1976), BMDP (Dixon 1977), or SPSS (Nie et al. 1975). These programs have the flexibility of allowing complicated curves to be fit to data sets, which is especially useful if differences in growth curves among different populations are to be tested statistically. For example, it might be necessary to fit different growth curves to several populations, but with the constraint that the t_0's be equal.

It should be remembered that LS solutions obtained iteratively may be local rather than global minimizations of $S(l_\infty, K, t_0)$. With this in mind, initial values provided to any iterative procedure must represent the best available information. I recommend that the Ford-Walford method be used to calculate initial values. This guarantees that any LS solution which is obtained has smaller residual sum of squares than the Ford-Walford estimates.

LEAST SQUARES METHODS OF ESTIMATION

Under differing assumptions on the error variance, four different LS methods of estimation are appropriate. When these assumptions are met, each method provides ML estimates under the likelihood model (Equation (1)).

Let l_{ij} be the length of the jth individual of age t_i, and let $\bar{l}_i$ and s_i^2 be the sample mean and sample variance of the lengths of individuals of age t_i, based on a sample size n_i. For each method, the assumption on the error variance and the appropriate sum of squares to be minimized when this assumption is correct, is given below.

(a) All l_{ij} have constant variance:

$$\Sigma(l_{ij} - \mu(t_i))^2 .$$

(b) All $\bar{l}_i$ have constant variance:

$$\Sigma(\bar{l}_i - \mu(t_i))^2 .$$

(c) The variance of l_{ij} varies with t_i, and at age t_i is equal to σ_i^2:

$$\Sigma(n_i/s_i^2)(\bar{l}_i - \mu(t_i))^2 .$$

(d) All l_{ij} have constant variance (i.e., the same assumption as (a) above):

$$\Sigma n_i(\bar{l}_i - \mu(t_i))^2 .$$

The dependent variables in methods (a) and (b) are formally of the form described by the likelihood model (Equation (1)). By this it is meant that they have constant variance, and assuming normality and independence, their likelihood is described by Equation (1). The dependent variables in methods (c) and (d) can be transformed into the form of Equation (1). This can be done by placing the weights $w_i = (n_i/s_i^2)$ (method (c)) and $w_i = n_i$ (method (d)) within the squared expressions. Doing so for method (c) gives the pseudoobservation $y_i = (\sqrt{n_i}/s_i)\bar{l}_i$ with expectation $E(y_i) = (\sqrt{n_i}/s_i)\mu(t_i)$ and variance asymptotically equal to unity (as $s_i \to \sigma_i$). Assuming normality and independence, the asymptotic likelihood of these y_i is described by Equation (1). Similarly for method (d), the pseudoobservation becomes $y_i = (\sqrt{n_i})\bar{l}_i$ with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$ and variance σ^2. Again assuming normality and inde-

pendence, the likelihood of these y_i is described by Equation (1). It follows that likelihood procedures applicable to unweighted methods (a) and (b) are also applicable to weighted methods (c) and (d) with few modifications. These arguments apply when fitting any function using LS estimation.

Selection of an appropriate LS method for a given problem can largely be made on the validity of the error assumption, but not solely on this basis. It is also useful to keep in mind the purpose of fitting the curve. For example, a curve fit with method (a) would do well in predicting the length of a randomly selected individual (if data were from random samples), and this property would be important in, say, modeling applications. Method (b), on the other hand, may best describe the growth of a species over its entire lifespan, a property which would be desirable when comparing growth among species. It should be noted that the practice of graphing the estimated curve and plotting average lengths observed at each age is visually biased toward method (b). Method (b) will generally look best on this type of plot.

Method (c) is appropriate when it is apparent that the variance at each age varies significantly. This assumption can be examined using Bartlett's or Cochran's tests (Dixon and Massey 1957) for the homogeneity of variance.

Method (d) is largely a computational device. In the following section it is shown that method (d) is nearly equivalent to method (a), but often requires much less computational effort.

NEAR EQUIVALENCE OF METHODS (A) AND (D)

Calculations for method (a) can be performed using method (d), with often a large savings in computational effort. It will be shown that methods (a) and (d) yield identical parameter estimates, and similar covariance matrix estimates of parameter estimates. These results are general properties of LS estimates under the assumptions of method (a), and are not dependent on the form of the function being fitted.

Identity of Parameter Estimates

For the von Bertalanffy curve using method (a), the sum of squares to be minimized is

$$S(l_\infty, K, t_0) = \sum_i \sum_j (l_{ij} - \mu(l_\infty, K, t_0, t_i))^2 .$$

The sum of squares to be minimized using method (d) is

$$S_w(l_\infty, K, t_0) = \sum_i n_i(\bar{l}_i - \mu(l_\infty, K, t_0, t_i))^2 .$$

The normal equation is derived for the parameter K say, using method (a), by taking the partial derivative of S with respect to K and setting the result equal to zero:

$$\frac{\partial S}{\partial K} = \sum_i \sum_j -2(l_{ij} - \mu(t_i))\mu_K'(t_i)$$

$$= -\sum_i 2\mu_K'(t_i) n_i(\bar{l}_i - \mu(t_i)) = 0 .$$

The normal equation is obtained for method (d) by taking the partial derivative of S_w with respect to K, yielding a result identical to that from method (a):

$$\frac{\partial S_w}{\partial K} = -\sum_i 2\mu_K'(t_i) n_i(\bar{l}_i - \mu(t_i)) = 0 .$$

Because this identity of the two normal equations is not due to any special property of K, normal equations obtained from methods (a) and (d) are identical, implying corresponding LS estimates are also identical.

Similarity of Covariance Matrix estimates

The asymptotic covariance matrix for parameters $\theta' = (\theta_1, \ldots, \theta_P)$ estimated using ML theory is the inverse information matrix $I(\theta)^{-1}$ (Kendall and Stuart 1973), where $I(\theta) = (I_{ij})$,

$$I_{ij} = -E\frac{\partial^2 L(\theta, X)}{\partial\theta_i \partial\theta_j} ,$$

$L(\theta, X) = \log(\ell(\theta, X))$, and $\ell(\theta, X)$ is the likelihood function.

For nonlinear LS estimates, $I(\theta)^{-1}$ can be estimated using

$$\hat{\Sigma} = (Z'Z)^{-1} s^2$$

which is the formula used by nonlinear LS computer programs. Generally, $Z = (Z_{ij})$, where Z_{ij} is the partial derivative of the expectation of the ith observation with respect to the jth parameter

evaluated at the ML estimates, and s^2 is the mean square error.

For estimates calculated using method (a),

$$Z' = \begin{bmatrix} \frac{\partial \mu(t_1)}{\partial l_\infty}, \ldots, \frac{\partial \mu(t_1)}{\partial l_\infty}, \ldots, \frac{\partial \mu(t_I)}{\partial l_\infty}, \ldots, \frac{\partial \mu(t_I)}{\partial l_\infty} \\ \frac{\partial \mu(t_1)}{\partial K}, \ldots, \frac{\partial \mu(t_1)}{\partial K}, \ldots, \frac{\partial \mu(t_I)}{\partial K}, \ldots, \frac{\partial \mu(t_I)}{\partial K} \\ \frac{\partial \mu(t_1)}{\partial t_0}, \ldots, \frac{\partial \mu(t_1)}{\partial t_0}, \ldots, \frac{\partial \mu(t_I)}{\partial t_0}, \ldots, \frac{\partial \mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3 \times N$$

evaluated at $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$, with $s^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/(N-3)$, $N = \Sigma_i\, n_i$ and I the number of age categories.

As was previously noted for method (d), it is often advantageous to view this model as being unweighted with transformed variables. From this point of view, $y_i = (\sqrt{n_i})\bar{l}_i$ is the dependent variable, with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$. Under this parameterization, $\text{var}(y_i) = \sigma^2$ with

$$Z_w' = \begin{bmatrix} \sqrt{n_1}\,\frac{\partial \mu(t_1)}{\partial l_\infty}, \ldots, \sqrt{n_I}\,\frac{\partial \mu(t_I)}{\partial l_\infty} \\ \sqrt{n_1}\,\frac{\partial \mu(t_1)}{\partial K}, \ldots, \sqrt{n_I}\,\frac{\partial \mu(t_I)}{\partial K} \\ \sqrt{n_1}\,\frac{\partial \mu(t_1)}{\partial t_0}, \ldots, \sqrt{n_I}\,\frac{\partial \mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3 \times I$$

again evaluated at $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$, with $s_w^2 = S_w(\hat{l}_\infty, \hat{K}, \hat{t}_0)/(I-3)$.

It is easily verified that $Z'Z = Z_w'Z_w$ and, therefore, any differences in the covariance matrix estimates of parameter estimates must be due to differences in the estimates s^2 and s_w^2 of σ^2. Although s^2 provides a better estimate than s_w^2 in terms of degrees of freedom ($N-3$ versus $I-3$), they should be similar in value, and hence it can be expected that methods (a) and (d) provide similar covariance matrix estimates of parameter estimates.

This analysis points out that good estimates of the covariance matrix of parameter estimates require having sufficient numbers of observations so that σ^2 is adequately estimated. From this point of view method (a) is superior to method (d). However, method (d) can be modified so that data are not completely collapsed (averaged) at each value of the independent variable. Instead, data can be partitioned so that there are several dependent variable averages, and weights, at each value of the independent variable. A similar technique can be applied to method (c).

Another possibility would be to estimate σ^2 independent of the LS calculations by pooling the s_i^2 values. However, this estimate based on pure error would tend to underestimate the true σ^2 which will often contain a lack of fit component (see the following section for a discussion concerning pure error and lack of fit).

FAILURE OF ASSUMPTIONS

There are two ways in which the assumed model can fail: 1) growth may not follow the von Bertalanffy curve; or 2) error assumptions may not hold.

Failure of the von Bertalanffy Curve

Even when growth follows the von Bertalanffy curve, expected lengths at age from sample data may not. Discrepancies can be caused by bias in sampling, bias in age determination, or size selective survival in the natural population. Because samples tend to be biased toward larger individuals, age readers tend to under-age older individuals, and larger individuals of an age group tend to have better survival, these factors may bias the observed size upward for a given age.

When a number of length specimens are available at each age, a statistical measure of lack of fit (departure from the von Bertalanffy curve) can be calculated using the procedure described by Draper and Smith (1966). For this analysis, it is

necessary to assume that the error variance of individuals is constant (i.e., the variance assumption of method (a) holds). It is also important to remember that for nonlinear models (such as the von Bertalanffy curve) the procedure is not strictly valid, but is analogous to calculations valid under linear models.

The residual sum of squares calculated using method (a) can be partitioned into a pure error component (S_{pe}) and a lack of fit components (S_{lof}). Estimates of these components are

$$S_{pe} = \Sigma(n_i-1)s_i^2$$

and

$$S_{lof} = S(\hat{l}_\infty,\hat{K},\hat{t}_0)-S_{pe} .$$

For a linear model with no lack of fit,

$$\hat{F} = (S_{lof}/(I-3))/(S_{pe}/(N-I))$$

would have an F-distribution with $\nu_1 = I-3$ and $\nu_2 = N-I$ degrees of freedom. While recognizing that the von Bertalanffy curve is not a linear model, this statistic may still serve as a tentative examination for lack of fit.

Even if the data show significant lack of fit, the von Bertalanffy curve may still provide the most useful growth analysis. Rejection of the von Bertalanffy curve must ultimately be based on superior alternative curves or methods of analysis.

Failure of Error Assumptions

When a number of length specimens are available at each age, parameter estimates should be robust against violations of the normality assumption. As was previously shown, estimates can be viewed as solutions to a LS problem with observations $y_i = (\sqrt{n_i})\bar{l}_i$ which are always approximately normally distributed due to the central limit theorem.

The most likely form of heteroscedasticity is the varying of variance with age. Method (c) provides an appropriate analysis for this case.

If observations are correlated, there will be no practical remedy. Efficient estimates will generally depend on the $N \times N$ correlation matrix of errors. This matrix will generally not be estimable.

CONSTRUCTING CONFIDENCE REGIONS

For method (a), confidence regions of approximate size $1-q$ around ML estimates $(\hat{l}_\infty,\hat{K},\hat{t}_0)$ can be constructed using the relationship

$$S(l_\infty,K,t_0) = S(\hat{l}_\infty,\hat{K},\hat{t}_0)\left[1+\frac{3}{N-3}F(3,N-3,1-q)\right] = c_q \text{ (Draper and Smith 1966)}$$

where $F(3,N-3,1-q)$ is the $(1-q)$th percentile of the F-distribution with $\nu_1 = 3$ and $\nu_2 = N-3$ degrees of freedom. That is, values of (l_∞,K,t_0) which satisfy $S(l_\infty,K,t_0) = c_q$ form a three-dimensional surface enclosing the true value of (l_∞,K,t_0) with approximate probability $1-q$. The probability level would be exactly $1-q$ if the growth model was linear, but for nonlinear models (such as the von Bertalanffy curve) this value is only approximated. Although methods exist which provide confidence regions with exact values for q (Hartley 1964), such methods are inferior to that of Draper and Smith in that they: 1) have a degree of arbitrariness in the selection of a region, 2) do not follow contours of equal likelihood, and 3) are more complex to apply.

The relationship defining a contour is

$$S(l_\infty,K,t_0)-c_q = 0$$

where

$$S(l_\infty,K,t_0) = \sum_u [l_u^2-2l_\infty l_u(1-\exp(-K(t_u-t_0))) + l_\infty^2(1-\exp(-K(t_u-t_0)))^2]$$

and $c_q = S(\hat{l}_\infty,\hat{K},\hat{t}_0)\left[1+\frac{3}{N-3}F(3,N-3,1-q)\right]$.

Therefore, $S(l_\infty,K,t_0)-c_q = Al_\infty^2 + Bl_\infty + C$

where $A = \sum_u (1-\exp(-K(t_u-t_0)))^2$

$$B = -2\sum_u l_u(1-\exp(-K(t_u-t_0)))$$

and $C = \sum_u l_u^2-c_q$.

Solutions exist for the three-dimensional contour problem whenever $B^2-4AC \geq 0$.

Points on the three-dimensional contour are easily calculated by conditioning on a value for t_0, and calculating the two-dimensional cross section (l_∞, K) by stepping through plausible values for K, and when $B^2-4AC \geq 0$, calculating $l_\infty = (-B \pm \sqrt{B^2-4AC})/(2A)$. By varying t_0 also, this algorithm will generate the entire three-dimensional confidence region.

Although points on the contour surface are easily calculated, the fact that three parameters are involved in the von Bertalanffy curve greatly limits the usefulness of confidence regions. This is due to the simple fact that three-dimensional regions are difficult to display.

The simplest solution to this problem is to condition on $\hat{t}_0$, and graph the resulting two-dimensional cross section $(\hat{l}_\infty, K)$. It must be remembered that this region is not a true confidence region since more extreme values of $(\hat{l}_\infty, K)$ may occur at a different value of t_0. Thus this procedure will give only a rough idea of our confidence in the estimates $(\hat{l}_\infty, \hat{K})$. A more time consuming solution is to graph a series of cross sections, or possibly a three-dimensional graph.

If method (b) is used to estimate parameters, the analysis follows as in method (a), by simply replacing l_u with $\bar{l}_u$ and N with I.

If weighted methods (c) or (d) is used to estimate parameters, confidence regions are defined by the relationship

$$S_w(l_\infty, K, t_0) = S_w(\hat{l}_\infty, \hat{K}, \hat{t}_0)\left[1 + \frac{3}{I-3}F(3, I-3, 1-q)\right] = c_q' .$$

Computations proceed as in the unweighted case, but with

$$A_w = \sum_u w_u(1-\exp(-K(t_u-t_0)))^2 ,$$

$$B_w = -2\sum_u w_u \bar{l}_u(1-\exp(-K(t_u-t_0))) ,$$

and $$C_w = \sum_u w_u \bar{l}_u^2 - c_q' .$$

For method (c) $w_u = n_u/s_u^2$, and for method (d) $w_u = n_u$.

APPLYING LIKELIHOOD RATIO TESTS

Likelihood ratio (LR) tests provide a general method for the statistical comparison of growth curves. It is a well-known and often exploited fact that once a general probability model has been specified (Ω), hypothesis tests of linear constraints on parameters in this model can be derived using the LR criterion. Alternatively viewed, linear constraints on parameters in Ω imply a simplified model ω. Tests of linear constraints on Ω are thus equivalent to testing ω against Ω.

The LR criterion can be used on the single sample problem, when it is desired to test whether a sample came from a population with some "known" values for any or all of the parameters (l_∞, K, t_0); or for the multisample problem comparing von Bertalanffy curves in different populations. The first problem will be solved by the simplest application of theory derived mainly in the context of the second problem. When a single parameter is being tested in the one or two sample problem, it makes good sense to simply use a Z-statistic (since ML estimates are asymptotically normal) and forego the more extensive calculations required for LR tests. One advantage that the Z test has over the LR test for the two sample problem is that σ^2 does not need to be equal in the two populations.

Consider I different populations each following the von Bertalanffy curve with parameters $(l_{\infty i}, K_i, t_{0i})$, $i = 1, \ldots, I$. These populations would typically be the same species in different habitats, males and females, etc. Let l_{ij} be the length of the jth observation in the ith population, of age t_{ij}, $j = 1, \ldots, n_i$, $N = \Sigma_i n_i$, with variance σ^2 independent of i. Note that the meaning of subscripts has been changed from what was used in previous sections.

Letting $S(l_\infty, \boldsymbol{K}, \boldsymbol{t}_0) = \Sigma_i \Sigma_j (l_{ij} - \mu(l_{\infty i}, K_i, t_{0i}, t_{ij}))^2$, the likelihood function under (Ω) can be written as

$$\ell(l_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2) = (2\pi\sigma^2)^{-N/2} \exp(-S(l_\infty, \boldsymbol{K}, \boldsymbol{t}_0)/2\sigma^2)$$

where $\boldsymbol{l}_\infty = (l_{\infty 1}, \ldots, l_{\infty I})$,
$\boldsymbol{K} = (K_1, \ldots, K_I)$,
and $\boldsymbol{t}_0 = (t_{01}, \ldots, t_{0I})$.

Although the above parameterization is appropriate for unweighted methods (a) and (b), the reader can verify that no additional problems arise using weighted methods (c) and (d).

Previously, it was shown that likelihood functions of the form $\ell(l_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2)$ are maximized by LS estimates $(\hat{l}_\infty, \hat{\boldsymbol{K}}, \hat{\boldsymbol{t}}_0)$, with the ML estimate of σ^2 being

$$\hat{\sigma}^2 = S(\hat{\boldsymbol{l}}_\infty, \hat{\boldsymbol{K}}, \hat{\boldsymbol{t}}_0)/N.$$

This is true whether or not there are any linear constraints placed on the parameters being estimated. Substituting $\hat{\sigma}^2$ into $\ell(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2)$ yields the maximum value of the likelihood function

$$\max\,(\ell(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2)) = (2\pi\hat{\sigma}^2)^{-N/2}\,\exp(-N/2).$$

The LR for the hypothesis

H_ω: that the parameters $(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0)$ satisfy some set of r linear constraints, say R

against the alternative

H_Ω: that the parameters $(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0)$ possibly satisfy no linear constraints

$$\max\,(\ell(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2))$$

$$\text{is } \Lambda = \frac{(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0),\ R}{\max\,(\ell(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0, \sigma^2))}.$$

$$(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0)$$

Letting $\hat{\sigma}^2_\omega$ and $\hat{\sigma}^2_\Omega$ be the ML estimates of σ^2 under ω and Ω, respectively, this LR becomes

$$\Lambda = \frac{(2\pi\hat{\sigma}^2_\omega)^{-N/2}\exp(-N/2)}{(2\pi\hat{\sigma}^2_\Omega)^{-N/2}\exp(-N/2)} = (\hat{\sigma}^2_\Omega/\hat{\sigma}^2_\omega)^{N/2}.$$

Under H_ω, the test statistic $-2\log(\Lambda) = -N\log(\hat{\sigma}^2_\Omega/\hat{\sigma}^2_\omega)$ will have asymptotically a X^2_r distribution. A derivation of this distribution given by Kendall and Stuart (1973) can be modified to accommodate the present model.

Because LR tests are based on statistics having asymptotically a X^2_r distribution, the validity of this test is dependent on the sample sizes used in calculating the test statistic. Assuming H_ω is true and that the error variance of individual observations is constant, the LR test statistic calculated using method (a) will be based on more observations than the LR test statistic calculated using method (d), and hence could be expected to better follow the X^2_r distribution. However, method (d) may be modified so that there are several dependent variable averages and weights at each value of the independent variable (see the section comparing methods (a) and (d)), and the number of observations maintained above the required level. A similar technique can be applied to method (c).

The problem of constructing LR tests thus reduces to one of finding LS estimates for a number of different probability models. These models are generated by placing appropriate linear constraints on the general model Ω, depending on the hypothesis being tested. For the single sample problem, linear constraints take the form of fixing any or all of the parameters $(\boldsymbol{l}_\infty, \boldsymbol{K}, \boldsymbol{t}_0)$ to their hypothesized values. In this case, the degrees of freedom of X^2_r is equal to the number of parameters fixed. For the multisample problem, linear constraints take the form of fitting von Bertalanffy curves so that any or all of the parameters are equal in any or all of the I populations. In this case, the degrees of freedom of X^2_r is equal to the number of linear equations needed to specify the particular constraints. For example, $I-1$ linear equations are needed to specify equality of any parameter over I populations.

AN EXAMPLE

As an example illustrating some of the methods that have been presented, growth data (Table 1) for Pacific hake, *Merluccius productus*, from Dark (1975), was analyzed using method (b). The reader can test his understanding of methods, as well as the correctness of his computer programs, by duplicating this analysis.

A first step in nonlinear LS analysis is the selection of a general purpose iterative nonlinear LS computer program. Such programs take initial estimates and attempt to find LS estimates. For the present analysis, BMDO7R of the BMD biomedical computer programs (Dixon 1976) was used. This choice was dictated by program availability.

TABLE 1.—Average length at various ages for male and female Pacific hake taken off California, Oregon, and Washington during 1965-69 (adopted from Dark 1975).

Age (years)	Female		Male	
	Sample size	Mean length (cm)	Sample size	Mean length (cm)
1 0	385	15 40	385	15.40
2 0	36	28 03	28	26 93
3 3	17	41 18	13	42 23
4 3	135	46 20	83	44 59
5 3	750	48 23	628	47 63
6 3	1,073	50 26	1,134	49 67
7 3	1,459	51 82	1,761	50 87
8 3	626	54 27	432	52 30
9 3	199	56 98	93	54 77
10 3	97	58 93	21	56 43
11 3	44	59 00	8	55 88
12 3	11	60 91	—	—
13.3	6	61 83	—	—

Suitable programs are also available in BMDP (Dixon 1977), SPSS (Nie et al. 1975), and from a number of other sources.

Inital values were obtained from Ford-Walford plots (Ricker 1975) which provided estimates $\hat{l}_\infty$ and $\hat{K}$; and from the weighted average

$$\hat{t}_0 = \frac{\sum_i [\log(1-\bar{l}_i/\hat{l}_\infty)/\hat{K} + t_i]\,(\hat{l}_\infty - \bar{l}_i)}{\sum_i (\hat{l}_\infty - \bar{l}_i)}$$

where $\bar{l}_i$ is the average length at age t_i. For these initial calculations, it was convenient to round ages to whole years. This disallows direct comparisons of Ford-Walford and LS estimates. Besides initial estimates, BMDO7R also requires a FORTRAN subroutine (provided in the Appendix) which evaluates $\mu(t_u)$ and its partial derivatives.

Table 2 contains the initial Ford-Walford estimates $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$ and the final LS estimates $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$ obtained from BMDO7R. LS fits of growth curves are graphed in Figure 1.

From Figure 1 there appears to be a difference in l_∞ between sexes. As a further examination of this difference, cross sections of the approximate 95% confidence regions around $(\hat{l}_\infty, \hat{K})$, generated by conditioning on $\hat{t}_0$, were graphed (Figure 2) using

TABLE 2.—Least squares (LS) estimates of von Bertalanffy parameters for male and female Pacific hake, based on data in Table 1.

Item	l_∞	K	t_0
Male			
Ford-Walford initial estimates	55.63	0.43	0.35
LS estimates	55.98	0.386	0.171
Standard deviation of LS estimates	1.083	0.039	0.142
Female			
Ford-Walford initial estimates	60.60	0.35	0.32
LS estimates	61.23	0.296	−0.057
Standard deviation of LS estimates	1.214	0.029	0.175

methods previously described. These regions not only show a difference in l_∞ between sexes, but also indicate a difference in K.

As a final step in this analysis, LR tests for equality of von Bertalanffy parameters between males (population 1) and females (population 2) were performed. It was necessary to fit data to five models corresponding to hypotheses of interest (Table 3).

The difficulty of fitting these models depends somewhat on the nonlinear LS program used. If derivative-free programs are available, the user will be saved the complex task of specifying derivatives. If programs allow for constraints, only the model Ω need be specified. Nonlinear LS programs available in BMDP have these features.

For BMDO7R, the Appendix provides FORTRAN subroutines which evaluate $\mu(t_u)$ and its

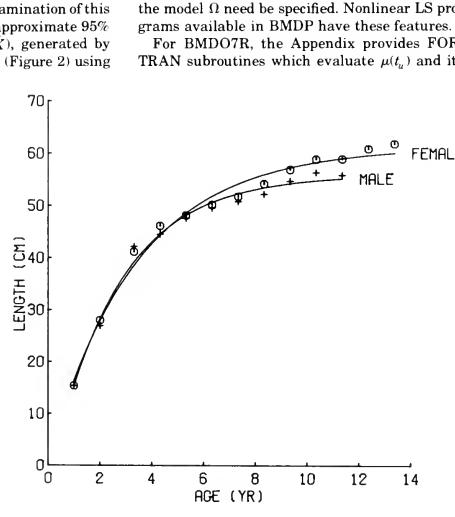


FIGURE 1.—Plots of average length at each age (from Table 1), for male and female Pacific hake, with graphs of estimated von Bertalanffy curves (from Table 2).

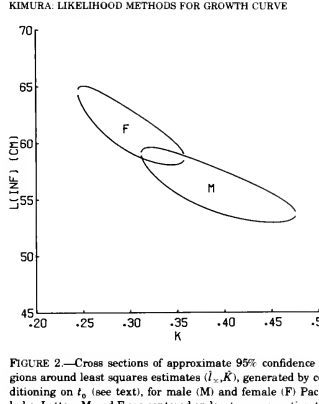


FIGURE 2.—Cross sections of approximate 95% confidence regions around least squares estimates $(\hat{l}_\infty, \hat{K})$, generated by conditioning on t_0 (see text), for male (M) and female (F) Pacific hake. Letters M and F are centered on least squares estimates.

partial derivatives for the five models. These subroutines are general in the sense that they allow comparisons of any number of populations. Probably these subroutines are compatible with the requirements of BMDP3R, but this program was not readily available for a test. Also, minor modifications may be necessary to comply with requirements of particular computer systems.

Results of LR tests (Table 3) indicate there is a significant difference ($\alpha = 0.002$) in l_∞ between sexes, a borderline significant difference ($\alpha = 0.05$) in K, but no significant difference in t_0.

ACKNOWLEDGMENTS

I thank R. J. Trumble of the Washington Department of Fisheries for bringing this problem to my attention. I also thank the referees for their helpful comments.

LITERATURE CITED

ALLEN, K. R.
1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23:163-179.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 10:181-213.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 533 p.

CHAPMAN, D. G.
1961. Statistical problems in dynamics of exploited fisheries populations. Proc. of the Fourth Berkeley Symp. Math. Stat. and Probability. Contrib. Biol. and Probl. Med., vol. 4:153-168. Univ. Calif. Press.

DARK, T. A.
1975. Age and growth of Pacific bake, *Merluccius productus*. Fish.Bull., U.S. 73:336-355.

DIXON, W. J. (editor).
1976. BMD biomedical computer programs. Univ. Calif. Press, 773 p.
1977. BMDP-77 biomedical computer programs P-series. Univ. Calif. Press, 880 p.

DIXON, W. J., AND F. J. MASSEY, JR.
1957. Introduction to statistical analysis. 2d ed. McGraw-Hill, N.Y., 488 p.

DRAPER, N. R., AND H. SMITH.
1966. Applied regression analysis. Wiley, N.Y., 407 p.

HARTLEY, H. O.
1964. Exact confidence regions for the parameters in nonlinear regression laws. Biometrika 51:347-353.

KENDALL, M. G., AND A. STUART.
1973. The advanced theory of statistics. Vol. 2, Inference and relationship. 3d ed. Hafner Publishing Co., N.Y., 723 p.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. SPSS statistical package for the social sciences. 2d ed. McGraw-Hill, N.Y., 675 p.

RICHARDS, F. J.
1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

TABLE 3.—Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) Pacific hake, based on data in Table 1 ($N = 24$ observations).

Hypothesis	Linear constraints	Equivalent model	$l_{\infty 1}$	$l_{\infty 2}$	K_1	K_2	t_{01}	t_{02}	Residual sum of squares ($N\sigma^2$)	$X_r^2 = -N \log (\sigma_{\Omega}^2/\sigma_{\omega}^2)$	df (r)	$P[X_r^2 > X_r^2]$
H_Ω	none	$l_{tj} = l_{\infty j}(1-\exp(-K_j(t_{tj}-t_{0j})))$	55 98	61 23	0 386	0 296	0 171	-0 057	48 22			
$H_{\omega 1}$	$l_{\infty 1} = l_{\infty 2}$	$l_{tj} = l_{\infty}(1-\exp(-K_j(t_{tj}-t_{0j})))$	59 40	59 40	0 297	0 337	-0 111	0 087	71 60	9 49	1 ($l-1$)	0 002
$H_{\omega 2}$	$K_1 = K_2$	$l_{tj} = l_{\infty j}(1-\exp(-K(t_{tj}-t_{0j})))$	57 44	60.14	0 330	0.330	-0.021	0.095	56 34	3 74	1 ($l-1$)	0 053
$H_{\omega 3}$	$t_{01} = t_{02}$	$l_{tj} = l_{\infty j}(1-\exp(-K_j(t_{tj}-t_0)))$	56 45	60 77	0 361	0.313	0 057	0 057	50.76	1 23	1 ($l-1$)	0 267
$H_{\omega 4}$	$l_{\infty 1} = l_{\infty 2}$ $K_1 = K_2$ $t_{01} = t_{02}$	$l_{tj} = l_{\infty}(1-\exp(-K(t_{tj}-t_0)))$	59 29	59 29	0 320	0 320	0 010	0 010	79 76	12 08	3 $3(l-1)$	0 007

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.
STEVENS, W. L.
1951. Asymptotic regression. Biometrics 7:247-267.
TOMLINSON, P. K., AND N. J. ABRAMSON.
1961. Fitting a von Bertalanffy growth curve by least squares including tables of polynomials. Calif. Dep. Fish Game, Fish Bull. 116, 69 p.

APPENDIX

This appendix contains FORTRAN subroutines required by BMDO7R to fit models corresponding to the five hypotheses in Table 3. These subroutines evaluate $\mu(t_a)$ and its partial derivatives. To use these subroutines, the following three instructions need to be understood.

1. The variable NG must be set equal to the number of populations to be compared.

2. The first NG variables of the data input must be "design variables," followed by age. That is, the first NG variables for observation l_{ij} must consist of NG-1 zeros and a single one, the one occurring in the ith position; followed by age (t_{ij}). Next comes length and statistical weights (if weighting is used).

3. The parameters to be estimated are referenced in the order all l_i's first, all K's second, and all t_0's last. Relative positions of l_i's, K's, and t_0's amongst themselves are simply the order of population number. It should be noted that the number of parameters fitted under the five hypotheses of Table 3 are H_{Ω}: $3 \times NG$; $H_{\omega 1}, H_{\omega 2}, H_{\omega 3}$: $(2 \times NG) + 1$; $H_{\omega 4}$: 3.

I. Subroutine FUN for hypothesis Ω.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS Ω:
C NG DIFFERENT GROWTH CURVES
      IND=NG+1
      XL=0.
      XK=0.
      XT=0.
      II=NG
      III=NG+NG
      DO 10 I=1,NG
      II=II+1
      III=III+1
      XL=XL+X(I)*P(I)
      XK=XK+X(I)*P(II)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=NG
      III=NG+NG
      DO 20 I=1,NG
      II=II+1
      III=III+1
      D(I)=0.
      D(II)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(II)=XL*XX*(X(IND)-XT)
      D(III)=-XL*XX*XK
20    CONTINUE
      RETURN
      END
```

II. Subroutine FUN for hypothesis $\omega 1$.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω1: l_i'S
C EQUAL
      IND=NG+1
      XK=0.
      XT=0.
      II=1
      III=1+NG
      DO 10 I=1, NG
      II=II+1
      III=III+1
      XK=XK+X(I)*P(II)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XL=P(1)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=1
      III=1+NG
      DO 20 I=1,NG
      II=II+1
      III=III+1
      D(II)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(II)=XL*XX*(X(IND)-XT
      D(III)=-XL*XX*XK
20    CONTINUE
      D(1)=1.-XX
      RETURN
      END
```

III. Subroutine FUN for hypothesis $\omega 2$.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω2: K'S
C EQUAL
      IND=NG+1
      INDX=NG+1
      XL=0.
      XT=0.
      III=NG+1
      DO 10 I=1,NG
      III=III+1
      XL=XL+X(I)*P(I)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XK=P(INDX)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      III=NG+1
      DO 20 I=1,NG
      III=III+1
      D(I)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(III)=-XL*XX*XK
20    CONTINUE
      D(INDX)=XL*XX*(X(IND)-XT)
      RETURN
      END
```

IV. Subroutine FUN for hypothesis $\omega 3$.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω3: t0'S
C EQUAL
      IND=NG+1
      INDX=NG+NG+1
      XL=0.
      XK=0.
      II=NG
      DO 10 I=1,NG
      II=II+1
      XL=XL+X(I)*P(I)
      XK=XK+X(I)*P(II)
10    CONTINUE
      XT=P(INDX)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=NG
      DO 20 I=1,NG
      II=II+1
      D(I)=0.
      D(II)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(II)=XL*XX*(X(IND)-XT)
20    CONTINUE
      D(INDX)=-XL*XX*XK
      RETURN
      END
```

V. Subroutine FUN for hypothesis $\omega 4$.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω4: ALL
C CURVES IDENTICAL
      IND=NG+1
      XL=P(1)
      XK=P(2)
      XT=P(3)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      D(1)=1.-XX
      D(2)=XL*XX*(X(IND)-XT)
      D(3)=-XL*XX*XK
      RETURN
      END
```

VERTICAL DISTRIBUTION AND DEVELOPMENT OF LARVAL FISHES IN THE NORTH PACIFIC CENTRAL GYRE DURING SUMMER

VALERIE J. LOEB[1]

ABSTRACT

Abundance data are presented on the mesopelagic fish larvae taken in 60 opening/closing bongo net samples from the North Pacific central gyre in late summer. Vertical abundance and size-depth distributions are described for 43 species of gonostomatids and myctophids and two sternoptychid genera. Developmental stages at which these fishes leave the surface layers (either moving deeper or beginning extensive vertical migration) are estimated from sizes of captured larvae.

Over 96% of the estimated larval water column abundance occurred within the upper 100 m. Maximum abundance and diversity were at 25-50 m, possibly related to the bottom of the seasonal mixed layer. Most of the abundant species had distinct depths of maximum abundance within one of the 25 m depth intervals sampled and demonstrated changes in size composition with depth. Different larval distributional patterns were found within and between the Gonostomatidae, Sternoptychidae, and Myctophidae. Larvae of the two myctophid subfamilies had significantly different overall vertical distribution patterns; Myctophinae larvae were more deeply distributed than Lampanyctinae larvae. The myctophids exhibited two patterns of ontogenetic migration: one group of species remains in the surface layers until transformation; the other leaves the surface layers in early stages of photophore development.

Mesopelagic fish species dominate the fish fauna in oceanic regimes, both in terms of numbers of species and numbers of individuals. The adults are important components of oceanic communities. The vertically migrating and more active species are known predators upon other nekton and upon zooplankton (Pearcy and Laurs 1966; Legand and Rivaton 1969; Merrett and Roe 1974). We know much about the depth distributions and diurnal migrations of adult fish species; comparatively little is known of the vertical distributions of their early life stages.

The larvae of most mesopelagic fish species are found within the upper several hundred meters of the water column (Ahlstrom 1969) where they are part of the zooplankton. This larval fish fraction of zooplankton assemblages is called the ichthyoplankton. Ahlstrom's (1959) study of vertical distributions of larval fishes in the California Current included some mesopelagic species. He found that the majority of the species occurred within the mixed layer and upper thermocline and that each species had a characteristic depth distribution; these depth distributions, however, varied with the highly variable (10-90 m) mixed layer depth.

Larval fishes grow and develop within the upper levels until some point of development when the individuals leave the plankton and adopt juvenile-adult roles. Changes in depth distribution with larval development and the stage(s) of development at which the young leave the upper levels and either descend to juvenile depths or begin extensive vertical migrations have not previously been reported.

The North Pacific central gyre is an excellent area in which to examine the vertical distribution of ichthyoplankton. Physically the upper several hundred meters are horizontally monotonous and vertically well stratified (McGowan and Hayward 1978; Gregg et al. 1973). In contrast to the California Current, the summertime mixed layer depth (ca. 40 m) is quite constant. The ichthyoplankton is composed of a diverse and rather equitably distributed assemblage of mesopelagic fish species. Overall species composition and relative abundance relations of larvae taken in integrating 0-300 m Isaacs-Kidd plankton trawl samples are similar from tow to tow within and between summers (Loeb 1979b); repeated patterns of species composition and abundance relations also occur in replicated bongo samples taken within the same depth interval (Loeb 1979a).

In this study I present catch information on a large number of larval fish species taken in 60

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093.

Manuscript accepted May 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1979

opening/closing bongo net samples during a stratified sampling program in the North Pacific central gyre (Scripps Institution of Oceanography 1974). I describe the vertical abundance and size-depth distributions of the more abundant families (Gonostomatidae, Sternoptychidae, and Myctophidae) and species. I also present estimates of the predescent stages of development of species for which there are sufficient catch data.

METHODS

All depth stratified samples were obtained during Climax I expedition (19-28 September 1968; Scripps Institution of Oceanography 1974) near lat. 28° N, long. 155° W. The physical, chemical, and biological properties at this locale have been shown to be stable over large time and space scales (McGowan and Walker in press) and are expected to be representative of the central gyre (Scripps Institution of Oceanography 1974). During this cruise, round-the-clock sampling was done with opening/closing bongo nets (Scripps Institution of Oceanography 1966) between a set of parachute drogues placed at 10 m depth about 10 km apart. The drogues traveled 346 km during the 10 days of sampling. The main depth intervals sampled were: 0-25 m, 25-50 m, 50-75 m, 75-100 m, 100-350 m, and 350-600 m; other intervals were also sampled. Paired 505 μm nets on the 70 cm diameter frames each had a mouth area of 0.396 m^2. They were opened at the bottom of the desired depth range and fished obliquely upward, closing near the top of the range. Maximum tow depths were determined by Benthos[2] depth-telemetering pinger and/or wire angle. The nets were closed automatically by a calibrated flowmeter after 400 m^3 of water had been filtered per net. Ship speed was nominally 2.5 kn.

All fishes were sorted from 60 samples representing 38 separate tows (one sample equals the catch from one of the paired nets). Samples included: ten each from 0-25 m, 25-50 m, 50-75 m, and 75-100 m; six from 100-225 m; six from 100-350 m; and eight from 350-600 m (Table 1).

To reduce biases due to net avoidance by larger individuals and more agile species (Bridger 1956; Ahlstrom 1959) most analyses were of "night" samples (taken between 2000 and 0600 local time). To provide enough replicate samples to allow statistical analyses of strata deeper than 50 m, I found it necessary to include 11 "day" samples; these were selected from tows taken as close to dawn or dusk as possible. As a result, this study does not include aspects of diurnal changes in depth distributions. Ahlstrom (1959) and Badcock and Merrett (1976) showed that the larvae of some midwater fishes (size or stage of development unreported) do undergo limited diurnal migrations.

I identified all fishes caught to the lowest taxon possible. These were categorized to stage of development (i.e., larval, metamorphic, post-metamorphic or juvenile, adult), enumerated and measured to the nearest 0.1 mm standard length (SL) (notochord length was measured for preflexion larvae). The data presented in this paper (unless otherwise noted) are based on larval to early

TABLE 1.—Opening/closing bongo net samples used for larval fish depth distribution analyses. Samples taken near lat. 28° N, long. 155° W in the North Pacific central gyre during September 1968. L and R designate left or right sample from paired net assembly. Mean and standard deviations of temperature at upper (T_U) and lower (T_L) limits of each interval based on 10 day and 7 night 0-500 m STD lowerings.

Depth interval (m)	Date (Sept 1968)	Time	Net	Temperature (C°) T_U	T_L
0-25	21	0250-0325	L & R	27 10 ± 0 20	26 85 ± 0 24
	22	0408-0445	L & R		
	23	0247-0330	R		
	26	2118-2137	L & R		
	27	0040-0103	R		
	27	0341-0404	L & R		
25-50	21	0250-0325	L & R	26 85 ± 0 24	24 94 ± 1 01
	22	0408-0445	L & R		
	23	0247-0330	L		
	24	0507-0540	L & R		
	26	2118-2137	R		
	27	0040-0103	R		
	27	0341-0404	L		
50-75	21	0250-0325	R	24 94 ± 1 01	21 45 ± 0 31
	22	0408-0445	R		
	26	1859-1922	L & R		
	26	2206-2230	L & R		
	27	0126-0156	L & R		
	27	0449-0510	L		
	27	0804-0838	R		
75-100	21	0250-0325	R	21 45 ± 0 31	20 51 ± 0 21
	22	0408-0445	R		
	24	0413-0500	L		
	26	1859-1922	L & R		
	26	2206-2230	L & R		
	27	0126-0156	R		
	27	0449-0510	L & R		
100-225	21	0529-0600	L	20 51 ± 0 21	15 28 ± 0 30
	21	1638-1656	L & R		
	22	0214-0234	L & R		
	24	0046-0111	L		
100-350	26	2010-2033	L & R	20 51 ± 0 21	10 52 ± 0 27
	27	0237-0255	L & R		
	27	0606-0633	L & R		
350-600	26	2010-2033	L & R	10 52 ± 0 27	Not available
	26	2328-2351	L & R		
	27	0237-0255	L & R		
	27	0606-0633	L & R		

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

metamorphic stages only; juvenile and adult information is provided separately. I was able to identify most of the abundant larvae to species. Some of the larvae, however, could not be identified with certainty. For these I assigned "probable" and "possible" species names. These designations were based on the accumulation of enough larvae to establish developmental links to known adult species (Loeb 1979b, >29,000 larval identifications) and a list of adult central gyre mesopelagic fish species and their relative abundances (Barnett 1975).

For analyses of abundance distributions with depth, the larval fish catches from each sample were converted to numbers per 1,000 m^3. These were averaged for each depth interval and then summed to provide estimated water column abundance. Individual species distributions are expressed as percent of their estimated water column abundance caught within each of the main depth intervals sampled. The 100-225 m catches were used in calculations only if they contained species not present in 100-350 m or 350-600 m samples. The 100-225 m and 100-350 m samples were compared to assess whether larval abundance was concentrated in the upper portion of the larger depth range.

Significance of differences in size composition with depth were determined, where sample sizes permitted, using the Kolmogorov-Smirnov test (Conover 1971) on cumulative size-frequency distributions of 0.5 mm (SL) categories of the total larvae taken (all samples combined) within each depth interval. A one-tailed probability of the maximum difference between cumulative size-frequency distributions in two depth strata ≤ 0.05 was deemed "significant." Rejection of the null hypothesis of no difference indicates that one of the size distributions being compared is significantly larger than the other. The results of these tests are in no case altered by the exclusion of larvae from the "day" samples in their calculation.

Descriptions of the developmental stages of myctophid larvae in the plankton include additional information obtained from six other central gyre cruises in the vicinity of lat. 28° N, long. 155° W. These cruises utilized Isaacs-Kidd plankton trawls (IKPT) fished obliquely from the surface to about 300 m (Loeb 1979b). Those data (24,500 identified larvae) provide a broader range of larval sizes and developmental stages, and development from early larvae to metamorphosis (transformation) has been traced for many species. I used this information as an aid for estimating levels of development reached while larvae are still in the upper water column, prior to descent to deeper juvenile-adult depths.

RESULTS

I identified a total of 5,448 larvae (Table 2). These included 94 generic and species identifications from 36 families, and one ordinal grouping. Three families (Gonostomatidae, Sternoptychidae, and Myctophidae) together contributed 91% of the individuals and 50% of the species.

Larvae were taken throughout the 600 m depth range (Figure 1a); however, over 97% of the estimated water column abundance was in the upper 100 m. Only 13 of the 95 kinds of larvae appeared to have maximum abundance below 100 m. Maximum larval abundance (and diversity, or number of species) occurred within the 25-50 m interval (Figure 1a); the bottom of the summer mixed layer (ca. 40 m) is within this interval (Figure 1b). Total larval abundance (Figure 1a) as well as individual species abundances were highly variable from tow to tow within each interval. Despite this variability, most species demonstrated a definite peak of abundance (generally >60% of their estimated water column abundance) and

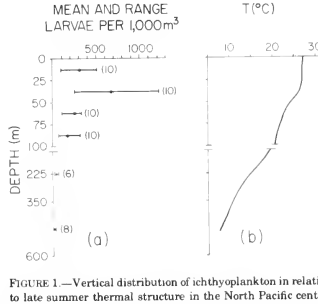


FIGURE 1.—Vertical distribution of ichthyoplankton in relation to late summer thermal structure in the North Pacific central gyre. (a) Mean and range of total numbers of larvae per 1,000 m^3 caught in replicate samples within each depth interval (bracketed values are numbers of replicate samples). (b) Temperature profile of upper water column during Climax I, based on average values from 10 day and 7 night STD lowerings.

TABLE 2.—Total numbers of individuals (N) and rank of numerical abundance (R) of larval fish species caught (n samples combined) within each of seven depth intervals in the North Pacific central gyre during late summer.

	0-25 m $n = 10$		25-50 m $n = 10$		50-75 m $n = 10$		75-100 m $n = 10$		100-225 m $n = 6$		100-350 m $n = 6$		350-600 m $n = 8$		Total	
Species	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R
Gonostomatidae																
Cyclothone alba	580	(1)	687	(1)	171	(1)	17	(12)	3	(13½)					1,458	(1)
C sp A (prob *pseudopalida*)	49	(5)	9	(26½)	2	(37)									60	(19)
C. atraria	1	(38)													1	(100)
C spp	76	(4)	78	(10)	28	(11)	4	(27½)			2	(11)	5	(1)	193	(7)
Diplophos taenia	13	(11)	1	(54)											14	(42½)
Gonostoma atlanticum							30	(6)	9	(3)	2	(11)			41	(29)
G. elongatum							10	(14)	2	(18½)	2	(11)			14	(42½)
Ichthyococcus ovatus							7	(18)	5	(8½)					12	(45)
Margrethia obtusirostra									4	(10½)					4	(73½)
Valenciennellus tripunctulatus									6	(6)	3	(7½)			9	(52)
Vinciguerria nimbaria	6	(18)	376	(2)	99	(2)	25	(8)	7	(4)	1	(19)			514	(2)
V. poweriae					2	(37)	60	(2)	5	(8½)	4	(5)			71	(16)
V spp	3	(25½)	90	(9)	61	(5)	34	(5)	3	(13½)	13	(1)			204	(6)
Woodsia sp							4	(27½)	1	(26½)					5	(67)
Sternoptychidae																
Argyropelecus spp											1	(19)	4	(2)	5	(67)
Sternoptyx diaphana									14	(1)	5	(3)			19	(38½)
S. pseudobscura							1	(46½)	4	(10½)			1	(4)	6	(61)
S. spp									6	(6)	4	(5)			10	(50)
Myctophidae																
Lampanyctinae																
Bolinichthys distofax			27	(17)											27	(30)
B. longipes	177	(2)	47	(11)	1	(46)									225	(5)
B spp	30	(6)	21	(21)											51	(23½)
Ceratoscopelus warmingi	15	(8)	235	(3)	47	(6)	2	(35)	1	(26½)					300	(3)
Diaphus andersoni	84	(3)	40	(13)	5	(25)					1	(19)			130	(12)
D. "slender B" (*D. mollis* B?)			2	(44½)	7	(21)	2	(35)							11	(48)
D. slender C" (*D. mollis* A?)	12	(12)	95	(8)	9	(17½)	2	(35)					1	(4)	119	(13)
D. brachycephalus	6	(18)	30	(16)	14	(15)	1	(46½)							51	(23½)
D. slender spp	10	(14½)			6	(23)	2	(35)	1	(26½)					19	(38½)
D. elucens (= *perspicillatus*)	18	(7)	164	(4)	46	(7)	2	(35)							230	(4)
D. rolfbolini (= *philipsi*)	2	(28½)	97	(7)	27	(12)	5	(24)	2	(18½)	1	(19)			134	(10)
D. stubby C" (*D. schmidti*?)	5	(21)	11	(24½)	7	(21)									23	(34½)
D. stubby spp							1	(46½)							1	(100)
Lampadena anomala	5	(21)	3	(39)											8	(55½)
L. luminosa	11	(13)	11	(24½)			1	(46½)							23	(34½)
Lampanyctus "big snout			16	(23)	2	(37)									18	(40)
L. "lacks pectorals"			4	(33½)	33	(9)	7	(18)	1	(26½)					45	(26)
L. nobilis	1	(38)	23	(19)	2	(37)									26	(31)
L. steinbecki	3	(25½)	123	(6)	12	(16)									138	(9)
L. spp			7	(29½)									1	(4)	8	(55½)
Lobianchia gemellari					29	(10)	26	(7)	2	(18½)					57	(21)
Notolychnus valdiviae					2	(37)	40	(4)			2	(11)			44	(27)
Triphoturus nigrescens	6	(18)	128	(5)	8	(19)	4	(27½)							146	(8)
Myctophinae																
Benthosema suborbitale							48	(3)	11	(2)	6	(2)			65	(17½)
Centrobranchus andreae							1	(46½)							1	(100)
C. brevirostris							1	(46½)							1	(100)
C. choerocephalus							5	(24)							5	(67)
Diogenichthys atlanticus							8	(15½)	2	(18½)	2	(11)			12	(45)
Hygophum proximum			26	(18)	95	(3)	11	(13)							132	(11)
H. reinhardti					45	(8)	19	(11)	1	(26½)					65	(17½)
Myctophum brachygnathum			17	(22)	3	(30½)	1	(46½)							21	(36½)
M. lychnobium			32	(15)	18	(13)	8	(15½)							58	(20)
M. nitidulum					1	(46)	6	(21)							7	(38½)
M. selenops					5	(25)									5	(67)
M spp									2	(18½)	1	(19)			3	(78½)
Symbolophorus evermanni			9	(26½)	76	(4)	22	(9)	1	(26½)					108	(14)
Other Larvae																
Congridae																
Ariosoma sp	1	(38)													1	(100)
Nemichthyidae																
Nemichthys scolopaceus	1	(38)	1	(54)											2	(84½)
Bathylagidae																
Bathylagus bericoides											1	(19)			1	(100)
B. longirostris									3	(13½)	1	(19)			4	(72½)
Stomiatoid fishes'	2	(28½)	22	(20)	16	(14)	2	(35)							42	(28)
Idiacanthidae																
Idiacanthus fasciola					1	(46)	7	(18)							8	(55½)
Paralepididae																
Type A (prob *Lestidium nudum*)	2	(28½)	1	(54)	2	(37)									5	(67)
Type B (like *L. interpacificum*)	7	(16)	7	(29½)	2	(37)									16	(41)
Type D (prob. Gen. nov. sp. nov.)					4	(28)									4	(73½)
Paralepis atlantica									2	(18½)					2	(84½)
Stemonosudis macrura	1	(38)	4	(33½)	4	(28)									9	(52)

TABLE 2—Continued.

Species	0-25 m n = 10 N	R	25-50 m n = 10 N	R	50-75 m n = 10 N	R	75-100 m n = 10 N	R	100-225 m n = 6 N	R	100-350 m n = 6 N	R	350-600 m n = 8 N	R	Total N	R
Sudis atrox			2	(44½)	2	(37)	2	(35)							6	(61)
Uncisudis advena			1	(54)	2	(37)	5	(24)							8	(55½)
Unidentified Paralepidids			1	(54)	2	(37)									3	(78½)
Alepisaundae																
Alepisaurus ferox					3	(30½)	2	(35)							5	(67)
Evermannellidae																
Evermannella indica			4	(33½)	1	(46)									5	(67)
Odontostomops normalops	2	(28½)	44	(12)	7	(21)									53	(22)
Unidentified evermannellids			2	(44½)											2	(84½)
Scopelarchidae																
Scopelarchus spp							4	(27½)	3	(13½)	4	(5)			11	(48)
Notosudidae																
Ahlesaurus brevis	10	(14½)	1	(54)											11	(48)
Scopelosaurus smithi	14	(9½)	8	(28)			3	(30)							25	(32)
Neoscopelidae																
Scopelengys sp (prob *clarkei*)			2	(44½)											2	(84½)
Giganturidae																
Bathyleptus lisae			1	(54)											1	(100)
Melanocetidae																
Melanocetus johnsoni	4	(23½)			1	(46)									5	(67)
M. sp	1	(38)													1	(100)
Oneirodidae																
Dolopichthys longicornis			3	(39)											3	(78½)
Oneirodid A (poss. *Lasiognathus* sp.)	1	(38)													1	(100)
Unidentified oneirodids			3	(39)											3	(78½)
Gigantactinidae																
Gigantactis sp (prob *vanhoeffeni*)	1	(38)	4	(33½)											5	
Ceratiidae																
Ceratias holboelli			1	(54)											1	(100)
Cryptopsaras couesi	5	(21)	4	(33½)											9	(52)
Caulophrynidae																
Caulophryne jordani					1	(46)									1	(100)
Unidentified ceratioids	4	(23½)	3	(39)											7	(58½)
Bregmacerotidae																
Bregmaceros spp					5	(25)	76	(1)	6	(6)	1	(19)			88	(15)
Ophidiidae																
Brotulid (poss. *Lamprogrammus niger*)			1	(54)											1	(100)
Macrouridae																
Mesobius berryi											1	(19)			1	(100)
Exocoetidae																
Unidentified exocoetids			3	(39)	1	(46)									4	(73½)
Melamphaeidae																
Melamphaes simus							6	(21)							6	(61)
M. sp. A (prtb. *indicus*)			1	(54)			1	(46½)							2	(84½)
M. spp.							1	(46½)							1	(100)
Scopeloberyx spp.							20	(10)	1	(26½)	3	(7½)			24	(33)
Scopelogadus mizolepis mizolepis							2	(35)							2	(84½)
Unidentified melamphaeids							1	(46½)							1	(100)
Anoplogastendae																
Anoplogaster cornuta			1	(54)											1	(100)
Zeidae																
Unidentified zeid									1	(26½)					1	(100)
Trachipteridae																
Trachipterus sp.			1	(54)											1	(100)
Stylephoridae																
Stylephorus chordatus											1	(19)			1	(100)
Apogonidae																
Howella sp.	1	(38)	39	(14)	9	(17½)									49	(25)
Bramidae																
Brama japonica	1	(38)	2	(44½)											3	(78½)
Coryphaenidae																
Coryphaena sp. (prob. *equiselis*)	1	(38)													1	(100)
Chiasmodontidae																
Unidentified chiasmodontid	1	(38)													1	(100)
Gempylidae																
Gempylus serpens	14	(9½)	4	(33½)	2	(37)	1	(46½)							21	(36½)
Trichiuridae																
Diplospinus multistriatus			1	(54)	4	(28)	6	(21)	1	(26½)					12	(45)
Type A (poss. *Aphanopus carbo*)									1	(26½)					1	(100)
Unidentified trichiurid							1	(46½)							1	(100)
Scombridae																
Acanthocybium sp.	1	(38)													1	(100)
Katsuwonus pelamis	1	(38)	2	(44½)											3	(78½)
Nomeidae																
Cubiceps caeruleus	1	(38)													1	(100)

TABLE 2.—Continued.

Species	0-25 m n = 10 N	R	25-50 m n = 10 N	R	50-75 m n = 10 N	R	75-100 m n = 10 N	R	100-225 m n = 6 N	R	100-350 m n = 6 N	R	350-600 m n = 8 N	R	Total N	R
Total larvae identified	1,190		2,563		932		557		111		63		12		5,448	
Unidentified larvae	143		347		89		106		22		11		8		726	
Total larvae	1,333		2,930		1,021		663		133		74		20		6,174	
Number of rankings	41		60		49		50		31		24		7		112	

[1]Stomiatoid fishes include Astronesthidae, Malacosteidae, Melanostomiatidae, and Stomiatidae

frequency of occurrence within one of the 25 m depth intervals. For many of the more abundant species, the catches in replicate tows within this interval were significantly greater (Mann-Whitney U test, $P \leq 0.05$) than those in adjacent intervals (Table 3).

TABLE 3.—Gonostomatidae, Sternoptychidae, and Myctophidae: Total estimated water column abundance of larval species during late summer in the North Pacific central gyre, based on summation of mean estimated abundances (numbers/1,000 m³) from each depth

Species	Total no. per 1,000 m³	0-25 m F (10)	%	Median length (mm)	Range (mm)	25-50 m F (10)	%	Median length (mm)	Range (mm)	50-75 m F (10)	%	Median length (mm)	Range (mm)
Gonostomatidae													
Cyclothone alba	365.0	10	39.7	5.6	3.2-12.6	10	47.0	4.5	2.5-12.2	10	11.7	7.9	2.2-12.4
C. sp. A	15.0	9	[1]81.7	5.9	3.2-13.8	6	15.0	7.6	4.9-13.9	2	3.3	9.4	5.0-13.7
C. atraria	0.2	1	100.0	4.6									
Diplophos taenia	3.5	7	[2]92.9	11.0	5.2-26.8	1	7.1	12.6					
Gonostoma atlanticum	8.3												
G. elongatum	3.3												
Ichthyococcus ovatus	3.8												
Margrethia obtusirostra	1.7												
Valenciennellus tripunctulatus	1.2												
Vinciguerria nimbaria	127.0	5	1.2	9.0	6.8-11.9	10	[1]74.1	7.2	3.7-14.5	10	19.5	14.0	3.7-17.5
V. poweriae	17.2									2	2.9	8.8	7.2-10.3
Woodsia sp.	1.4												
Sternoptychidae													
Argyropelecus spp.	1.7												
Sternoptyx spp.	4.3												
Myctophidae													
Lampanyctinae													
Bolinchthys distofax	6.8					5	100.0	5.7	3.2-8.8				
B. longipes	56.2	10	[1]78.7	4.6	3.1-8.4	8	20.9	5.1	3.4-8.2	1	0.4	8.7	
Ceratoscopelus warmingi	75.2	4	5.0	4.0	3.2-4.7	10	[1]78.2	5.0	2.7-7.7	10	15.6	6.3	4.8-8.3
Diaphus andersoni	32.7	10	[1]64.3	4.2	2.7-6.5	7	30.6	4.5	3.2-7.1	2	3.8	7.0	5.3-11.6
D. "slender B"	2.8					2	18.2	3.6	2.5-4.6	2	63.6	5.6	3.5-6.3
D. "slender C"	29.8	3	10.1	3.8	2.6-5.0	9	[1]79.7	4.5	2.3-6.5	4	7.6	4.9	4.5-6.3
D. brachycephalus	12.8	3	11.8	4.0	3.7-4.6	6	58.8	4.2	2.6-5.9	5	27.4	5.4	4.3-8.7
D. elucens	57.5	8	7.8	3.5	2.8-4.8	10	[1]71.3	4.0	2.6-8.7	6	20.0	5.5	2.6-8.6
D. rolfbolini	33.2	1	1.5	3.4	3.3-3.5	10	[1]73.1	4.0	2.7-6.6	8	20.4	4.7	2.9-7.7
D. "stubby C"	5.8	2	21.7	3.5	3.2-3.8	2	47.8	3.7	3.0-4.2	2	30.4	3.6	3.3-3.8
Lampadena anomala	2.0	5	62.5	5.1	3.4-5.8	3	37.5	3.7	2.9-6.2				
L. luminosa	5.8	4	47.8	5.0	3.7-5.9	4	47.8	6.8	3.4-8.6				
Lampanyctus "big snout"	4.5					7	[1]88.9	4.0	2.8-7.1	2	11.1	5.6	3.9-7.4
L. "lacks pectoralis"	11.4					3	8.8	4.0	3.5-5.9	9	[1]72.2	4.4	2.6-6.2
L. nobilis	6.5	1	3.8	5.4		5	88.5	4.8	2.9-10.5	2	7.7	7.8	5.4-10.2
L. omanbecki	34.5	3	2.2	3.2	3.2-4.2	10	[1]89.1	3.4	2.1-5.5	4	8.7	4.4	2.9-6.9
Lobianchia gemellari	14.6									8	49.7	4.4	2.8-5.8
Notolychnus valdiviae	11.3									2	4.4	4.0	3.1-10.5
Triphoturus nigrescens	36.5	4	4.1	5.0	2.3-7.4	10	[1]87.7	4.4	2.7-8.1	4	5.5	6.7	5.2-7.9
Myctophinae													
Benthosema suborbitale	14.5												
Centrobranchus andreae	0.2												
C. brevirostris	0.2												
C. choerocephalus	1.2												
Diogenichthys atlanticus	2.8												
Hygophum proximum	33.0					9	19.7	3.8	2.8-5.9	10	[1]72.0	4.5	2.3-8.7
H. reinhardti	16.4									9	[1]68.5	6.5	3.8-9.4
Myctophum brachygnathum	5.2					6	81.0	2.9	2.3-4.1	2	14.3	3.9	2.5-4.8
M. lychnobium	14.5					7	55.2	3.7	2.8-5.6	5	31.0	3.6	2.5-4.6
M. nitidulum	1.8									1	14.3	3.9	
M. selenops	1.2									2	100	4.7	3.4-5.4
Symbolophorus evermanni	27.2					3	8.3	5.5	3.9-6.2	9	[1]69.9	4.5	2.8-5.6

[1]Designates abundances which, based on abundances within replicate tows, are significantly greater (Mann-Whitney U-test, $P < 0.05$) than in any other depth interval

[2]Denotes use of 100-225 m instead of 100-350 m samples

Gonostomatid and myctophid larvae made up most of the ichthyoplankton in the upper 100 m (Figure 2). The "other larvae" were a low, constant percent of the total from the surface to 75 m, but their percent contribution was markedly increased between 75 and 350 m. Below 350 m most of the larvae were sternoptychids and gonostomatids.

Family Gonostomatidae

The gonostomatids (8 genera, 12 species) composed 48% of the identified larvae. The family was an important fraction of the total larvae in all strata (Figure 3a); 97% of the estimated family abundance occurred above 100 m. Maximum abundance was at 25-50 m due to concentrations of the two most abundant species *Cyclothone alba*

interval, and frequency of occurrence (F) in (*n*) samples, percent of total estimated water column abundance, median length, and size range (mm standard length) within each depth interval.

	75-100 m				100-350 m				350-600 m			
Species	F (10)	%	Median length (mm)	Range (mm)	F (6)	%	Median length (mm)	Range (mm)	F (8)	%	Median length (mm)	
Gonostomatidae												
Cyclothone alba	5	1 2	9 2	3 7-14 7	[2]2	0 3	4 1	3 8-4 7				
C. sp. A												
C. atraria												
Diplophos taenia												
Gonostoma atlanticum	7	90 0	6 1	2 7-16 3	1	10 0	6 5	2 7-12 9				
G. elongatum	5	75 1	5 4	3 7-12 2	2	24 9	6 5	4 3-8 2				
Ichthyococcus ovatus	3	45 7	8 0	5 8-13 2	[2]3	54 3	11 0	4 0-16 3				
Margrethia obtusirostra					[2]3	100	4 6	2 8-8 2				
Valenciennellus tripunctulatus					2	100	8 6	7 1-9 9				
Vinciguerria nimbaria	9	4 9	14 2	3 9-17 8	1	0 3	4 5	3 7-7 1				
V. poweriae	9	87 4	10 8	6 5-19 2	2	9 7	12 1	6 8-19 7				
Woodsia sp.	2	70 4	5 9	3 7-6 2	[2]1	29 6	3 2					
Sternoptychidae												
Argyropelecus spp.					1	25 2			2	75 8		
Sternoptyx spp.	1	5 8			4	87 0			1	7 2		
Myctophidae												
Lampanyctinae												
Bolinichthys distofax												
B. longipes												
Ceratoscopelus warmingi	2	0 7	10 7	8 6-12 8	[2]1	0 5	11 8					
Diaphus anderseni					1	1 3	10 5					
D. "slender B"	2	18 2	8 8	6 2-10 0								
D. "slender C"	2	1 7	6 6	4 3-8 9					1	1 0	4 9	
D. brachycephalus	1	2 0	6 1									
D. elucens	2	0 9	6 8	4 8-8 9								
D. rolfbolini	3	3 8	6 9	4 9-9 9	1	1 3	4 7	2 9-7 8				
D. "stubby C"												
Lampadena anomala												
L. luminosa	1	4 4	12 7									
Lampanyctus "big snout"												
L. "lacks pectorals"	4	15 3	5 7	3 2-6 8	[2]1	3 7	4 3					
L. nobilis												
L. steinbecki												
Lobianchia gemellari	9	44 6	3 8	3 2-7 9	[2]2	5 7	4 0	3 7-4 2				
Notolychnus valdiviae	8	[1]88 3	5 2	3 3-8 0	2	7 3	6 2	6 1-6 4				
Triphoturus nigrescens	[2]	2 7	7 6	6 2-11 8								
Myctophinae												
Benthosema suborbitale	4	82 8	3 6	2 5-7 8	3	17 2	3 9	1 8-8 0				
Centrobranchus andreae	1	100	5 9									
C. brevirostris	1	100	5 3									
C. choerocephalus	3	100	6 2	3 4-7 1								
Diogenichthys atlanticus	4	70 7	4 9	4 3-5 8	2	29 3	4 2	3 8-4 6				
Hygophum proximum	5	8 3	5 5	2 2-10 8								
H. reinhardti	7	28 9	6 5	2 4-13 1	[2]1	2 6	4 6					
Myctophum brachygnathum	1	4 7	7 5									
M. lychnobium	3	13 8	3 6	2 2-4 2								
M. nitidulum	3	85 7	3 7	2 7-4 9								
M. selenops												
Symbolophorus evermanni	8	20 2	4 4	3 3-10 5	[2]1	1 6	4 7					

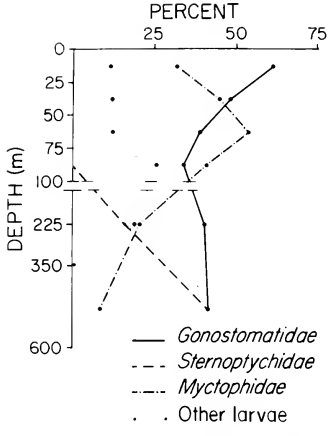


FIGURE 2.—Percent contribution of major families and "other larvae" to the total ichthyoplankton caught within each depth interval of the North Pacific central gyre during summer.

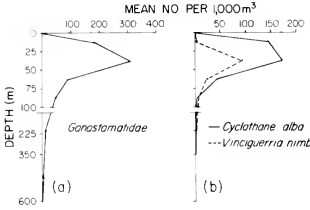


FIGURE 3.—Vertical distributions of larval gonostomatids in the North Pacific central gyre during summer. Concentrations of (a) gonostomatid larvae (12 species combined) and of (b) *Cyclothone alba* and *Vinciguerria nimbaria* larvae by depth interval.

and *Vinciguerria nimbaria* (Figure 3b). Maximum diversity occurred at 75-225 m.

CYCLOTHONE SPP.—*Cyclothone alba* is a numerous larval fish species in the central gyre throughout the year, ranking second in abundance only to *Vinciguerria nimbaria* (Loeb 1979b). It was the most abundant species taken during this cruise (27% of all larvae), and was present in all samples from 0 to 75 m; below 75 m it was rare (Table 2). Eighty-seven percent of the estimated water column abundance was from the upper 50 m, with highest concentrations at 25-50 m (Figure 3b). Abundances in replicate tows within the 0-25 m and 25-50 m intervals were not significantly different from each other; they were, however, significantly greater (Mann-Whitney U test, $P < 0.01$) than those in deeper intervals.

A wide range of larval lengths was found within each depth interval from 0 to 75 m and the cumulative size-frequency curves differed significantly (Kolmogorov-Smirnov test, $P < 0.05$) between all three intervals (Figure 4). There was no simple increase in standard length with depth: smaller sizes dominated at 25-50 m, larger lengths at 50-75 m, and intermediate sizes at 0-25 m. Although median standard length was largest in the 75-100 m interval, the cumulative size-frequency curve was not significantly different from that at 50-75 m, possibly because of the paucity of larvae captured at 75-100 m. The three largest larvae present in 75-100 m samples (11.6-14.7 mm) were in the prometamorphic (white photophore) stage (Ahlstrom and Counts 1958) of development. Only three small larvae were caught between 100 and 350 m, and 57 metamorphosed individuals were caught at 350-600 m.

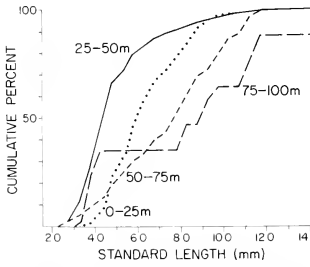


FIGURE 4.—Cumulative size-frequency curves for *Cyclothone alba* larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

Most of the smallest *C. alba* larvae apparently occur near the bottom of the mixed layer, and move first up and then downward with increasing size and development; the most advanced stage attained in 0-100 m is prometamorphic. A rapid descent may then occur, indicated by the near absence of any individuals in 100-225 m and 100-350 m samples. Photophore completion and metamorphosis probably occur at depths >350 m, in agreement with Ahlstrom's (1974) report that only the white photophore stage of *Cyclothone* spp. is found above 200 m, and that more advanced stages occur deeper in the water column.

Kobayashi (1973) gives a 300-1,000 m depth range for adult Pacific *C. alba*. He found that the individuals occurring in the range of maximum abundance (400-600 m) were smaller than those occurring shallower or deeper; intermediate-sized adults were shallower and largest adults were deeper. This size distribution of the adults parallels that found herein for the larvae, although shifted well downwards in the water column.

Cyclothone sp. A is probably the larval form of *C. pseudopallida*, and is the only other larval *Cyclothone* species found in abundance in the central gyre (Loeb 1979b). Fifty-nine of the sixty larvae caught were from the upper 50 m, and maximum abundance was at 0-25 m (Table 3). Median standard lengths increased with depth but, due to the small sample sizes, significance of differences in size-frequency distributions could not be tested. No metamorphic stages were taken either in the stratified tows or among the 365 *Cyclothone* sp. A larvae taken in 0-300 m IKPT samples during other gyre cruises. Most of early larval development may occur at 0-50 m, with a subsequent rapid descent to the juvenile-adult depth ranges (500-900 m; Kobayashi 1973).

VINCIGUERRIA SPP.—*Vinciguerria nimbaria* was the second most abundant species caught (9% of all larvae). On a year-round basis it is the most abundant larval fish species taken in the gyre (Loeb 1979b). The larvae occurred in samples from 0 to 350 m (Figure 3b), but were consistently present (29 out of 30 samples) only between 25 and 75 m. Ninety percent of the estimated water column abundance was between 25 and 75 m (74% at 25-50 m). Abundances in replicate tows within the 25-50 m depth interval were significantly greater ($P<0.01$) than in any other interval (Table 3).

Samples from 25 to 100 m contained a wide range of larval sizes. However, median standard length increased with depth (Table 3) and cumulative size-frequency curves from 25-50 m and 50-75 m (Figure 5) were significantly different from each other. The proportion of metamorphosing individuals increased below 50 m (Table 4). These included the prometamorphic (white photophore), midmetamorphic (rapid body shape change), and postmetamorphic (photophore completion and body pigmentation) stages described by Ahlstrom and Counts (1958). All *V. nimbaria* present in 0-25 m samples were early larvae, as were most in the 25-50 m samples (only 3% from 25-50 m were pro- or midmetamorphic). In contrast, 75% from 50-75 m were in metamorphic stages. Size distribution at 75-100 m was essentially bimodal: 40% of the larvae were very small (3.5-6.0 mm) and 50% were metamorphic (10.5-17.5 mm). No juveniles or adults were taken.

Vinciguerria poweriae was much less abundant, and had a deeper distribution than did its congener; it occurred from 50 to 350 m (Table 3), with maximum abundance at 75-100 m. There was a trend for increased size with depth (Table 3). Only four metamorphosing individuals were caught.

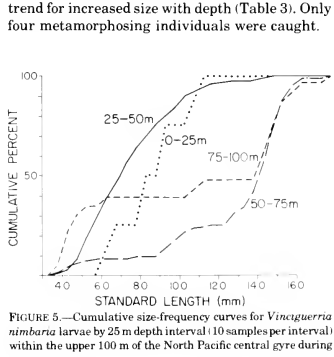


FIGURE 5.—Cumulative size-frequency curves for *Vinciguerria nimbaria* larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

TABLE 4.—Abundance of metamorphic stages of *Vinciguerria nimbaria* by depth during late summer in the North Pacific central gyre.

Depth interval (m)	Total individuals	Pro-	Mid-	Post- metamorphic stages	Percent metamorphic
0-25	6				
25-50	376	5	6		2.9
50-75	99	25	15	34	74.7
75-100	25	2	4	7	52.0
100-350	1				

OTHER GONOSTOMATIDS.—The eight other gonostomatid species caught were rare; together <4% of the family total (Tables 2, 3). *Diplophos taenia* had the shallowest distribution of any gonostomatid species, occurring mostly at 0-25 m. *Gonostoma atlanticum, G. elongatum, Ichthyococcus ovatus*, and *Woodsia* sp. were present in the 75-350 m range, with maxima at 75-100 m. *Margrethia obtusirostra* and *Valenciennellus tripunctulatus* were caught only at 100-225 m and 100-350 m.

Family Sternoptychidae

The Sternoptychidae is the third most abundant family in the central gyre in terms of total larval abundance on a year-round basis (Loeb 1979b). Peak abundances occur during winter months, when this family makes up more than 6% of the total larvae. Minimal catches occur in late summer, so the 40 individuals taken during the present (late summer) cruise can provide only a very sketchy description of the vertical distributions of this otherwise abundant family.

The two genera (*Sternoptyx* and *Argyropelecus*) almost always occurred deeper than 100 m (Figure 2) and were abundant relative to other larvae in the 100-600 m depth range. *Sternoptyx* spp. appeared to have a shallower distribution than *Argyropelecus* spp. (Table 2). All but 2 of the 35 *Sternoptyx* larvae were taken between 100 and 350 m, with largest catches at 100-225 m (24 larvae distributed among all six samples). Four of the five *Argyropelecus* larvae were caught at 350-600 m. This is in contrast with the depth distributions found in the eastern Atlantic (Badcock and Merrett 1976) where *Argyropelecus* larvae were found from 100 to 500 m and *Sternoptyx* from 500 to 1,000 m.

A variety of developmental stages of both genera were found in the stratified samples. *Sternoptyx diaphana* from 100 to 225 m ranged from early larvae (3.8 mm) to larvae with abdominal and isthmal photophores (7.7 mm). The four *Argyropelecus* spp. from 350-600 m ranged from very small undeveloped larvae to one individual with an almost complete photophore complement.

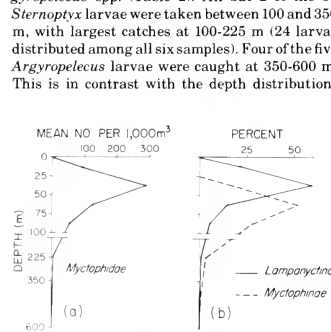


FIGURE 6.—Vertical distributions of larval myctophids in the North Pacific central gyre during summer. (a) Concentrations of myctophid larvae (31 species combined) by depth interval. (b) Percent of estimated water column abundances of Lampanyctinae and Myctophinae larvae in each depth interval.

Family Myctophidae

The myctophids (14 genera, 31 species) contributed over 42% of the total larvae. Over 98% of the estimated water column abundance was in the upper 100 m with maximum abundance at 25-50 m (Figure 6a). Diversity was highest (21 to 23 species) between 25 and 100 m (Table 2). The larval depth distributions of the two subfamilies differed (Figure 6b). Ninety-four percent of the Lampanyctinae estimated water column abundance was in the upper 75 m, with peak abundance at 25-50 m; only two (*Lobianchia gemellari* and *Notolychnus valdiviae*) of the 19 species were not taken in the 25-50 m interval (Table 3). This subfamily contributed 78% of the myctophid individuals and therefore greatly influenced the shape of the family distribution curve (Figure 6a). Myctophinae larvae were never caught in the upper 25 m, and contributed only 7% of the total myctophid larvae in the 25-50 m interval. The subfamily was most abundant from 50-225 m, contributing 49%, 58%, and 71% of the total myctophid larvae in the 50-75 m, 75-100 m, and 100-225 m intervals, respectively; peak abundance occurred at 50-75 m (Figure 6b). Only 4 of the 12 myctophine species taken were found at 25-50 m, while 7 were taken at 50-75 m and 11 at 75-100 m (Table 3). Significant differences were found between the cumulative frequency versus depth distributions of the two subfamilies (Kolmogorov-Smirnov test, $P << 0.01$).

Aspects of abundance, size distributions, and development of the more abundant species are considered below. For some species a variety of developmental stages was found. Because of the diverse patterns of photophore development exhibited by myctophid larvae (Moser and Ahlstrom 1970) only very general terminology is used to denote these stages. These include: early larvae (=

no photophore development); early photophore development larvae (= photophores developing); late photophore development larvae (= lacking full photophore complement and still having larval morphology); transforming, or metamorphosing, individuals (= those completing photophore development and undergoing changes in pigmentation and morphology); and transformed, or early juvenile, stages (= adult morphology and photophore patterns, but still lightly pigmented). Additional information from other gyre cruises on developmental stages is included here.

Subfamily Lampanyctinae

BOLINICHTHYS SPP.—*Bolinichthys longipes* was the fifth-ranked species taken, occurring primarily in the upper 50 m, with peak abundance at 0-25 m; abundances in replicate tows within the 0-25 m interval were significantly greater (Mann-Whitney U test, $P<0.01$) than in other depth intervals (Table 3). Median standard lengths increased with depth (Table 3) and 0-25 m and 25-50 m cumulative size-frequency curves were significantly different from each other. The largest specimen (8.7 mm, from 50-75 m) was still in early photophore development. The largest *B. longipes* larva (10.8 mm) of the 670 taken from IKPT samples was also in early photophore development. No transforming individuals were taken, although juveniles ≥12.8 mm were caught.

Bolinichthys distofax had a narrower distribution than did *B. longipes*; all individuals came from 25-50 m (Table 3). Larval size ranges and developmental stages found in bongo and IKPT samples were comparable with those of *B. longipes*.

CERATOSCOPELUS WARMINGI.—*Ceratoscopelus warmingi* was the third-ranked species, >5% of total larvae, and is also third-ranked species on a year-round basis (Loeb 1979b). Although present at 0-225 m (Figure 7), 94% of the estimated water column abundance was at 25-75 m. Abundances in replicate samples within the 25-50 m interval were significantly greater ($P<0.01$) than in other intervals; the species made up 9% of the total larvae in this interval. Median standard lengths increased with depth and cumulative size-frequency curves for 0-25 m, 25-50 m, 50-75 m, and 75-225 m (Figure 8) were all significantly different from each other. The three largest larvae (8.6-12.8 mm), taken at 75-225 m, were still in early photophore development stages. No later photophore development stages or transforming specimens of *C. warmingi* were found among the 1,806 larvae (to 16.7 mm) examined from 0-300 m IKPT samples; a few early juveniles (≥18.0 mm) were taken.

DIAPHUS SPP.—Seven *Diaphus* species were taken on this cruise. They fell into the two morphological categories described by Moser and Ahlstrom (1974): the "slender" form (which as adults possess a suborbital photophore) and the

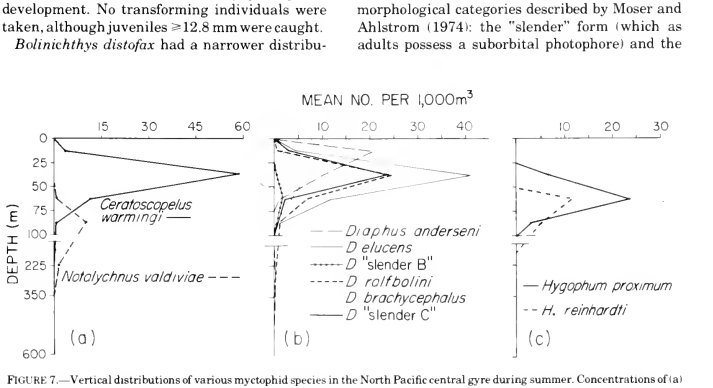


FIGURE 7.—Vertical distributions of various myctophid species in the North Pacific central gyre during summer. Concentrations of (a) *Ceratoscopelus warmingi* and *Notolychnus valdiviae*, (b) *Diaphus* spp., and (c) *Hygophum* spp. larvae by depth interval.

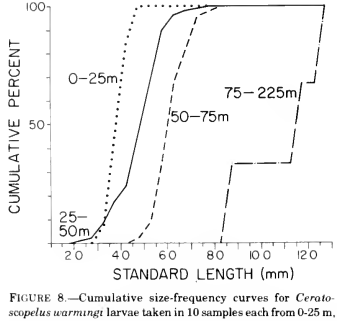


FIGURE 8.—Cumulative size-frequency curves for *Ceratoscopelus warmingi* larvae taken in 10 samples each from 0-25 m, 25-50 m, 50-75 m, and in combined samples from 75-100 m (10) and 100-225 m (6) of the North Pacific central gyre during summer.

"stubby" form (without this photophore). The presence of transforming specimens of most of these species in plankton samples facilitated their probable identifications. The "slender" species were *D. anderseni*, *D. brachycephalus*, and the *D. mollis* complex. The "stubby" species were *D. elucens*, *D. rolfbolini*, and the possible larvae of *D. schmidti*.

Diaphus anderseni had the shallowest distribution among *Diaphus* species, with 96% of the abundance from the upper 50 m and significant ($P<0.05$) peak abundance at 0-25 m (Figure 7b; Table 3). Median standard lengths increased slightly from 0-25 m to 25-50 m, with a much greater increase between 25-50 m and 50-75 m (Table 3); cumulative size-frequency curves were significantly different for all three intervals. The largest individuals (11.3 and 11.6 mm), caught at 50-75 m, were transforming. One recently transformed (10.5 mm) individual was taken at 100-350 m. The entire developmental sequence of *D. anderseni* was found in 0-300 m IKPT samples; transforming individuals were 11.3-11.8 mm.

Diaphus "slender C" (probably the "B" form of *D. mollis*; Clarke 1973), *D. brachycephalus*, *D. elucens*, and *D. rolfbolini* all had similar distributions centered around maximum abundances at 25-50 m (Figure 7b); for all but *D. brachycephalus* the abundances in replicate tows within this interval were significantly greater than in other depth intervals (Table 3). Within the 25-50 m interval, *D. elucens*, *D. rolfbolini*, and *D.* "slender C" ranked 4, 7, and 8, respectively, in total larval abundance; *D. elucens* was the fourth-ranked species taken overall during this cruise (Table 2). For each species, median standard lengths increased with depth (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other.

No transforming individuals of these species were taken in tows considered here, although a transforming *D.* "slender C" (10.5 mm) was caught in a 0-100 m sample, and one recently transformed *D. elucens* (11.8 mm) was caught at 0-25 m. Oblique IKPT hauls (ranging in depth from 0-180 m to 0-360 m) on other central gyre cruises have caught late larval, transformational, and early juvenile stages of all four species. Transforming individuals of *D. brachycephalus* were 9.8-10.5 mm; *D. elucens*, 10.3-11.7 mm; *D.* "slender C," 11.2-12.7 mm; and *D. rolfbolini*, 11.7-12.5 mm.

The two other *Diaphus* species taken were both rare in stratified tows (Table 2). Most of *D.* "slender B" (probably the "A" form of *D. mollis*; Clarke 1973) occurred at 50-75 m, the deepest distribution of the genus (Figure 7b). Transforming specimens (10.0-11.3 mm) have been caught in 0-300 m IKPT hauls. *Diaphus* "stubby C" may be the larval form of *D. schmidti*; the larvae have been taken in the central gyre only in small numbers and sizes. Most were caught at 25-50 m during this cruise.

LAMPADENA SPP.—*Lampadena anomala* and *L. luminosa* were caught in low numbers within the upper 50 m. Eleven *L. luminosa* larvae occurred in four tows from both 0-25 m and 25-50 m; one large larva (12.7 mm) was also taken at 75-100 m (Table 3). There was a trend for increased size with depth. *Lampadena anomala* was taken (one per sample) in five 0-25 m and three 25-50 m samples (Table 3). All *Lampadena* spp. individuals were in early stages of photophore development. No late-stage specimens of these relatively rare central gyre species have been taken in any of the samples examined.

LAMPANYCTUS SPP.—*Lampanyctus steinbecki*, most abundant of the larval *Lampanyctus* species taken, ranked ninth for this cruise (Table 2). It was caught at 0-75 m, but 89% of the estimated water column abundance was at 25-50 m; abundances in replicate samples within this interval were significantly higher ($P<0.01$) than

in other intervals (Table 3). Only early-stage larvae (2.1-6.9 mm) were taken. Median standard length increased only slightly with depth (Table 3).

The three other *Lampanyctus* species caught in stratified tows were rare. These included: *L.* "big snout," probably of the *L. niger* complex; *L.* "lacks pectorals," a larval stage of an undescribed *Lampanyctus* species (E. H. Ahlstrom[3]); and *L. nobilis*. The larvae of *L.* "big snout" and *L. nobilis* were most abundant at 25-50 m, while *L.* "lacks pectorals" was taken mostly at 50-75 m (Table 3). All three species showed a trend for increased size with depth (Table 3); only early photophore development stages were taken. No late larval or transformational stages of any *Lampanyctus* species were found in 0-300 m IKPT samples (1,477 specimens examined).

LOBIANCHIA GEMELLARI—The larvae of *L. gemellari* occurred deeper than most lampanyctine species, only at depths >50 m (Table 3). Over 94% of the estimated water column abundance was between 50 and 100 m; larvae were similar in frequency of occurrence in samples and in abundance at 50-75 m and 75-100 m. Cumulative size-frequency curves for 50-75 m and 75-100 m were significantly different from each other and indicated more small and fewer large individuals in the deeper interval. The largest larvae taken in stratified tows (6.7 and 7.9 mm) were in early photophore development. Stages from early larvae through transformation (10.8-12.7 mm) were caught in 0-180 m IKPT hauls.

NOTOLYCHNUS VALDIVIAE.—Both the adult and larval *N. valdiviae* differ from other lampanyctine species in several respects, and Moser and Ahlstrom (1974) suggested placement of the species in a separate subfamily. The larvae are also unusual in their depth distributions as compared with other lampanyctine species (Figure 7a). *Notolychnus valdiviae* was absent at 0-50 m and rare at 50-75 m; maximum abundance (40 of the 44 larvae caught) occurred at 75-100 m where the species ranked fourth (Table 2).

All stages of development of *N. valdiviae* were found between 50 and 100 m. The largest pretransformation specimen (8.0 mm) was from 75-100 m. A 10.5 mm transforming specimen plus nine other individuals ranging from recently transformed to adult (10.8-21.8 mm) were caught at 50-75 m. Three other metamorphosed individuals were found in other intervals: a recently transformed individual (11.3 mm) at 25-50 m; and two juveniles (15.7 and 17.3 mm) at 75-100 m.

TRIPHOTURUS NIGRESCENS.—*Triphoturus nigrescens* was the fourth-ranked myctophid (eighth ranked species overall) taken. The larvae were distributed from 0 to 100 m, with 88% of the estimated water column abundance at 25-50 m; abundances in replicate samples within this interval were significantly greater ($P<0.01$) than in other intervals (Table 3). Median standard lengths increased below 50 m (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other. The 11.8 mm larva, from 75-100 m (Table 3), was one of the largest *T. nigrescens* larvae taken in any central gyre plankton sample; it still lacked photophore development. Nine metamorphosed individuals were also caught in stratified tows: six (14.7-17.0 mm) at 25-50 m; one (17.9 mm) at 50-75 m; and two (17.0 and 21.3 mm) at 75-100 m. No late-stage larvae have been found among the 612 specimens collected from central gyre IKPT samples.

Subfamily Myctophinae

BENTHOSEMA SUBORBITALE.—*Benthosema suborbitale* occurred at 75-350 m, and was an important component of the deeper ichthyoplankton, ranking third in 75-100 m samples and second in 100-225 m and 100-350 m samples (Table 2). Largest numbers occurred at 75-100 m, but 46 of the 48 larvae from this interval came from only 2 of 10 samples; frequency of positive samples was highest at 100-225 m (five of six samples). Size ranges, median lengths, and cumulative size-frequency curves were similar for all depth intervals. The largest larva (8.0 mm) was in early photophore development. Seven recently transformed juveniles were caught: five (11.1-12.1 mm) at 25-50 m and two (10.8 and 12.7 mm) at 50-75 m. Developmental stages to early transformation (10.8-11.3 mm) were found in 0-300 m IKPT samples.

CENTROBRANCHUS SPP.—Three species of *Centrobranchus* were caught at 75-100 m (Table

[3]E. H. Ahlstrom, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. 1977.

3). *Centrobranchus andrae* and *C. brevirostris* were represented by single specimens. The five *C. choerocephalus* individuals (3.4-7.1 mm) occurred in three samples. All specimens were early photophore stage larvae.

DIOGENICHTHYS ATLANTICUS.—The 12 *D. atlanticus* larvae (all early photophore stage larvae) were caught between 75 and 350 m; 8 came from 75-100 m (Table 2). During other central gyre cruises, *D. atlanticus* was abundant in IKPT samples, and developmental stages from early larvae to transformation (11.3-12.8 mm) were found.

HYGOPHUM SPP.—*Hygophum proximum* was the most numerous larval myctophine (Table 2). It occurred from 25 to 100 m, with maximum abundance and significantly larger catches in replicate tows ($P<0.01$) at 50-75 m (Table 3). Median standard length increased with depth (Table 3) and 25-50 m and 50-100 m size-frequency curves were significantly different from each other. The largest larva (10.0 mm, from 75-100 m) was in early photophore development. No late-stage *H. proximum* larvae have been found among the 490 examined from 0-300 m IKPT samples.

Hygophum reinhardti larvae were more deeply distributed than those of *H. proximum*, occurring from 50 to 225 m. As with its congener, maximum estimated water column abundance and significantly larger catches ($P\leq0.05$) were at 50-75 m, but the larvae were also frequently taken (7 of 10 samples) at 75-100 m (Figure 7c). There were no apparent trends in size with depth (Table 3). No late photophore development larvae were caught, but two recently transformed individuals (12.3-13.3 mm) were found in 0-300 m IKPT samples from other cruises.

MYCTOPHUM SPP.—Four *Myctophum* species were caught (Table 2). The 58 *M. lychnobium* larvae occurred between 25 and 100 m, with maximum abundance at 25-50 m; *M. brachygnathum* had a similar distribution. All five *M. selenops* were caught at 50-75 m, and six of the seven *M. nitidulum* at 75-100 m. All of the larvae were small (<8.0 mm) and in early photophore development; only those of *M. brachygnathum* appeared to have increased size with depth (Table 3). A total of 393 *Myctophum* larvae, of all four species, have been examined from central gyre IKPT samples; none exceeded 10.0 mm or were in advanced stages of photophore development.

SYMBOLOPHORUS EVERMANNI.—*Symbolophorus evermanni* occurred from 25 to 225 m; over 90% of the estimated water column abundance was between 50 and 100 m; abundances in replicate samples within the 50-75 m interval were significantly greater ($P<0.05$) than in other intervals (Table 3). Although the largest larva (10.5 mm) was from 75-100 m, the median standard length was smaller there than at shallower depths (Table 3). The 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other, indicating decreased size with increased depth. Only early photophore development stages were caught by stratified tows. This was also the case for all 0-300 m IKPT samples examined, where the largest prejuvenile (15.5 mm) of 369 individuals was in the earliest stages of photophore development.

Other Larvae

Other families contributed only 9% of the identified larvae and included a wide assortment of mesopelagic fishes; only 3 of the 33 families identified were epipelagic. These "other larvae" were found in samples taken from 0 to 350 m (Figure 2). Total abundance was low in the upper 75 m, but increased greatly below 75 m (due primarily to peak abundances of two families), and made up 25% and 19% of the ichthyoplankton in 75-100 m and 100-350 m samples, respectively. Maximum diversity occurred at 25-50 m.

None of these "other" species was abundant. Of the 49 kinds of larvae represented only 3 were caught in even moderate numbers: *Bregmaceros* spp. (Bregmacerotidae), *Odontostomops normalops* (Evermannellidae), and *Howella* sp. (Aponogonidae). Only *Bregmaceros* spp. is abundant in the central gyre ichthyoplankton on a year-round basis (Loeb 1979b). Together these three kinds made up 39% of the other larvae; the remaining 61% was contributed by 1 order and 30 families (42 species). Catch information on the other larvae is presented in Table 2; more detailed distributional data is provided in Loeb (1979a).

DISCUSSION AND CONCLUSIONS

The overall vertical distribution pattern of central gyre ichthyoplankton conforms to that described by Ahlstrom (1959) for the California Current. Most species and individuals were in the upper 100 m, with maximum abundance and di-

versity at 25-50 m, possibly related to the bottom of the mixed layer. A distinct change in species composition and relative abundances occurred below 75 m. This involved a shift from dominance by *Cyclothone alba*, *Vinciguerria nimbaria*, and lampanyctine myctophids to other gonostomatid species, myctophine myctophids, and other families. Ahlstrom (1959) previously had found groups of species (in the California Current) to be either predominantly within the mixed layer and upper thermocline or mostly within or below the thermocline.

None of the abundant larvae were taken only in one 25 m interval, and most were found over at least a 75 m depth range. However, almost all species taken in the upper 100 m had distinct maxima of catch frequency and abundance within one of the 25 m depth intervals sampled; for many species, despite high catch variability due to patchiness, the abundances in replicate tows within this interval were significantly higher than in any other interval. Almost twice as many larvae and half again as many kinds were found in 100-225 m samples as in 100-350 m samples, indicating that most deeper species may be distributed above 225 m.

Significant changes were found in cumulative size-frequency distributions with depth for many of the abundant species. There was a general trend for those species with peak abundance in the upper 50 m to have significant increases in larval size with depth. Species with maximum abundance below 50 m tended to exhibit no size-depth changes, or had significant decreases in size with depth. With these deeper larvae, the apparent lack of size change with depth may be the product of small sample sizes outside the depth of maximum abundance and the broader depth ranges sampled below 100 m.

The gonostomatids exhibited two different distributional patterns. *Cyclothone* spp., *V. nimbaria*, and *Diplophos taenia* occupied the topmost 50 m. The other seven species were distributed below 75 m, with maximum abundances in the 75-225 m range. The nighttime depth distribution patterns of juveniles and adults (from Clarke 1974) of the migratory gonostomatid species relative to each other are, with the exception of *Gonostoma elongatum*, generally the same as for the larvae (Figure 9). Both larval and adult *Diplophos taenia* had the shallowest distribution and *Valenciennellus tripunctulatus* the deepest distribution within the family. Also, except for *G. elongatum*,

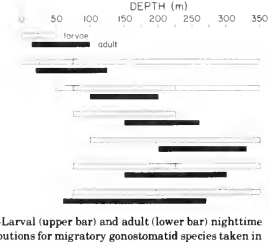


FIGURE 9.—Larval (upper bar) and adult (lower bar) nighttime depth distributions for migratory gonostomatid species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates intervals where >90% of the estimated water column abundance occurred. Adult depth distributions from Clarke (1974).

the upper depth distributions of the adults (usually small adults; Clarke 1974) tend to overlap the lower ranges of peak larval abundance. Although Clarke's (1974) adult information is from a different oceanic regime (offshore Hawaiian waters), his general patterns of depth distribution may still be valid for the central gyre adults.

The night depth patterns of larval and adult myctophid species are more complex than those of the gonostomatids. The larvae of subfamily Lampanyctinae generally occupy shallower depths than do those of subfamily Myctophinae (Figure 6b). The opposite is generally true of the night distributions of the adults from the two subfamilies. Clarke (1973) presented adult depth distributions for 46 myctophid species taken near Hawaii. Of the 15 myctophine species he listed, 8 had upper night distribution limits at 0-25 m (5 of these were taken in substantial numbers by dip nets); 2 others occurred at 25-50 m. In contrast, only 10 of the 31 lampanyctine species listed by Clarke (1973) were caught in the upper 50 m. Ahlstrom and Stevens (1976) also found that neuston (surface) samples taken in the California Current caught only myctophine juveniles and adults and lampanyctine larvae.

Different night adult and larval depth patterns are apparent for the two subfamilies (Figure 10). Lampanyctine adults, generally overlap, or are distributed below, their depths of maximum larval abundance. The shallowest lampanyctine individuals (which share the larval depth range) are usually small adults or juveniles (Clarke 1973). This contrasts strongly with myctophine adults

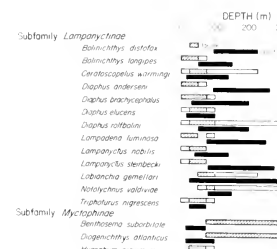


FIGURE 10.—Larval (upper bar) and juvenile and adult (lower bar) nighttime depth distributions for the more abundant lampanyctine and myctophine (Myctophidae) species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates depth intervals where ≥90% of the estimated water column abundance occurred. Adult depth distributions from Clarke (1973).

(except for *Hygophum* spp.), wherein all sizes tend to be distributed above the depths of maximum larval abundance. In most cases the largest adults of both subfamilies are vertically separated from the larvae, and, where overlap occurs, the smallest juveniles are in similar depth ranges with the largest larvae.

A variety of patterns of early developmental stages were found. Among the gonostomatids, metamorphic stages of *Cyclothone alba* and *Vinciguerria* spp. were found in stratified samples. Apparently *C. alba* leaves the larval depth range once it has reached the prometamorphic stage of development. *Vinciguerria* spp. go through all early metamorphic stages while in the larval depth range and presumably descend to greater depths once the postmetamorphic stage is completed. For both *C. alba* and *V. nimbaria* the advanced stages of larval development were found in the lower portion of the larval depth range. Gradual downward migration with development, as seen in *V. nimbaria*, may also occur in *Valenciennellus tripunctulatus* and *Gonostoma* spp. (Badcock and Merrett 1976).

The myctophid species exhibited different levels of photophore development before descending to juvenile depths. Developmental series from early larvae to transforming individuals were found from ≤350 m for 11 of the 31 myctophid species taken in Climax I. These include: six of the seven *Diaphus* species (all but *D. schmidti*), *Lobianchia gemellari*, *Notolychnus valdiviae*, *Benthosema suborbitale*, *Diogenichthys atlanticus*, and *Hygophum reinhardti*. At least some individuals of *Diaphus* spp., *L. gemellari*, *N. valdiviae*, and *D. atlanticus* complete transformation before descent to juvenile depths or else begin extensive migrations before transformation. The presence of lightly pigmented juveniles of *D. anderseni*, *D. elucens*, *N. valdiviae*, *B. suborbitale*, and *H. reinhardti* in the upper 100 m at night indicated that, if these are not predescent individuals, some members of these species may undergo early juvenile migration.

No late photophore stage larvae were found for *Bolinichthys* spp., *Ceratoscopelus warmingi*, *Lampadena* spp., *Lampanyctus* spp., *Triphoturus nigrescens*, *H. proximum*, *Myctophum* spp., or *Symbolophorus evermanni* in either the Climax I samples or 0-300 m IKPT samples taken on other gyre cruises. These larvae appear to leave the upper 300 m of the water column at varying levels of early photophore development prior to transformation. The late stages of photophore development probably occur at the juvenile day depth range for each species. The developmental state at descent appears to be a generic characteristic within both subfamilies. Except for *Hygophum* spp., congeners achieved similar levels of photophore development while in the upper 300 m.

Due to small numbers of other larvae captured, little can be ascertained about their distributional patterns. Most species occurred in the upper 100 m, with greatest numbers of species at 25-50 m. Basic trends in depth distribution appeared to exist on a familial or ordinal level: Notosudidae were most abundant at 0-25 m; five families of ceratioid fishes occurred in the upper 50 m; four families of stomiatoid fishes and the Evermannellidae occurred most frequently at 25-75 m; Bregmacerotidae and Melamphaeidae were most abundant at 75-100 m; and Scopelarchidae, Bathylagidae, and Sternoptychidae occurred below 100 m. The paralepidids (much like the myctophids) exhibited a variety of depth distributions through the upper 225 m.

The depth distributions described are for the late summer central gyre ichthyoplankton assemblage. Surface temperature is 6°-7° C lower in winter and the mixed layer depth increases from ca. 40 m in late summer to 110-140 m in winter (McGowan and Williams 1973). There are also

definite seasonal changes in larval fish species composition and abundance relations. As larval depth distributions are apparently affected by temperature distribution and mixed layer depth (Ahlstrom 1959) spatial patterns in winter gyre waters may be different from those portrayed here.

ACKNOWLEDGMENTS

This work was supported by grants from the Institute of Marine Resources of Scripps Institution of Oceanography and the Oceanic Biology Program (Code 484) of the Office of Naval Research. Ship time was in part supported by the U.S. National Science Foundation and the Marine Life Research Program of the State of California. I greatly appreciate the assistance in larval fish identification provided by E. H. Ahlstrom and Betsy Stevens of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif. Special thanks go to Eric Shulenberger of the Office of Naval Research for his excellent editorial advice. Thanks also to John A. McGowan and R. H. Rosenblatt of Scripps Institution of Oceanography for their editorial suggestions.

LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.
1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Rep. 13:39-44.
1974. The diverse patterns of metamorphosis in gonostomatid fishes—an aid to classification. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 659-674. Springer-Verlag, N.Y.

AHLSTROM, E. H., AND R. C. COUNTS.
1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 58:363-416.

AHLSTROM, E. H., AND E. STEVENS.
1976. Report of neuston (surface) collections made on an extended CalCOFI cruise during May 1972. Calif. Coop. Oceanic Fish Invest. Rep. 18:167-188.

BADCOCK, J., AND N. R. MERRETT.
1976. Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog. Oceanogr. 7:3-58.

BARNETT, M. A.
1975. Studies on the patterns of distribution of mesopelagic fish faunal assemblages in the central Pacific and their temporal persistence in the gyres. Ph.D. Thesis, Scripps Institution of Oceanogrpaphy, Univ. California, San Diego, 145 p.

BRIDGER, J. P.
1956. On day and night variation in catches of fish larvae. J. Cons. 22:42-57.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish Bull., U.S. 72:337-351.

CONOVER, W. J.
1971. Practical nonparametric statistics. John Wiley and Sons, N.Y., 462 p.

GREGG, M. C., C. S. COX, AND P. W. HACKER.
1973. Vertical microstructure measurements in the central North Pacific. J. Phys. Oceanogr. 3:458-469.

KOBAYASHI, B. N.
1973. Systematics, zoogeography, and aspects of the biology of the bathypelagic fish genus *Cyclothone* in the Pacific Ocean. Ph.D. Thesis, Scripps Institution of Oceanography, Univ. California, San Diego, 487 p.

LEGAND, M., AND J. RIVATON.
1969. Cycles biologiques des poissons mésopélagiques de l'est de l'Ocean Indien. Trosième note: action predatrice des poissons micronectoniques. Cah. O.R.S.T.O.M. Sér. Oceanogr. 7:29-45.

LOEB, V. J.
1979a. The icthyoplankton assemblage of the North Pacific central gyre: spatial and temporal patterns. Ph.D. Thesis, Scripps Instittution of Oceanography, Univ. California, San Diego, 220 p.
1979b. Larval fishes in the zooplankton communtiy of the North Pacific central gyre. Mar. Biol. (Berl.) 53:173-191.

MCGOWAN, J. A., AND T. L. HAYWARD.
1978. Mixing and oceanic productivity. Deep-Sea Res. 25:771-793.

MCGOWAN, J. A., AND P. W. WALKER.
In press. Structure in the copepod community of the central North Pacific gyre. Ecol. Monogr.

MCGOWAN, J. A., AND P. M. WILLIAMS.
1973. Oceanic habitat differences in the North Pacific. J. Exp. Mar. Biol. Ecol. 12:187-217.

MERRETT, N. R., AND H. S. J. ROE.
1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. (Berl.) 28:115-126.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narroweyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.
1974. Role of larval stages in systematic investigations of marine teleosts: The Myctophidae, a case study. Fish. Bull., U.S. 72:391-413.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

SCRIPPS INSTITUTION OF OCEANOGRAPHY.
1966. A new opening - closing paired zooplankton net. Scripps Inst. Oceanogr., SIO Ref. 66-23, 56 p.
1974 Physical, chemical and biological data. Climax I Expedition, 19 September - 28 September 1968 Scripps. Inst. Oceanogr., SIO Ref. 74-20, 41 p.

RESISTANCE OF DIFFERENT STOCKS AND TRANSFERRIN GENOTYPES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, AND STEELHEAD TROUT, *SALMO GAIRDNERI*, TO BACTERIAL KIDNEY DISEASE AND VIBRIOSIS[1]

GARY W. WINTER,[2] CARL B. SCHRECK,[2] AND JOHN D. MCINTYRE[3]

ABSTRACT

Juvenile coho salmon and steelhead trout of different stocks and three transferrin genotypes (AA, AC, and CC), all reared in identical or similar environments, were experimentally infected with *Corynebacterium* sp., the causative agent of bacterial kidney disease, or with *Vibrio anguillarum*, the causative agent of vibriosis. Mortality due to the pathogens was compared among stocks within a species and among transferrin genotypes within a stock to determine whether there was a genetic basis for resistance to disease. Differences in resistance to bacterial kidney disease among coho salmon stocks had a genetic basis. Stock susceptibility to vibriosis was strongly influenced by environmental factors. Coho salmon or steelhead trout of one stock may be resistant to one disease but susceptible to another. The importance of transferrin genotype of coho salmon in resistance to bacterial kidney disease was stock specific; in stocks that showed differential resistance of genotypes, the AA was the most susceptible. No differences in resistance to vibriosis were observed among transferrin genotypes.

Bacterial kidney disease (BKD) caused by *Corynebacterium* sp. is a major cause of serious losses among salmon reared in freshwater hatcheries of the Pacific Northwest (Leitritz and Lewis 1976), and epizootics caused by *Vibrio anguillarum* in the marine environment are particularly devastating to salmonids maintained in saltwater impoundments (Fryer et al. 1972). Externally applied antibiotics are relatively ineffective in the treatment of these diseases. Immunization with bacterins for the control of vibriosis has been shown to be feasible (Fryer et al. 1976), but attempts to produce a bacterin for BKD have been unsuccessful (Evelyn 1977). The use of disease resistant populations of fish may conceivably reduce the incidence and severity of these diseases. Fish that inherit natural resistance to a disease normally maintain that resistance throughout their lives (Snieszko et al. 1959). In addition, information on the resistance of donor stocks, for use in transplants to infected waters, would be valuable.

The existence of disease resistant strains within a species has been demonstrated. Stock or strain refers to a population of fish of one species which shares both a common environment (a particular stream) and common gene pool (discrete breeding group) and, as such, can be considered as a self-perpetuating system (Larkin 1972). Differences in susceptibility to ulcer disease and furunculosis have been observed among different strains of brook trout, *Salvelinus fontinalis* (Wales and Berrian 1937; Wolf 1954; Snieszko 1957; Snieszko et al. 1959), and Gjedrem and Aulstad (1974) noted significant differences in resistance to vibriosis, which they showed to be slightly heritable, between different strains of Atlantic salmon, *Salmo salar*, parr in Norway. Unfortunately, in most previous studies of disease resistance, fish of the different stocks were not reared in a common environment. Since phenotypic expression is a combination of genotype, environment, and interactions between these two variables, different stocks must be reared under identical conditions if one is to be certain that differences in resistance to disease are genetic in origin and not due, for example, to previous exposure of a particular stock to the disease in question or some other factor such as nutritional history. One objective of the present study was to determine whether there are differences in resistance to BKD and vibriosis

[1]Oregon Agricultural Experimental Station Technical Paper No. 4862.

[2]Oregon Cooperative Fishery Research Unit, Oregon State University, Corvallis, OR 97331. Cooperators are Oregon State University, Oregon Department of Fish and Wildlife, and U.S. Fish and Wildlife Service.

[3]Oregon Cooperative Fishery Research Unit; present address: U.S. Fish and Wildlife Service, Box 1050, Tyler Road, Red Bluff, CA 96080.

Manuscript accepted May 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980.

among stocks of coho salmon, *Oncorhynchus kisutch*, and steelhead trout, *Salmo gairdneri*, and whether these differences have a genetic basis.

Suzumoto et al. (1977) reported differences in resistance to BKD among three genotypes of transferrin (an iron-binding plasma protein) in coho salmon. In mammals, iron is known to increase the growth and virulence of some pathogens. Transferrin may reduce infection by binding the metal, thereby reducing its availability to invading bacteria, a process known as nutritional immunity (Weinberg 1974). No iron requirement has been demonstrated for BKD bacteria, although it is likely that one exists, judging by the fastidiousness of the organisms. Hershberger (1970) observed differences in iron binding capacity among transferrin genotypes in brook trout and suggested that individuals more efficient in the uptake and release of iron might fare better under "adverse conditions" such as disease. A second objective of this study was to compare resistance to BKD and vibriosis among transferrin genotypes, to evaluate earlier results with BKD, and to determine whether transferrin increases the tolerance of bacterial diseases of salmonids in general. We also sought to determine whether differences in resistance of transferrin genotypes exist among different stocks of coho salmon and steelhead trout.

MATERIALS AND METHODS

Juvenile coho salmon were obtained as eyed eggs from the Fall Creek (Alsea) and Big Creek salmon hatcheries, Oreg. The Big Creek hatchery was also the source of two crosses, Big Creek × Sol Duc (B × S) and Big Creek × Umpqua (B × U). All stocks were reared at Corvallis, Oreg.—the Big Creek stock at Oregon State University's Smith Farm; the Alsea stock at the Oregon Department of Fish and Wildlife's Research Section; and the two crosses at Oregon State University's Fish Disease Laboratory. These rearing facilities presented similar, though not identical, environments for the fish. Because we lacked sufficient fish of the two crosses to include them in all studies, we used them only in the BKD study.

Steelhead trout were obtained as green eggs from the following Oregon State hatcheries: Alsea (winter run), Roaring River (Siletz summer run), Cole Rivers (Rogue summer run), and Marion Forks (North Santiam winter run). All four stocks were reared under identical conditions at Smith Farm.

For determination of the transferrin genotypes of the experimental fish, we withdrew about 0.1 ml of blood from the caudal vein of anesthetized fish with a 1 ml tuberculin syringe and ejected it into heparinized hematocrit tubes, which were then centrifuged. The plasma from the salmon was frozen until the time of analysis. Blood samples from steelhead trout were placed on ice and processed within 4 h after collection because we found that frozen storage reduces the stability of transferrin in this species. Fish were individually identified by dangler tags applied immediately behind the dorsal fin. We used starch-gel electrophoresis, adapting the discontinuous buffer system described by Ridgeway et al. (1970), to determine transferrin genotypes. Only the AA, AC, and CC genotypes were considered, and in some stocks only two of these were used. The transferrins of Siletz and North Santiam steelhead trout stocks were not included in this study because resolution on the electrophoretic gels was poor. After the fish were bled, they were given a recovery period of at least 2 wk before they were transferred to experimental tanks.

Bacterial Kidney Disease

All experimental fish were held indoors in 70 l fiber glass tanks supplied with flowing, aerated, chilled (12° ± 2° C), dechlorinated water. The fish were allowed to acclimate in these tanks for 2 wk. Fish were fed once daily with Oregon Moist Pellet. Each stock of coho salmon and steelhead trout consisted of 125 fish divided into two test replicates of 50 each plus 25 control fish. Included in the steelhead trout experiment was one group of 34 fish of hatchery-reared (Cole Rivers) Rogue River stock, without a replicate. The respective transferrin genotypes were distributed randomly among all tanks.

The BKD (*Corynebacterium* sp.) strain (RB-1-73) used was isolated on cysteine serum agar from a spring chinook salmon, *O. tshawytscha*, at the Round Butte Oregon State Hatchery by J. E. Sanders, fish pathologist, Oregon Department of Fish and Wildlife. A stock culture was maintained on Mueller-Hinton agar (Difco Laboratories,[4] Detroit, Mich.) enriched

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

with cysteine (0.1%) and calf serum (20%). Before each experiment, cells were passed once in the species being tested to produce a fresh isolate, and this isolate was further cultured until sufficient cells were available for an inoculum.

All test fish received an intraperitoneal injection of 0.1 ml of a suspension of kidney disease bacteria in phosphate-buffered saline (PBS), and all control fish received a 0.1 ml intraperitoneal injection of only PBS. The approximate inocula were 9×10^7 cells for the coho salmon (mean weight, 23 g), and 3×10^8 cells for the steelhead trout (mean weight, 36 g). The coho salmon were injected on 17 March 1977 and the steelhead trout on 12 September 1977. We examined all fish that died and identified BKD as the causative agent on the basis of presumptive diagnosis, using gram stains of kidney smears. In addition, kidney smears from 10% of the fish that died were cultured on Mueller-Hinton media. Experiments were terminated at the end of 4 mo or earlier, depending on the progress of infection.

One week after the coho salmon had been injected, an accidental exposure of the fish, including the controls, to chlorine resulted in mortalities as high as 50% in some stocks. The study was nevertheless continued, but a second, abbreviated test was begun on 24 August 1977. Only Alsea and Big Creek stocks (mean weight, 33.2 g) were used; the Big Creek fish were obtained directly from the hatchery. The inoculum for this second experiment was increased to 3×10^8 cells.

Vibriosis

The *V. anguillarum* strain (LS-174) used in these experiments was isolated on brain heart infusion agar from a coho salmon at Lint Slough, Waldport, Oreg., by J. S. Rohovec. The inocula were either prepared from lyophilized cells or recent passage isolates. Experimental fish were exposed to the pathogen in 93 l stainless steel tanks at Oregon State University's Fish Disease Laboratory.

Two experiments were undertaken with the coho salmon. In the first (8 October 1976), 225 fish (mean weights for Big Creek and Alsea stocks were 10.4 g and 14.5 g, respectively) from each stock were divided equally among two test replicates and an untreated control. The three tanks contained fish from each stock to insure identical treatment. The fish in this experiment, having not been bled and tagged for transferrin genotype identification, were freeze branded to differentiate the stocks in each tank. In the second experiment (10 June 1977) the number of fish per tank was reduced to about 25 (mean weight, 36.6 g) because larger numbers were not available, but transferrin genotypes had been determined.

In the steelhead trout phase of the study (21 October 1977), 75 fish from each stock (mean weight, 36 g) were divided equally among three test replicates and 15 from each stock were placed in a fourth tank for controls. A hatchery-reared Rogue stock was also used in this steelhead trout experiment. In a second experiment (27 December 1977) in which we used steelhead trout from the Cole Rivers (Rogue), Alsea, and Marion Forks (North Santiam) hatcheries, 50 fish (mean weight, 42.2 g) were divided equally between two replicates. Transferrin genotypes were distributed randomly among the tanks.

The initial temperature in all experimental tanks was 12.2° C, to which all fish had been acclimated. The temperature was then raised to 17.7° C over a period of 1.5 h, and at this temperature water flow was discontinued in all tanks for 15 min. The bacteria suspended in brain heart infusion broth (Difco Laboratories) were then introduced into the test tanks (other than those of the controls). The inocula were 5×10^6 cells/ml for the first coho salmon exposure and 8.6×10^6 cells/ml for the second; the steelhead trout received concentrations of 8.8×10^6 cells/ml in the first experiment and 7.2×10^6 cells/ml in the second. All fish that died were necropsied and kidney smears were cultured on brain heart infusion agar. Positive diagnosis of *V. anguillarum* was confirmed by slide agglutination with specific antiserum. The experiments were terminated at the end of 1 wk.

Statistical comparison of three or more stocks involved a one-way analysis of variance based on arcsin transformations of percentages and least significant difference, and comparisons of transferrin genotypes of two stocks were based on χ^2 test employing a $2 \times k$ contingency table (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

Bacterial Kidney Disease

In the first experiment in which coho salmon were infected with BKD, the Alsea stock and B × U cross were about twice as resistant to the disease

as were fish of the Big Creek stock and B × S cross (see totals, Figure 1A). The difference in mortality between the B × U and each of the two more susceptible groups (Big Creek and B × S), was significant ($P<0.05$), but the Alsea mortality was significantly lower than that of only the B × S, cross ($P<0.06$). A comparison of mean times to death (days) revealed a similar pattern: B × S, 79.5; B × U, 99.9; Big Creek, 88.4; and Alsea, 95.4. The mean times to death for the B × U and Alsea coho salmon were significantly greater than the B × S ($P<0.05$). The differential resistance of coho salmon stocks to BKD probably has a genetic basis because the stocks were reared in similar environments.

Among transferrin genotypes, only the B × S cross and Alsea stock showed any important differences in resistance to BKD (Figure 1A). In both groups the AA genotype was the most susceptible, and the AC and CC both showed lower, similar mortalities. The difference in resistance was significant ($P<0.07$) between the AA and AC genotypes within the B × S cross. The Alsea transferrin results, though not significant due to small sample size, are substantiated by a previous study in which Suzumoto et al. (1977)

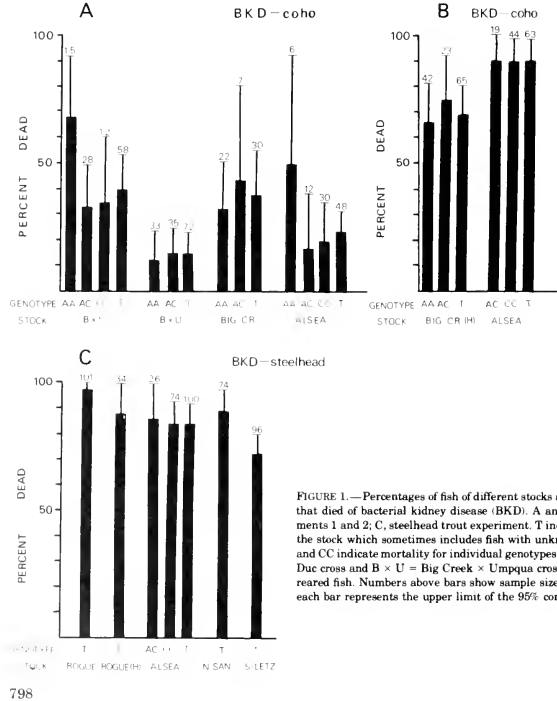


FIGURE 1.—Percentages of fish of different stocks and transferrin genotypes that died of bacterial kidney disease (BKD). A and B, coho salmon experiments 1 and 2; C, steelhead trout experiment. T indicates total mortality for the stock which sometimes includes fish with unknown genotypes; AA, AC, and CC indicate mortality for individual genotypes; B × S = Big Creek × Sol Duc cross and B × U = Big Creek × Umpqua cross; (H) indicates hatchery-reared fish. Numbers above bars show sample sizes; the vertical line above each bar represents the upper limit of the 95% confidence interval.

used Alsea coho salmon in which the AA genotype was also the most susceptible to BKD. Because of similar transferrin results in the B × S cross and Alsea stock, the data were combined. For the combined data, the AC (28% mortality) and CC (24% mortality) genotypes were significantly ($P<0.01$) more resistant to BKD than was the AA genotype (62% mortality). Within both the stocks and transferrin genotypes, differences between replicates were not significant.

The second BKD experiment with coho salmon gave results similar to those of the first on the basis of transferrin genotypes (Figure 1B). Unfortunately, the AA genotype was not included in the Alsea comparison because we lacked sufficient fish. No stock comparison was made because the Big Creek stock came directly from the hatchery, at a time when 91.5% of the mortalities in production fish at Big Creek were due to BKD (J. Conrad[5]). The probability that the Big Creek coho salmon used in the experiment had previously been exposed to BKD was therefore very high.

In the third BKD study, which involved the four steelhead stocks and a second Rogue stock reared at the hatchery (Figure 1C), mortalities in all the test groups began to increase at a high rate 3 wk after the study began because of a secondary infection with *Aeromonas hydrophila*. This trend continued for another 4 wk, at which time mortalities leveled off, and the study was terminated. A comparison of the resistance of the different stocks is not fully valid because the fish in the different test tanks were obviously not challenged equally with a secondary infection of *A. hydrophila*. However, there were no significant differences ($P>0.10$) between replicates, and the mortality of the Siletz steelhead trout (72%) was significantly lower ($P<0.05$) than that of all other stocks except the Alsea. Because mortality in the Rogue stock was extremely high (96%), a transferrin genotype comparison was not considered. The AC and CC genotypes within the Alsea stock were equally susceptible to the double infection of BKD and *A. hydrophila*. Although percentage mortality is a better measure of an organism's ability to tolerate disease, mean time to death is also an indication of resistance to diseases, especially chronic ones such as BKD. There were no differences in mean time to death (days) among either the Rogue or Alsea steelhead transferrin genotypes (numbers of fish in parentheses): Rogue—AA, 28.5 (30); AC, 30.0 (41); and CC, 29.7 (19); Alsea—AC, 30.4 (21); and CC, 30.0 (62). The importance of transferrin was probably reduced by the double infection.

[5]J. Conrad, Oregon Department of Fish and Wildlife, Clatskanie, OR 97015, pers. commun. February 1978.

Vibriosis

In the first experiment in which coho salmon were exposed to *V. anguillarum* (Figure 2A), the Big Creek stock (38% mortality) was significantly more resistant ($P<0.005$) than the Alsea stock (62% mortality) (transferrin was not considered in this comparison). There was a significant difference ($P<0.005$) in mean weight (t'-test, Snedecor and Cochran 1967:114) between the Alsea and Big Creek fish. However, there were no significant differences ($P>0.10$) in resistance to vibriosis among four weight classes (5.1-10.0, 10.1-15.0, 15.1-20.0, and 20.1-25.0 g) within either stock. The difference in resistance between the two stocks appears to be genetic. In a second test, the resistance trend between the Alsea and Big Creek stocks was reversed (Figure 2B), though at a lower level of significance ($P<0.07$) than the previous experiment. However, the Alsea coho salmon used in this second test came directly from the hatchery. Though it is unlikely that any of these fish would have been previously exposed to *V. anguillarum* in freshwater, a difference in susceptibility to vibriosis still existed. These conflicting results thus demonstrate that the environment has a strong effect in determining resistance to vibriosis. In both the Alsea and Big Creek stocks, no differential resistance was shown by the transferrin genotypes, although the AA genotype was not included in the Alsea transferrins (Figure 2B).

In the first of the two vibriosis experiments with steelhead trout (Figure 2C), the North Santiam steelhead trout were the least susceptible to vibriosis of all the stocks ($P<0.05$). The Alsea steelhead trout, though exhibiting a higher mortality (87%) than the North Santiam fish, were still significantly more resistant than the remaining two stocks ($P<0.05$). Because mortality was high in the Smith Farm- and hatchery-reared Rogue stocks (96%), transferrin genotype differences and the effects of rearing environment on resistance were not considered. However, no differences in resistance were observed among genotypes within the Alsea stock. These results using steelhead trout are similar to those observed in the coho salmon exposed to vibriosis.

The second vibriosis experiment (Figure 2D),

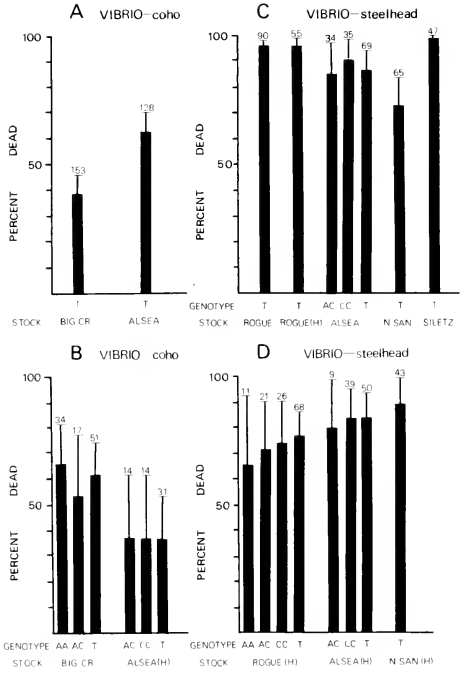


FIGURE 2.—Percentages of fish of different stocks and transferrin genotypes that died of vibriosis. A and B, coho salmon experiments 1 and 2; C and D, steelhead trout experiments 1 and 2. For interpretation of other features see Figure 1.

involving hatchery-reared steelhead trout from the Rogue, Alsea, and North Santiam, revealed the same results as did the first, with respect to transferrin genotypes. No differential resistance was shown among genotypes, including the AA's, within either the Alsea or Rogue stocks. Although resistance to vibriosis among the three stocks was similar, the North Santiam stock showed the highest mortalities this time—which again emphasizes the importance of environmental factors in the determination of resistance and the need for eliminating environmental differences in making genetic comparisons. There was a significant difference in vertebral number between North Santiam steelhead trout reared at the hatchery and at Smith Farm, indicating an environmental difference (our unpubl. data). The Rogue replicates in this experiment were significantly different ($P<0.025$) with respect to stock mortality; consequently a genetic comparison was invalid. Except for the hatchery-reared Rogue replicates in the last vibriosis experiment using steelhead trout, there were no significant differences between replicates for stocks or genotypes in all four vibriosis tests; consequently we combined replicates in the data analysis.

Perhaps stock resistance to acute diseases such as vibriosis depends more on which stock has an environmental advantage at the time of infection, rather than on genetic make-up. Also, when mortalities in experiments are high, resistance comparisons are difficult to make because any immunity that was present may have been overwhelmed. Genetic factors are probably more important in chronic diseases such as BKD. For example, Zinn et al. (1977) observed apparent genetic resistance to infection by *Ceratomyxa shasta*, normally not an acute condition, among hatchery strains of chinook salmon.

It is also evident that a stock may be resistant to one disease and not to another. Although the Siletz steelhead trout were most resistant to the double infection of BKD and *A. hydrophila*, they showed the greatest susceptibility to *V. anguillarum*. Ehlinger (1977) observed that certain selected brook trout strains, though resistant to furunculosis, were more susceptible to gill disease than was the native stock. Consequently selection of stocks for resistance to several diseases would be difficult (McIntyre 1977), except possibly when the pathogens are closely related (Hutt 1970).

Judging by the present results, it appears that the importance of transferrin genotypes in resistance to disease is stock specific. Differences among genotypes were only observed in the Alsea and B × S coho salmon infected with BKD. Weinberg (1974) noted that different host species may vary in the extent to which they rely on iron-specific nutritional immunity. Although only the most common genotypes were compared within each stock, it is unlikely that other genotypes would have shown greater resistance to BKD; their frequencies within the stocks would have been increased by natural selection if the disease plays an important role as a selective agent. However, it is apparent that factors other than disease may select for different transferrin genotypes. In Ukranian carp, *Cyprinus carpio*, general survival rates were highest among individuals with the AC genotype (Balakhnin and Galagan 1972). There is also an association of transferrin phenotype with weight gain in juvenile rainbow trout that may be due to the linkage of the transferrin locus with a gene or gene complex affecting growth (Reinitz 1977). The association of resistance to BKD with transferrin genotype may also be due to a gene linkage; if so, transferrin serves only as a marker. McIntyre and Johnson (1977) observed higher growth rates and better survival in AA than in AC transferrin genotypes of Big Creek coho salmon. While the frequency of the C allele is high in the Alsea stock, that frequency is depressed in a mixed population at Big Creek where Alsea coho salmon have been used to supplement the broodstock (J. D. McIntyre unpubl. data). Although BKD selects for the C allele in the Alsea coho salmon, the advantage of this allele is offset by some other more important selective factor, such as growth rate, within the Big Creek stock.

It is also conceivable that transferrin genotypes provide resistance to different diseases, or not at all—as with vibriosis. The ability to synthesize iron chelators—compounds necessary to remove iron from transferrin—is considered a virulence factor for certain pathogens (Arnold et al. 1977). Perhaps the iron chelators of *V. anguillarum* remove iron from transferrin more efficiently than do those of BKD bacteria. This more efficient removal would explain to some extent the lack of differential resistance to vibriosis among genotypes within both coho salmon and steelhead trout stocks. Pratschner (1978) observed differential resistance among transferrin phenotypes to vibriosis and several other diseases in coho salmon from the Skagit River, Wash. The AA phenotype exhibited greater susceptibility to vibriosis and cytophagosis but greater resistance to furunculosis while the CC phenotype was most resistant to vibriosis and very susceptible to furunculosis and cytophagosis. The disparity between Pratschner's and our results with respect to vibriosis may be due to the stock-specific nature of transferrin. Possibly differences among transferrin genotypes are more significant in a chronic disease such as BKD, and less so in an acute disease such as vibriosis—or perhaps the rapid death rate following exposure to *V. anguillarum* compressed the results too much to allow differences to be observed. Because of the short time span involved to vibriosis infections, the benefit of such differences to individual fish would be negligible.

Keeping in mind such considerations as selection for transferrin genotypes by different factors such as growth or disease, it becomes clear (as with stocks) that selectively breeding for certain transferrin genotypes would not be advisable. Though selection for one particular genotype might provide resistance to BKD, it might also entail lower growth rates or even greater susceptibility to other diseases. McIntyre (1977) cautiously recommended selective breeding for disease resistance only in propagated fish being held under

carefully controlled conditions or when one particular pathogen is a recurrent problem. Otherwise, it seems advisable to maintain variability in a stock to meet the demands of a variable environment.

LITERATURE CITED

ARNOLD, R. R., M. F. COLE, AND J. R. MCGHEE.
1977. A bactericidal effect for human lactoferrin. Science (Wash., D.C.) 197:263-265.

BALAKHNIN, I. A., AND N. P. GALAGAN.
1972. Distribution and survival rate of individuals with different transferrin types among carp offspring from various combinations of parents. Hydrobiol. J. 8(3):41-45.

EHLINGER, N. F.
1977. Selective breeding of trout for resistance to furunculosis. N.Y. Fish Game J. 24:25-36.

EVELYN, T. P. T.
1977. Immunization of salmonids. *In* Proceedings from the International Symposium of Diseases of Cultured Salmonids, April 4-6, 1977, p. 161-176. Tavolek, Inc., Seattle, Wash.

FRYER, J. L., J. S. NELSON, AND R. L. GARRISON.
1972. Vibriosis in fish. *In* R. W. Moore (editor), Progress in fishery and food science, p. 129-133. Univ. Wash. Publ. Fish., New Ser. 5.

FRYER, J. L., J. S. ROHOVEC, G. L. TEBBIT, J. S. MCMICHAEL, AND K. S. PILCHER.
1976. Vaccination for control of infectious diseases in Pacific salmon. Fish Pathol. 10:155-164.

GJEDREM, T., AND D. AULSTAD.
1974. Selection experiments with salmon. I. Differences in resistance to vibrio disease of salmon parr (*Salmo salar*). Aquaculture 3:51-59.

HERSHBERGER, W. K.
1970. Some physicochemical properties of transferrins in brook trout. Trans. Am. Fish. Soc. 99:207-218.

HUTT, F. B.
1970. Genetic resistance to infection. *In* R. H. Dunlop and H. W. Moon (editors), Resistance to infectious disease, p. 1-11. Saskatoon Modern Press, Sask.

LARKIN, P. A.
1972. The stock concept and management of Pacific salmon. *In* R. C. Simon and P. A. Larkin (editors), The stock concept in Pacific salmon, p. 11-15. H. R. MacMillan Lectures in Fisheries, Univ. B.C., Vancouver.

LEITRITZ, E., AND R. C. LEWIS.
1976. Trout and salmon culture (hatchery methods). Calif. Dep. Fish Game, Fish Bull. 164, 197 p.

MCINTYRE, J. D.
1977. Heritable tolerance of disease in salmonids. *In* Proceedings from the International Symposium on Diseaaes of Cultured Salmonids, April 4-6, 1977, p. 87-90. Tavolek, Inc., Seattle, Wash.

MCINTYRE, J. D., AND A. K. JOHNSON.
1977. Relative yield of two transferrin phenotypes in coho salmon. Prog. Fish-Cult. 39:175-177.

PRATSCHNER, G. A.
1978. The relative resistance of six transferrin phenotypes of coho salmon (*Oncorhynchus kisutch*) to cytophagosis, furunculosis, and vibriosis. M.S. Thesis, Univ. Washington, Seattle, 71 p.

REINITZ, G. L.
1977. Tests for association of transferrin and lactate dehydrogenase phenotypes with weight gain in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 34:2333-2337.

RIDGWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS.
1970. Polymorphism in the esterasea of Atlantic herring. Trans. Am. Fish. Soc. 99:147-151.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods, 6th ed. Iowa State Univ. Press, Ames, 593 p.

SNIESZKO, S. F.
1957. Disease resistant and susceptible populations of brook trout (*Salvelinus fontinalis*). *In* J. C. Marr (coordinator), Contributions to the study of subpopulations of fishes, p. 126-128. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 208.

SNIESZKO, S. F., C. E. DUNBAR, AND G. L. BULLOCK.
1959. Resistance to ulcer disease and furunculosis in eastern brook trout, *Salvelinus fontinalis*. Prog. Fish-Cult. 21:111-116.

SUZUMOTO, B. K., C. B. SCHRECK, AND J. D. MCINTYRE.
1977. Relative resistance of three transferrin genotypes of coho salmon (*Onchorhynchus kisutch*) and their hematological responses to bacterial kidney disease. J. Fish. Res. Board. Can. 34:1-8.

WALES, J. H., AND W. BERRIAN.
1937. The relative susceptibility of various strains of trout to furunculosis. Calif. Fish Game 23:147-148.

WEINBERG, E. D.
1974 Iron and susceptibility to infectious disease. Science (Wash., D.C.) 184:952-956.

WOLF, L. E.
1954. Development of disease-resistant strains of fish. Trans. Am. Fish. Soc. 83:342-349.

ZINN, J. L., K. A. JOHNSON, J. E. SANDERS, AND J. L. FRYER.
1977. Susceptibility of salmonid species and hatchery strains of chinook salmon (*Oncorhynchus tshawytscha*) to infections by *Ceratomyxa shasta*. J. Fish. Res. Board Can. 34:933-936.

REMARKS ON SYSTEMATICS, DEVELOPMENT, AND DISTRIBUTION OF THE HATCHETFISH GENUS *STERNOPTYX* (PISCES, STOMIATOIDEI)

JULIAN BADCOCK[1] AND RONALD C. BAIRD[2]

ABSTRACT

Sternoptyx pseudodiaphana Borodulina is reported from the eastern North Atlantic in sympatry with *S. diaphana*, providing conclusive evidence that the former represents a species distinct from *S. diaphana*. Patterns of geographic variation among various characters are apparent in species of *Sternoptyx* as is allometric growth. These patterns render species identification difficult in certain allopatric populations, particularly those from the Atlantic and Pacific Oceans. Each species has distinct patterns of horizontal and vertical distribution and where species occur in sympatry, their centers of abundance do not coincide. Members of the genus *Sternoptyx* inhabit the "lower mesopelagic depth zone" (sensu Baird) from 500 to 1,500 m. Geographic variation in depth of maximum abundance for various species can be demonstrated. These appear correlated with variations in temperature and light although competitive interactions may also contribute to observed depth ranges. Photophore development is similar in the three species described and postlarval individuals of *S. diaphana* and *S. pseudodiaphana* are readily distinguishable. Characters useful in distinguishing the various species are presented in relation to patterns of geographic variation.

A single ancestral species which gave rise to the four presently recognized species, each exhibiting slight morphological divergence, is advanced as a parsimonious initial hypothesis of evolutionary relationship.

The genus *Sternoptyx* has, until recently, been thought to contain but a single polymorphic species (Schultz 1961, 1964). However, Baird (1971), and more recently Haruta and Kawaguchi (1976), have demonstrated the validity of three morphologically similar species, *S. diaphana* Hermann, *S. obscura* Garman, and *S. pseudobscura* Baird, each with broad but distinct geographic ranges. Baird (1971) also noted a morphologically distinct population of *S. diaphana* from the subtropical convergence region of the South Pacific. In view of the degree of character similarity and lack of sympatry with other populations of *S. diaphana*, he considered his data insufficient to substantiate the Southern Ocean form as a distinct species. Borodulina (1977) subsequently described the Southern Ocean form as *S. pseudodiaphana* and has recently published a synopsis of the hatchetfish genera *Argyropelecus* and *Sternoptyx* based on Russian collections (Borodulina 1978).

Sternoptyx pseudodiaphana from the eastern tropical Atlantic occurs in sympatry with *S. diaphana*. Our new data provide conclusive evidence that *S. pseudodiaphana* represents a species distinct from *S. diaphana*. Patterns of geographic variation are not well known in deep-sea fishes and patterns occur in the genus *Sternoptyx* which tend to obscure species distinctions among certain allopatric populations. Characters found useful in distinguishing among various species and populations are presented which complement and expand the treatments of Baird (1971) and Borodulina (1978). We describe metamorphic and postlarval development for various species and include comparisons among species. Additional data on the geographic and vertical distribution of the genus, including information from discrete-depth trawling studies, are presented which add considerably to our knowledge of the distribution of this widespread group of mesopelagic fishes.

METHODS

All four species of *Sternoptyx* were examined. The material and its sources are listed in Appendix Table 1. The specimens were fixed in Formalin[3] and preserved either in alcohol (70% ethyl or

[1]Institute of Oceanographic Sciences, Wormley, Godalming, Surrey, U.K. Authorship alphabetical.
[2]Department of Marine Science, University of South Florida, St. Petersburg, Fla.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted June 1979
FISHERY BULLETIN VOL 77, NO 4, 1980

40% isopropyl) or in aqueous storage fluid (10% propylene glycol, 1% Formalin, 0.5% phenoxytol, based upon Steedman 1974). Generally, specimens were taken by various open midwater nets; however, a number of samples were taken with opening/closing nets of various designs (Clarke 1969; Baker et al. 1973; Hopkins et al. 1973).

Photophore Nomenclature

The unique pattern of photophore clustering in the family Sternoptychidae (sensu Baird 1971) has resulted in a different system of nomenclature from that used for other stomiatoid families (Figure 1). Weitzman (1974) suggested a revised nomenclature for stomiatoid taxa to include the hatchetfishes and for convenience, both appear in Table 1 (Weitzman's slightly modified). The distinct and unusual specializations in external morphology in the hatchetfishes (sensu Baird 1971) make determinations of homology among photophore groups difficult. We regard the new terms, therefore, as a convenience rather than as suggestions of homologies between similarly named photophore groups throughout the Stomiatoidei. For instance the preorbital photophore (PO) of the genus *Sternoptyx* differs from that of either *Argyropelecus* or *Polyipnus* morphologically, and probably functionally, and is perhaps more aptly termed an oral organ (Herring 1977). Nevertheless, for convenience, the term PO (ORB of Weitzman) is retained.

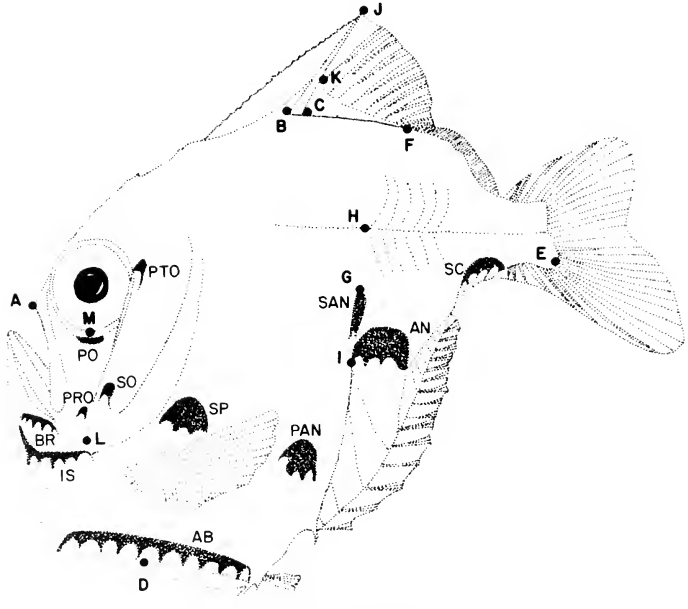


FIGURE 1.—Nomenclature of photophores and basic measurements for *Sternoptyx* spp.

TABLE 1.—Photophore development of *Sternoptyx pseudodiaphana* and *S. diaphana*, expressed in stages. Asterisk denotes earliest stage for photophore group completion; parentheses indicate photophore nomenclature in Baird 1971.

Stage	SL range (mm)	Number of photophores per photophore group (each side)											No. of specimens
		OP$_2$ (SO)	ORB (PO)	BR (BR)	PV (AB)	IP (I)	OV (SP)	OP$_1$ (PTO)	AN (AN)	VAV (PAN)	SC (SC)	OP$_1$ (PRO)	SAN (SAN)	
						S. pseudodiaphana eastern North Atlantic								
1	10.0-10.2	1*	1*	2	6	3-4	2	1*	0	0	0	0	0	2
2	8.3- 9.7	1	1	2	8- 9	4	3*	1	1	0	0	0	0	2
3	7.6- 9.2	1	1	2	8-10*	4	3	1	1	1	0	0	0	5
4	7.9-10.0	1	1	2	10	4-5*	3	1	2	1-2	1-2	0	0	14
5	9.8-10.5	1	1	3*	10	5	3	1	3*	3*	2	0	0	2
6	9.5-11.1	1	1	3	10	5	3	1	3	3	2-3	1*	0	13
7	11.2-14.1	1	1	3	10	5	3	1	3	3	3	1	1*	22
8	[1]13.0?16.2	1	1	3	10	5	3	1	3	3	4*	1	1	
						S. pseudodiaphana southeastern Pacific								
2	6.5- 8.4	1	1	2	7- 8	4	3	1	1	0	0	0	0	3
4	7.6- 9.6	1	1	2	8-10*	4-5*	3	1	1-2	1-2	1-2	0	0	12
6	9.6- 9.9	1	1	3	10	5	3	1	3*	2-3*	1-2	1	0	2
7	9.7-14.3	1	1	3	10	5	3	1	3	3	2-3	1	1	7
						S. diaphana western North Atlantic								
2	7.0	1*	1*	2	8	4	3*	1*	1	0	0	0	0	1
3	7.0- 7.6	1	1	2	9-10*	4	3	1	1-2	1-2	0	0	0	7
4	7.6- 8.3	1	1	2	9-10	4-5*	3	1	2	2	1-2	0	0	4
5	7.8- 9.4	1	1	2-3*	10	5	3	1	2-3*	3*	2	0	0	6
6	8.8-10.5	1	1	3	10	5	3	1	2-3*	3*	2	1*	0	11
7	9.8-13.2	1	1	3	10	5	3	1	3	3	2-3	1	1*	22
8	[1]12.8?13.6	1	1	3	10	5	3	1	3	3	4*	1	1	

[1]Smallest observed size
[2]All specimens equal or larger have all photophores

In this account, where reference to a particular photophore within a group is made, numbering is in an anteroposterior direction (e.g., AB(PV) 10 is the posteriormost photophore pair).

Measurements and Counts

The peculiar morphology of marine hatchetfishes has necessitated a number of modifications to measurements commonly used to describe teleost fishes. While most of those used here have been described by Baird (1971), it is difficult to precisely determine reference points in the genus *Sternoptyx*. All measurements used here are defined as the shortest distance between two stated points. Standard length (SL) in juveniles and adults was measured to the nearest 1 mm, but in postlarvae, to the nearest 0.1 mm. Other measurements of all specimens were taken to 0.1 mm. Measurements were as follows (letters refer to points on Figure 1):

Standard length (SL): from the tip of the snout (A) to the furthermost extension of the caudal peduncle (E);

Body depth: from the dorsal blade origin (B) to the midpoint of the ventral body margin (D);

SAN photophore depth: from the dorsalmost point (G) of the photophore SAN to the dorsal body margin (F) at the base of the posteriormost dorsal ray;

Midline height: from the anteroventral edge (I) of the photophore group AN to the trunk midline of horizontal septum (H) on a line passing through the photophore SAN;

SAN photophore height: from the anteroventral edge (I) of the photophore group AN to the dorsalmost point (G) of the photophore group SAN;

Trunk depth (TD): from the posterior end of the dorsal fin base (F) to the anteroventral edge (I) of the photophore group AN;

Trunk length: from the point of the trunk midline defined by the midline height measurement (H) to the posteriormost extent of the caudal peduncle (E);

Photophore lengths (AN and SC): the distance between the farthest extensions of the darkly pigmented photophore margins;

Dorsal fin base: from the origin of the first (K) to that of the last (F) dorsal ray;

Dorsal blade height: from the dorsal body margin (C) to the blade tip (J), along blade axis;

Orbital diameter: the length of the longest orbital axis (fleshy orbit);

Suborbital length: from the midventral point of the orbit (M) to the tip (L) of the preopercular spine.

It was not possible for one person to measure or take counts on all the specimens examined. The results obtained, however, were in good agreement, although it is inevitable that some variation

expressed may have been due to the individual measurer. All postlarval measurements and comparisons were made by one person (i.e., SL <18 mm). The postlarval phase was considered concluded at the attainment of a full complement of pigmented photophores (ca. 14-18 mm), at which stage individuals were classified as subadults. Meristic counts were made in accordance with Baird (1971) and vertebral counts included all separated vertebrae with the exception of the urostylar complex.

SYSTEMATIC REMARKS

Species Distinction

Morphological distinctions among species of *Sternoptyx* are relatively slight and distinctive characters tend to be obscured in allopatric populations, making identification difficult in the absence of other species. As an aid to the identification of specimens with a full complement of photophores (ca. 18 mm SL), the distinctive species characteristics reported by Baird (1971), Haruta and Kawaguchi (1976), and Borodulina (1978) are combined and expanded in relation to observed patterns of geographic variation. Characters used in distinguishing the four species are discussed below and each species is illustrated (Figures 2-5). Selected meristic and morphometric data are presented in Tables 2 and 3. Table 4 provides a synopsis of characters useful in differentiating adults and subadults.

The genus can be divided into two morphological groups or species pairs. In one, containing *S. pseudodiaphana* (Figure 2) and *S. diaphana* (Figure 3), the AN photophores completely fill the anal fin base, the horizontal part of the ventral body margin extends very little posterior to AN, and the posterior anal fin pterygiophores are relatively short. The second group, with *S. obscura* (Figure 4) and *S. pseudobscura* (Figure 5) is characterized by species having an appreciable extension of the horizontal part of the ventral body margin posterior to AN, long posterior anal fin pterygiophores, and smaller AN and SC (Table 3).

Within these two groups, species may be readily separated from one another, albeit more through a combination of characters than by virtue of a single one. *Sternoptyx pseudodiaphana* and *S.*

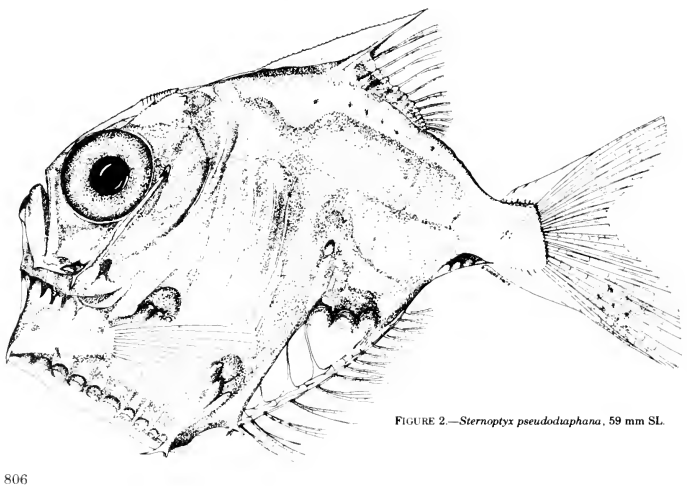


FIGURE 2.—*Sternoptyx pseudodiaphana*, 59 mm SL.

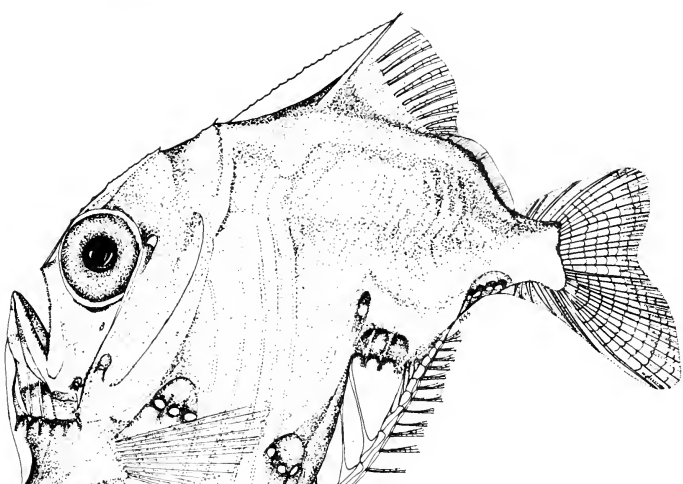


FIGURE 3.—*Sternoptyx diaphana*, 32 mm SL.

TABLE 2.—Meristic counts of *Sternoptyx* species.

Species	Vertebral no						Dorsal rays					Anal rays					Gill rakers (1st arch)			
	27	28	29	30	31	32	9	10	11	12	13	12	13	14	15	16	6	7	8	9
S. diaphana[1]	2	30	12	—	—	—	7	7	3	—	—	—	2	9	4	—	2	39	3	—
S. pseudobscura[2]	1	8	19	1	—	—	3	4	3	—	—	—	3	5	2	—	—	18	34	3
S. obscura[3]	—	—	2	8	—	—	3	5	1	—	—	3	7	—	—	—	—	9	4	3
S. pseudodiaphana[4]	—	—	4	40	53	8	4	11	54	53	4	—	1	21	5	1	2	68	11	—
S. pseudodiaphana[5]	—	—	3	20	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. pseudodiaphana[6]	—	—	—	1	21	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[1]Atlantic and Pacific populations represented
[2]Atlantic and central Pacific populations represented
[3]East Pacific populations only
[4]Northeastern and southern Atlantic and southeastern Pacific populations represented
[5]Tropical Atlantic subset (included in 4)
[6]Southeastern Pacific subset (included in 4)

diaphana (>18 mm SL) can be distinguished on the basis of vertebral number 29-32 versus 27-29, respectively, Table 2; see also Borodulina 1978), and the placement of the photophore SAN (described by SAN depth/SL and trunk depth/SAN height, Figures 6, 7) which is appreciably raised in *S. pseudodiaphana*. Overlap of more than one of these three characters in any given specimen was rarely observed. Other differences, most noticeable in sympatric populations, occur in body shape and pigmentation. *Sternoptyx diaphana* is generally deeper in body and especially trunk, appreciably less pigmented, and lacks streaks on the outer ventral caudal fin margin in larger individuals (Tables 3, 4).

Sternoptyx obscura is distinguished from *S.*

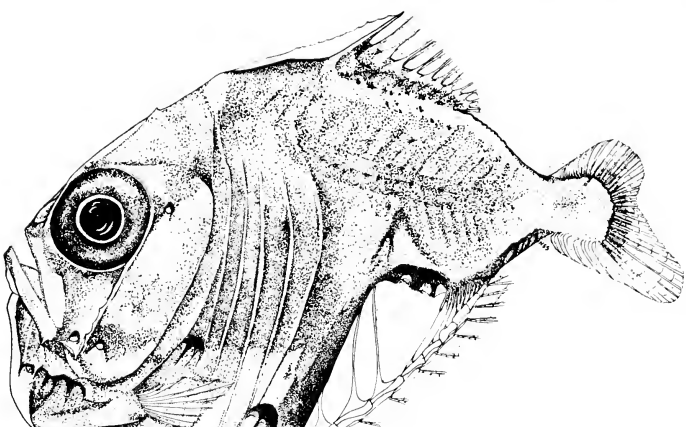


FIGURE 4.—*Sternoptyx obscura*, 39 mm SL.

TABLE 3.—Proportional measurements of *Sternoptyx* species for various size classes.

	11-16 mm SL[1] *S. diaphana*			17-47 mm SL *S. diaphana*			16-55 mm SL *S. pseudobscura*		
Item	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Body depth[2]	85 2	80 8-90 0	7	87 1	75 7-96 7	74	87 4	73 2-96 2	52
AN length[2]	10 1	8 2-11 4	11	12 0	9 4-13 9	58	8 6	5 5-10 5	45
SC length[2]	5 5	4 2-6 4	6	7 3	5 9-11 2	55	5 3	3 8-6 7	41
SAN depth[2]	29 8	28 3-31 8	10	33 2	27 0-39 7	88	20 8	14 4-30 7	66
Trunk depth[2]	38 0	34 2-40 8	11	44 1	38 3-49 5	88	39 5	33 7-46 7	56
Trunk length[2]	36 1	34 2-38 2	11	36 1	32 0-43 8	86	35 6	27 0-41 5	54
Trunk depth/trunk length	1 05	1 00-1 12	11	1 21	0 94-1 37	86	1 12	0 95-1 33	64
Dorsal base/dorsal blade	—	—	—	0 76	0 56-1 00	72	0 79	0 56-0 94	19
Trunk depth/SAN height	4 4	3 8-6 0	11	3 8	2 9-6 1	86	2 0	1 6-2 5	56
Orbit diameter/suborbital length	0 89	0 83-0 95	11	1 03	0 89-1 21	57	0 85	0 72-1 04	37
	13-17 mm SL[1] *S. pseudodiaphana*			18-61 mm SL *S. pseudodiaphana*			15-40 mm SL *S. obscura*		
Item	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Body depth[2]	78 6	70 1-89 4	27	80 8	70 5-92 6	131	74 9	68 4-82 1	18
AN length[2]	9 8	7 6-11 8	36	11 4	8 8-13 7	120	8 5	6 0-11 1	11
SC length[2]	6 3	5 3-7 6	19	7 6	5 0-11 7	120	5 1	4 0-7 7	11
SAN depth[2]	24 4	22 3-31 8	36	25 3	21 7-33 2	132	22 9	20 3-26 2	18
Trunk depth[2]	35 8	31 4-41 2	36	38 8	33 5-46 6	132	31 6	27 5-35 1	18
Trunk length[2]	37 4	32 9-43 8	36	37 7	33 2-43 4	132	37 7	32 5-42 2	18
Trunk depth/trunk length	0 95	0 83-1 11	34	1 03	0 86-1 24	131	0 83	0 75-0 94	26
Dorsal base/dorsal blade	—	—	—	0 90	0 65-1 12	51	1 14	1 03-1 43	14
Trunk depth/SAN height	2 8	2 3-3 4	32	2 7	2 1-3 4	132	3 6	2 6-5 1	18
Orbit diameter/suborbital length	1 06	0 96-1 21	36	1 07	0 92-1 45	108	1 05	0 89-1 30	10

[1]Subadults
[2]Percent standard length

pseudobscura (and indeed, all other species of *Sternoptyx*) by the narrow shape and configuration of the trunk and also the high dorsal fin base/dorsal blade ratio. The trunk is markedly longer than it is deep, while the dorsal blade height is usually much shorter than dorsal fin base length

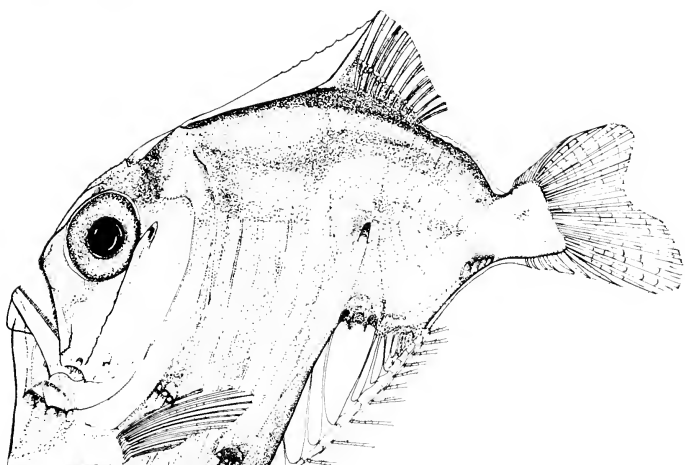


FIGURE 5.—*Sternoptyx pseudobscura*, 54 mm SL.

(Table 3). *Sternoptyx obscura* is further distinguished from *S. pseudobscura* by its lower placement of the photophore SAN and by uniformly dark pigment of body and trunk, as well as the presence of a dark corona along the caudal fin rays, radiating from the fin base.

Geographic Variation

The degree of genetic differentiation and nature of geographic variation in populations of midwater fishes have not been thoroughly explored, though evidence is now accumulating that such variation does exist and may be widespread in species with broad geographic ranges (e.g., Naftaktitis 1968; Baird 1971; Pertseva-Ostroumova 1974; Karnella and Gibbs 1977). Baird (1971) was able to distinguish separate populations in several species of the related hatchetfish genus *Argyropelecus*. Populations tended to remain distinct over time and differences among populations were generally associated with zoogeographic boundaries. The present evidence indicates that similar patterns of geographic variation occur in species of *Sternoptyx*, the extent of which awaits more extensive investigation.

Geographic variation is apparent in both *S. pseudobscura* and *S. pseudodiaphana*. The systematic problems arising from such variation are illustrated in Figures 6 and 7. In addition to the indicated allometry, the suitability of the two character complexes (trunk depth/SAN photophore height and SAN photophore depth) for distinguishing species differs, depending on the populations being compared. Both characters are distinctive among the three species illustrated (*S. diaphana*, *S. pseudodiaphana*, and *S. pseudobscura*) for sympatric populations in the North Atlantic. However, where southeast Pacific populations of *S. pseudodiaphana* are compared with

TABLE 4.—Characters useful in differentiating species of the genus *Sternoptyx*.

Character	*S. pseudodiaphana*	*S. diaphana*	*S. obscura*	*S. pseudobscura*
Anal pterygiophore configuration	No appreciable pterygiophore extension posterior to anal photophores (<18 mm SL)	Similar to *S. pseudodiaphana* (>18 mm SL)	Extension posterior to anal photophores (see Haruta and Kawaguchi 1976)	Similar to *S. obscura* (see Haruta and Kawaguchi 1976)
SAN position	About 3 or less times in trunk depth, not more than 3½ times in subadults	More than 3 times in trunk depth more than 4 times in subadults (< ca 17 mm)	As in *S. diaphana*	About 1½ to 2½ times in trunk depth, raised to midtrunk line in Atlantic populations
Ratio dorsal base to dorsal blade	Dorsal base normally shorter than blade, occasionally about equal to or slightly longer	Dorsal base usually less than 0.9 of blade	Dorsal base longer than dorsal blade	As in *S. pseudodiaphana*
Trunk dimensions	Trunk depth about equal to trunk length, in subadults often less	Trunk depth conspicuously greater than trunk length, in subadults can be equal	Trunk depth conspicuously less than trunk length	Trunk width greater than trunk length
Trunk pigmentation	Dark bar above midline, little pigment near midline	Light in region of midline	Uniformly dark over whole trunk region	Nonuniform dark pigment in trunk region
Caudal fin pigmentation	Light pigment streaks at ventral outermost margin of caudal rays of larger adults (ca 40 mm)	Little or no pigment on caudal rays	Corona of dark pigment spreading from base of caudal fin rays	Dark pigment restricted to innermost margin of caudal fin rays
Pectoral fin pigmentation	Absent in adults, present at ray bases in juveniles and subadults	Not present	Not present	Not present
Vertebral number	30-32, rarely 29	28, occasionally 27 or 29	30, occasionally 29	29, ocasionally 28 or 30
Anal rays	14-15, rarely 13	14-15, occasionally 13	12-13	13-15
Anal photophores	In adults longer than peduncle depth, little horizontal extension of ventral body margin above anal fin	Similar to *S. pseudodiaphana*, anal photophores fill pterygiophore "gap"	Shorter than peduncle depth, body margin extends posteriorly above anal fin	Similar to *S. obscura*
Eye size	Orbit diameter greater than suborbital length, rarely less	Orbit diameter about equal to, often less than, suborbital length	Orbit diameter usually greater than suborbital length	Orbit diameter less than suborbital length, equal to it
Dorsal rays	9-13, usually 11-12	9-11, usually 11	9-11, usually 11	9-11
Maximum size (SL)	60 mm	50 mm	45 mm	55 mm

Atlantic forms of *S. diaphana* the trunk depth character exhibits overlap particularly in smaller individuals. Likewise, while the SAN depth character is distinctive for *S. diaphana* and *S. pseudodiaphana*, there is considerable overlap when Pacific populations of *S. pseudobscura* are compared with *S. pseudodiaphana*. The lower position of the SAN photophore has been illustrated by Haruta and Kawaguchi (1976, figure 6) for western Pacific forms of *S. pseudobscura* and can be compared with the Atlantic form illustrated here (Figure 5). Differences in vertebral number between Pacific and tropical Atlantic forms of *S. pseudodiaphana* are indicated (Table 2) and the character should be useful in distinguishing the Pacific population from *S. obscura*.

Postlarval Development

Characters useful in distinguishing later life stages are often less suitable or ineffective for metamorphosing and postlarval stages or indeed small (<18 mm) subadults. Geographic variation and allometric growth further complicate identification. The present data, while substantiating the presence of both allometry and geographic variation (Table 3; Figure 7), cannot be considered comprehensive and intensive studies of collections from numerous geographic regions are yet to be done. The extension of the ventral trunk margin, size of AN photophore group, and elongate posterior pterygiophores appear to be neotenic characters established from mid- to late-metamorphic stages (Figures 8, 9) and are consequently less useful as species-distinctive characters for early life stages.

When present, the location of photophore SAN is diagnostic, though the placement tends to be somewhat lower on the body in postlarvae. SAN is closely associated with photophores AN in *S. diaphana* and not markedly raised in *S. obscura*. For *S. pseudodiaphana* and *S. pseudobscura* it is vertically separated from the AN group. In Atlantic populations of *S. pseudobscura* the photophore SAN is raised to the midtrunk line, distinguishing it from other congeners. The lower SAN position in Indo-Pacific populations of *S. pseudobscura* make this character less useful in separating it from *S. pseudodiaphana*. The smaller eye (noted by Günther 1887) in *S. pseudobscura* (Table 3) is

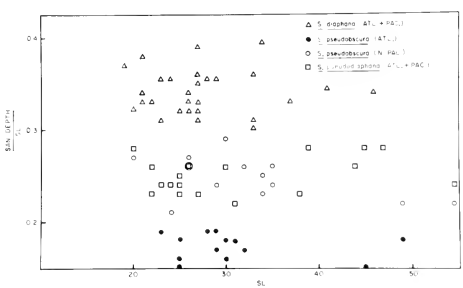


FIGURE 6.—Scattergram of ratio of SAN photophore depth/SL and SL (millimeters) for three species of *Sternoptyx*.

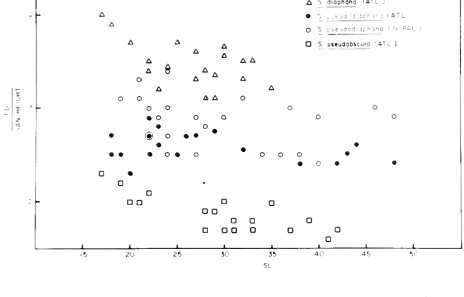


FIGURE 7.—Scattergram of ratio of trunk depth (TD)/SAN photophore height and SL (millimeters) for three species of *Sternoptyx*.

diagnostic while small individuals of the two species may be separated on the basis of pectoral fin ray pigment present in *S. pseudodiaphana*. The young of *S. obscura* are uniformly pigmented and have the characteristically narrow trunk at quite small sizes.

The sequence of numbered "stages" in which photophore groups appear and are completed is listed in Table 1 for *S. pseudodiaphana* and *S. diaphana*. The sequential pattern is identical in both species, and limited data suggest *S. pseudobscura* also conforms to this pattern though the early-metamorphic forms of these species are as yet undescribed. For ease of reference a sequence of stages based on the order of appearance of photophores during development is presented in Table 1. The brief account given below is intended primarily to outline the major anatomical landmarks during metamorphosis and to indicate some of the distinctions among species during postlarval development.

Sternoptyx pseudodiaphana

The least developed specimen observed of *S. pseudodiaphana* from the Atlantic (10.2 mm SL) is elongate, with the head about 25% of SL. Dorsal and pelvic fins are undeveloped, while the pectoral fin has six and the anal seven rays developing. The caudal has 19 rays. The postlarva is relatively transparent and pigment is restricted to certain areas: a symphysial pair of spots, two isthmus spots, the pectoral fin, and a caudal peduncle spot. Internally, the swim bladder is pigmented dorsad, as is the posterior part of the stomach. Meningeal pigment is present both as a melanophore in the

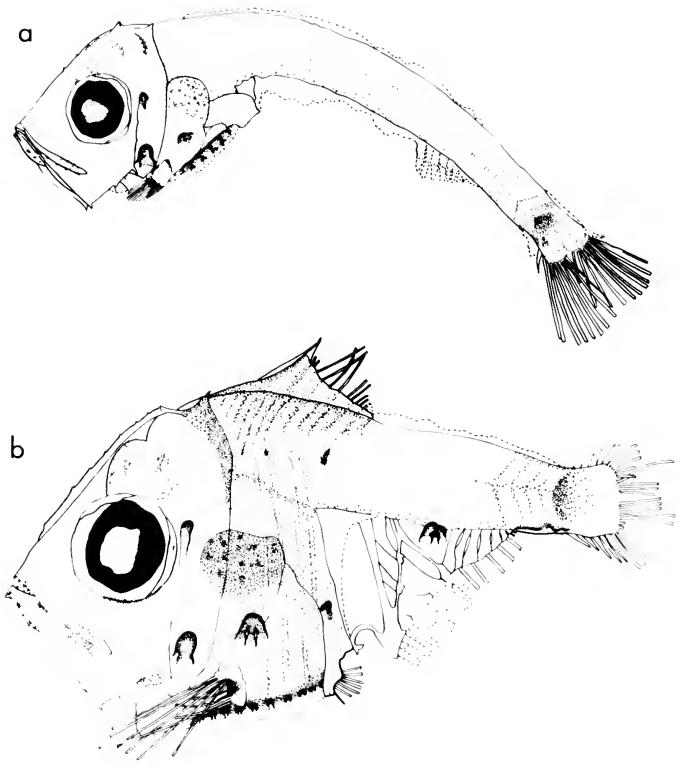


FIGURE 8.—Development of *Sternoptyx pseudodiaphana*: (a) Stage 1, 10.0 mm SL; (b) Stage 4, 8.9 mm SL.

pineal region and as scattered melanophores posterior to it. In the most advanced Stage 1 specimen (Figure 8a) additional pigment occurs anterior to the stomach. Stomach pigmentation is completed by Stage 3 and during this stage new pigment sites develop along the ventral margin of the orbit, in the opercular region, and along the predorsal crest. Light abdominal pigmentation appears during Stage 4 and the caudal pigment extends anteriorly along the dorsum (Figure 8b), reaching the dorsal fin base later in this stage. As development progresses, pigmentation spreads and intensifies

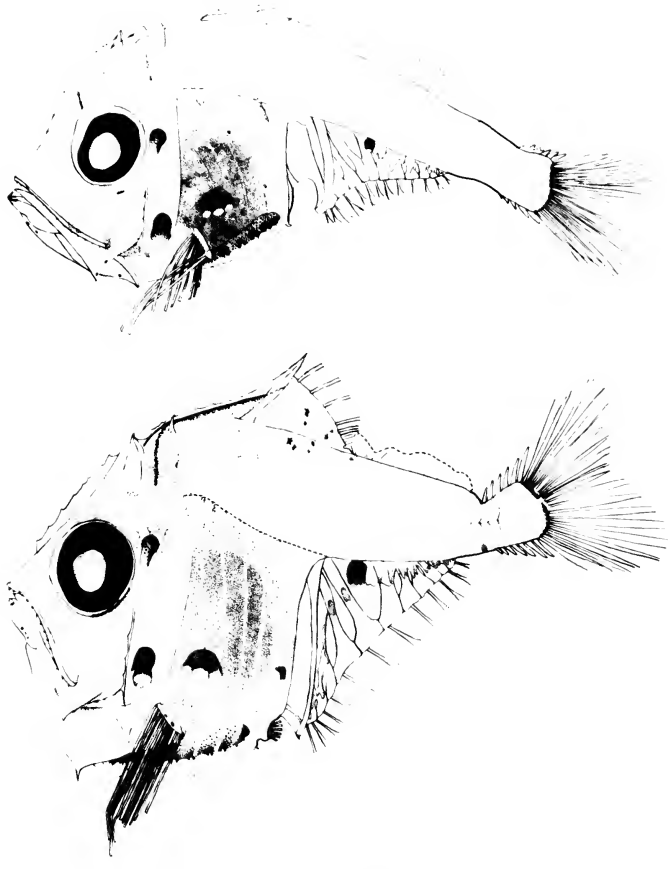


FIGURE 9.—Development of *Sternoptyx diaphana*: (upper) Stage 2, 7.0 mm SL; (lower) Stage 3, 7.2 mm SL.

leading to the adult condition. The rays of the dorsal fin first develop during Stage 3; the rays of the pelvic fin first appear in Stage 4.

A series of *S. pseudodiaphana* taken from the southeastern Pacific (lat. 33°-39° S, long. 80°-120° W) show a similarity in morphology and pattern of development to North Atlantic forms. The data indicate that the sequences of both appearance and completion of the various photophore groups are similar, although the relative timing of completion for certain groups may differ slightly. For example, while the completion of PV in North Atlantic forms apparently occurs prior to the initiation of SC, in southeastern Pacific forms it occurs afterwards (Table 1). Pigmentation in specimens from these two populations is essentially alike, but a small pigment spot located near the posterior end of the dentary in Pacific forms was not noted in the Atlantic material. As in the adults, differences between postlarvae from the two areas, then, does occur.

Slight differences in larval characteristics between populations of the same species have been shown for certain lanternfishes (Pertseva-Ostroumova 1974) and do occur in the genus *Sternoptyx*, differences which we suspect, based on *Argyropelecus*, may be more extensive than indicated here. They can render species differentiation difficult in certain areas. Early-metamorphic individuals of *S. diaphana* and *S. pseudobscura* are superficially similar and in tropical Atlantic collections only late-metamorphic stages can be separated with certainty. Metamorphic individuals of *S. pseudodiaphana*, on the other hand, are highly distinctive. A series of *S. diaphana* taken off Bermuda, an area where *S. pseudobscura* is apparently rare, allowed for some comparison between the midmetamorphic forms of this species and *S. pseudodiaphana*.

The caudal spot so conspicuous in the young of *S. pseudodiaphana* at Stage 1 (Table 1) is found neither in *S. diaphana* nor *S. pseudobscura* prior to completion of photophore development. Pigmentation of the pectoral fin rays has been found in *S. diaphana*, although not consistently, up to Stage 3. At any given stage, *S. diaphana* appears to be in a more advanced state both morphologically and in terms of pigmentation. Thus the configuration of the anal fin pterygiophores attains the juvenile appearance during Stage 3, appearing in Stage 4 in *S. pseudodiaphana*; the pelvic fins differentiate earlier (Stage 3 versus 4), as does the pigmentation of *S. diaphana* in general (Figure 9). Even so, the pigmentation of *S. pseudodiaphana* tends to be denser in the more advanced specimens, which are conspicuous by the dark color of the dorsum. Elbert H. Ahlstrom[4] recognizes three forms of postlarval *Sternoptyx* spp. in his North Pacific collections, none of which bear a caudal melanophore. As populations of *S. pseudodiaphana* are unknown north of the Equator in the Pacific, then, tentatively, postlarval *S. obscura* also lack caudal pigment. *Sternoptyx pseudodiaphana* may, therefore, be distinguished from congeners by this character.

General Comments

During metamorphosis postlarval *Sternoptyx* (ca. 6-14 mm) undergo extensive change from an elongate premetamorphic form to a deep-bodied juvenile. In earlier stages, metamorphic individuals are somewhat shorter than premetamorphic forms, a pattern of apparent loss in length also observed in the related hatchetfish genus *Argyropelecus* (e.g., Brauer 1906; Jespersen 1915; and others). While the sequential pattern of photophore addition appears identical among the species examined, timetables for the differentiation of other external characters do not necessarily coincide. As indicated, *S. diaphana* appears in a more advanced state of morphological differentiation and development than *S. pseudodiaphana* at comparable photophore stages. A similar pattern has been observed by Baird (unpubl. data) among species of *Argyropelecus*. Geographic variation both among and within species is apparent. It appears that there can be appreciable flexibility among species in the timing of photophore addition in relation to the development of other morphological characters, though the adaptive significance of these observations is presently unclear. Growth rate, the functional significance of photophore presence at a given size, and broader ecological considerations such as predation or resource availability, are likely complexly related to patterns of photophore development.

GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION OF *STERNOPTYX* SPECIES

The genus is widespread, occurring in all oceans

[4]E. H. Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. November 1975.

and apparently excluded only from polar seas and the Mediterranean (Jespersen 1915; Geistdoerfer et al. 1970; Baird 1971; Haruta and Kawaguchi 1976; Borodulina 1978). The geographic distributions of the species are presented in Figures 10 and 11 and, when coupled with the recent Russian data (Borodulina 1978), exhibit certain distinct patterns. The species tend to be limited to areas with hydrographically similar characteristics (sensu Baird 1971) and often exhibit mutually exclusive distributions. The horizontal distributions conform in general to zoogeographically distinct regions in the oceans (e.g., Baird 1971; McGowan 1977; Backus and Craddock 1977), the nature and limits of which are only generally defined. From the limited number of observations of vertical distribution in areas of sympatry, species which share the water column tend to have separate depths of maximum abundance.

Sternoptyx obscura is confined to the Indo-Pacific. In the eastern Pacific and Indian equatorial regions, it is the sole representative of the genus. In the periphery of its distribution, it can be relatively abundant (e.g., basins off southern California) and can occur in sympatry with *S. diaphana* and *S. pseudobscura* (Figures 10, 11). In general the geographic distribution resembles that of a number of other species, e.g., *Myctophum aurolanternatum*, *Cyclothone acclinidens*, *Scopelarchoides signifer*, *Rosenblattichthys alatus* (Nafpaktitis and Nafpaktitis 1969; Parin et al. 1973; Johnson 1974; Mukhacheva 1974; Quero 1974; Becker and Borodulina 1976), that are apparent equatorial Indo-Pacific endemics.

Sternoptyx diaphana and *S. pseudobscura* occur in the Atlantic and Indo-Pacific and overlap for much of their ranges (Figures 10, 11). *Sternoptyx pseudobscura*, however, is apparently uncommon in the western North Atlantic and the Caribbean, where *S. diaphana* is abundant, yet it is well represented in the Gulf of Mexico. The occurrence of all three species in Indonesian basin regions is indicative of the zoogeographic complexity of the mesopelagic ichthyofauna of that area.

Sternoptyx pseudodiaphana is widely distributed in the Southern Ocean (see also Borodulina 1978) and associated boundary currents in the Southern Hemisphere (Figure 11). Evidence from other studies (e.g., Alvarino 1965; Gibbs 1968; Krefft and Parin 1972; Nafpaktitis 1973; Mayer 1975; Bertelsen et al. 1976) has indicated that the subtropical convergence area, at least in the South Pacific, is a distinct zoogeographic region with a number of endemic or characteristic species. The occurrence of *S. pseudodiaphana* off South Australia, in the Indian Ocean, and across the South Atlantic between lat. 32°-40° S reinforces the concept that many elements of the subtropical con-

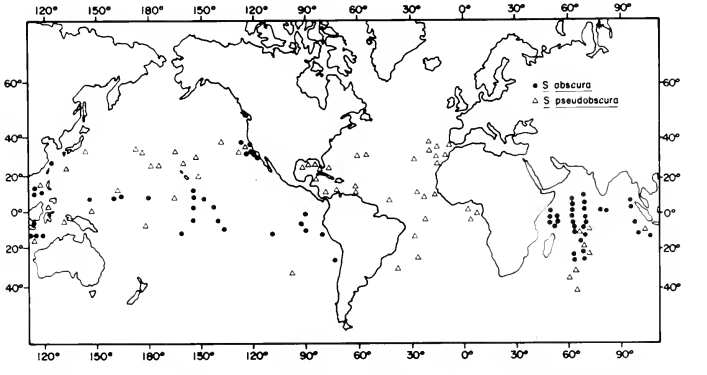


FIGURE 10.—Distribution of *Sternoptyx obscura* and *S. pseudobscura* (also from Baird 1971; Haruta and Kawaguchi 1976).

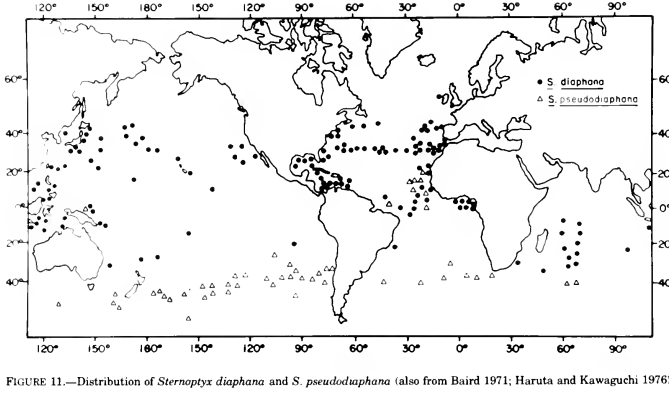


FIGURE 11.—Distribution of *Sternoptyx diaphana* and *S. pseudodiaphana* (also from Baird 1971; Haruta and Kawaguchi 1976).

vergence fauna in the Pacific have circum-Southern Ocean distributions (Craddock and Mead 1970). McGinnis (1974) has presented evidence in support of counterclockwise circulation in the Pacific subantarctic with observed endemism in mesopelagic fishes resulting from zoogeographic isolation of that region. *Sternoptyx pseudodiaphana* from this area can be distinguished from Atlantic forms and the evidence presented here is not in conflict with the McGinnis hypothesis. In the tropical eastern North Atlantic *S. pseudodiaphana* extends as far north as lat. 20° N, long. 21° W (where it exists in sympatry with *S. diaphana*) and it is not unlikely that it occurs in the Gulf of Guinea (Figure 11). Although some specimens have been taken in the Benguela Current area, the general paucity of material at present available from the South Atlantic precludes judgment as to whether a link exists between the North Atlantic and Subtropical Convergence populations. A potentially disjunct distribution, in a manner less extreme than is expressed by *Stomias boa boa* (Gibbs 1969), is given some tentative support by the apparent differences observed between postlarvae from the North Atlantic and South Pacific. Thus it is possible that the North Atlantic population of *S. pseudodiaphana* is a diverging form of the Subtropical Convergence stock. Finally, mention should be made of the single specimen apparently caught near the Philippines. There is no obvious mistake in the station labelling for this individual (*Challenger* Stn. 218). The species range extends considerably northward in the Atlantic and future studies may also confirm a more complex distribution pattern in the Pacific than present data would indicate.

The species of *Sternoptyx* are the deepest dwelling of the marine hatchetfishes and do not exhibit marked diel vertical migration. There are few capture records from opening/closing nets but new data are provided from recent comprehensive surveys (0-2,000 m) at three locations, in the eastern North Atlantic and Gulf of Mexico, where discrete-depth trawls were taken (Hopkins and Baird 1973; Badcock and Merrett 1976). *Sternoptyx diaphana* and *S. pseudobscura* occur sympatrically at all three locations. *Sternoptyx pseudodiaphana* was found only at the eastern Atlantic stations where it was the least abundant species at lat. 18° N but more common at lat. 11° N. Individuals of all species were taken over a broad depth range (ca. 500-2,000 m) but were only abundant over a much more restricted depth zone (Table 5). Thus, *S. diaphana* and *S. pseudobscura*, which have broad areas of sympatry, tend to have distinctly separate zones of maximum abundance while *S. pseudodiaphana*, at the limits of its distribution, is somewhat intermediate and overlaps

TABLE 5.—Range of depths of maximum abundance of species of *Sternoptyx* in sympatry at three locations (subadults and adults) (Hopkins and Baird 1973; Badcock and Merrett 1976).

Species	Lat 27° N, long 86° W	Lat 18° N, long 25° W	Lat 11° N, long 20° W
S. diaphana	600-750 m	600-800 m	500-700 m
S. pseudobscura	850-1,000 m	800-1,500 m	800-1,000 m
S. pseudodiaphana	Not present	600-1,500 m	600-1,000 m

both congeners (Table 5). The shoaling of *Sternoptyx* spp. between lat. 18° N and 11° N is not a function of developmental state and is a feature shown by many species of midwater fishes (Badcock and Merrett 1977).

In other areas of the eastern North Atlantic and also in the Gulf of Mexico where *S. pseudobscura* and *S. diaphana* share the water column, populations of *S. pseudobscura* are always centered below those of *S. diaphana*. Data presented by Baird (1971) indicated that *S. pseudodiaphana* is usually taken in 800-1,200 m depth in the Southern Ocean. Evidence from recent collections from the South Atlantic imply a similar pattern of vertical distribution.[5] In general, then, *S. pseudodiaphana* and *S. pseudobscura* may be regarded as deeper dwelling species of *Sternoptyx* while *S. diaphana* is a shallower living form. In certain areas of the Atlantic, discrete sampling has shown *S. diaphana* to be centered deeper than indicated above (Badcock 1970; Badcock and Merrett 1976; Roper et al.[6]). *Sternoptyx pseudobscura* has been shown to be of low abundance in these areas but the deepening of *S. diaphana* is likely to be a consequence of the sinking of isotherms relative to other areas. The role of competitive interactions among these species is yet undocumented and these may also exert an effect on geographic patterns of vertical distribution. Data on *S. obscura* are not comprehensive, but a preliminary survey of maximum depth of open trawl collections indicate a depth range similar to *S. diaphana* (500-1,000 m) in basins off southern California.

An analysis of the vertical distribution of mid- and late-metamorphic stages in the eastern North Atlantic was possible only for *S. pseudodiaphana* because of the problems in distinguishing between such individuals of the other two species examined. As with subadults and adults, individuals of like developmental stage lay shallower in the water column at lat. 11° N, long. 20° W than at lat. 18° N, long. 25° W (400-800 m versus 500-900 m depth). Although the data are sparse, there is evidence for ontogenetic vertical stratification among metamorphic stages. At lat. 11° N, long. 20° W, Stages 1-3 occurred only in 400-500 m depth; Stage 4 in 400-600 m; Stage 5 in 500-700 m; and Stage 6 in 500-800 m. A similar relationship is implied for metamorphic stages from lat. 18° N, long. 25° W, although stratification occurred deeper in the water column.

CONCLUSIONS

The evidence presented shows *Sternoptyx* to contain four closely related species. Morphological distinctions between them are relatively slight, but are consistent among the populations examined. The four species have broad geographic ranges and the limited data indicate the occurrence of geographic variation in *S. pseudobscura* and *S. pseudodiaphana* at adult and postlarval levels. Thus systematic difficulties arise in that certain characters useful in distinguishing species in sympatry may overlap when measurements from other populations are included.

Characters subject to allometric growth similarly present systematic problems. Nevertheless, most of the morphological criteria used here to separate species are maintained irrespective of population or developmental state. When found in sympatry, distinctions are clear and species consistently separable by many characters.

While we distinguish two species pairs on the basis of anal fin pterygiophore configuration, no hypothesis of cladistic relationship among the species is advanced. Considering the highly specialized and peculiar morphology of the genus (Baird 1971; Baird and Eckhardt 1972; Weitzman 1974; for discussion of family relationships), the most parsimonious hypothesis advanced is that a single ancestral species evolved which diverged considerably from a more generalized hatchetfish stock. Subsequent speciation in the genus probably involved the isolation of populations which now show very slight morphological divergence, exhibit various degrees of geographic variation, and have distinct horizontal and vertical patterns of distribution.

ACKNOWLEDGMENTS

Our thanks go to R. H. Gibbs, Jr. (Smithsonian

[5]G. Krefft, Institut für Seefischerei, Hamburg, West Germany, pers. commun. 1976.

[6]Roper, C. F. E., R. H. Gibbs, Jr., and W. Aron. 1970. Ocean acre: an interim report. Report to the U.S. Navy Underwater Sound Laboratory. Contract No. N00140-69-C-0166. Smithson. Inst., Wash., D.C., 22 p.

Institution), A. C. Wheeler (British Museum, Natural History), R. J. Lavenberg (Los Angeles County Museum), M. M. Dick and K. Leim (Museum of Comparative Zoology), R. H. Backus (Woods Hole Oceanographic Institute), J. Nielsen (Zoologiske Museum, Copenhagen), and G. Krefft (Institut für Seefischerei, Hamburg) and their institutions for making material available. We are also grateful to P. M. David, N. R. Merrett, R. J. Gibbs, Jr., and R. J. Lavenberg for their valuable comments and discussions of the manuscript. Finally, our thanks to R. A. Larcombe and Nancy Smith (illustrations). Partial support was provided by the National Science Foundation under grant DES 75-03845.

LITERATURE CITED

ALVARINO, A.
1965. Chaetognaths. Oceanogr. Mar. Biol. Annu. Rev. 3:115-194.

BACKUS, R. H., AND J. E. CRADDOCK.
1977. Pelagic faunal provinces and sound-scattering levels in the Atlantic Ocean. *In* N. R. Andersen and B. J. Zahuranec (editors), Oceanic sound scattering prediction, p. 529-547. Plenum Press, N.Y.

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the Sond cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BADOCK, J., AND N. R. MERRETT.
1976. Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog. Oceanogr. 7:3-58.
1977. On the distribution of midwater fishes in the eastern North Atlantic. *In* N. R. Andersen and B. J. Zahuranec (editors), Oceanic sound scattering prediction, p. 249-282. Plenum Press, N.Y.

BAIRD, R. C.
1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (family Sternoptychidae). Bull. Mus. Comp. Zool. Harv. Univ. 142:1-128.

BAIRD, R. C., AND M. J. ECKHARDT.
1972. Divergence and relationship in deep-sea hatchetfishes (Sternoptychidae). Syst. Zool. 21:80-90.

BAKER, A. DE C., M. R. CLARKE, AND M. J. HARRIS.
1973. The N.I.O. combination net (RMT 1+8) and further developments of rectangular midwater trawls. J. Mar. Biol. Assoc. U.K. 53:167-184.

BECKER, V. E., AND O. D. BORODULINA.
1976. Taxonomy and distribution of the lanternfishes of the genus *Myctophum* (materials to the revision of the genus). [In Russ.] Tr. Akad. Nauk. SSSR Inst. Okeanol. 104:113-143.

BERTELSEN, E., G. KREFFT, AND N. B. MARSHALL.
1976. The fishes of the family Notosudidae. Dana Rep. Carlsberg Found. 86, 114 p.

BORODULINA, O. D.
1977. A new species, *Sternoptyx pseudodiaphana* Borodulina (Sternoptychidae, Osteichthyes) from waters of the southern hemisphere. [In Russ.] Vopr. Ikhtiol. 17:938-941.
1978. Materials on the systematics and distribution of the oceanic hatchetfishes genera *Argyropelecus* and *Sternoptyx* (Sternoptychidae, Osteichthyes). [In Russ.] Tr. Akad. Nauk. SSSR Inst. Okeanol. 3:27-59.

BRAUER, A.
1906. Die Tiefsee-Fische I. Systematischer Teil. Wiss. Ergeb. Dtsch. Tiefsee-Exped. Dampfer VALDIVIA, 1898-99. 15:69-122.

CLARKE, M. R.
1969. A new midwater trawl for sampling discrete depth horizons. J. Mar. Biol. Assoc. U.K. 49:945-960.

CRADDOCK, J. E., AND G. W. MEAD.
1970. Midwater fishes from the eastern South Pacific Ocean. Scientific Results of the SE Pacific Exped. Anton Bruun, Rep. 31:1-46.

GEISTDOERFER, P., J. C. HUREAU, AND M. RANNOU.
1970. Liste Préliminaire des espèces de poissons de profondeur récoltées au cours de la Compagne Noratlante de N. O. "Jean Charcot" en Atlantique Nord (Août-Octobre 1969). Bull. Mus. Natl. Hist. Nat., Bot. Ser. II, 42(6):1177-1185.

GIBBS, R. H., JR.
1968. *Photonectes munificus*, a new species of melanostomiatid fish from the South Pacific subtropical convergence, with remarks on the convergence fauna. Los Ang. Cty. Mus. Contrib. Sci. 149:1-6.
1969. Taxonomy, sexual dimorphism, vertical distribution and evolutionary zoogeography of the bathypelagic fish genus *Stomias* (Stomiatidae). Smithson. Contrib. Zool. 31:1-25.

GUNTHER, A.
1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873-1876. Rep. Sci. Results Voyage H.M.S. Challenger 22, 335 p.

HARUTA, C., AND K. KAWAGUCHI.
1976. Taxonomy and geographical distribution of the fishes of the genus *Sternoptyx* (family Sternoptychidae) from the western North Pacific Ocean. [In Jpn., Engl. summ.] Jpn. J. Ichthyol. 23:143-152.

HERRING, P. J.
1977. Oral light organs in *Sternoptyx* with some observations of biolumineacence in hatchetfishes. *In* M. V. Angel (editor), A voyage of discovery, p. 553-567. Deep-Sea Res. 24 (Suppl.)

HOPKINS, T. L., AND R. C. BAIRD.
1973. Diet of the hatchetfish *Sternoptyx diaphana*. Mar. Biol. (Berl.) 21:34-46.

HOPKINS, T. L., R. C. BAIRD, AND D. MILLIKEN.
1973. A messenger-operated closing trawl. Limnol. Oceanogr. 18:488-490.

JESPERSEN, P.
1915. Sternoptychidae (*Argyropelecus* and *Sternoptyx*). Report of the Danish Oceanographic Expedition to the Mediterranean. II. Biology A2:1-41.

JOHNSON, R. K.
1974. A revision of the alepisauroid family Scopelarchidae (Pisces, Myctophiformes). Fieldiana, Zool. Mem. 66, 249 p.

KARNELLA, C., AND R. H. GIBBS, JR.
1977. The laternfish *Lobianchua dofleini*: an example of the importance of life-history information in prediction of oceanic sound scattering. *In* N. R. Andersen and B. J.

Zahuranec (editors), Oceanic sound scattering prediction, p. 361-379. Plenum Press, N.Y.

KREFFT, G., AND N. V. PARIN.
1972. Ergebnisse der Forschungsreisen des FSS "Walther Herwig" nach Sudamerika. XXV. *Diplophos rebaini* n. sp. (Osteichthyes, Stomiatoidei, Gonostomatidae), a new gonostomatid fish from Southern Seas. [In Engl., Germ. summ.] Arch. Fischereiwiss. 23:94-100.

MAYER, G. F.
1975. Results of the research cruises of FRV "Walther Herwig" to South America. XXXIX. The epigonine fauna of the South Atlantic, with a key to the genera and a redescription of *Rosenblattia rubusta* Mead and De Falla. [In Engl., Germ. Abst.] Arch Fischereiwiss. 26:13-28.

MCGINNIS, R. F.
1974. Counterclockwise circulation in the Pacific subantarctic sector of the Southern Ocean. Science (Wash., D.C.) 186:736-738.

MCGOWAN, J. A.
1977. What regulates pelagic community structure in the Pacific? *In* N. R. Andersen and B. J. Zahuranec (editors), Oceanic sound scattering prediction, p. 423-443. Plenum Press, N.Y.

MUKHACHEVA, V. A.
1974. Cyclothones (genus *Cyclothone*, fam. Gonostomatidae. Pisces) of the World Ocean and their distribution. *In* T. S. Rass (editor), Ichthyoplankton, deep-sea fishes and squids of the tropical waters of the World Ocean. [In Russ.] Tr. Akad. Nauk. SSSR Inst. Okeanol. 96:189-254.

NAFPAKTITIS, B. G.
1968. Taxonomy and distribution of the laternfishes, genera *Lobianchia* and *Diaphus*, in the North Atlantic. Dana Rep., Carlsberg Found. 73, 131 p.
1973. A review of the laternfishes (family Myctophidae) described by Á. Vedel Tåning. Dana Rep., Carlsberg Found. 83, 46 p.

NAFPAKTITIS, B. G., AND M. NAFPAKTITIS.
1969. Laternfishes (family Myctophidae) collected during Cruises 3 and 6 of the R/V *Anton Bruun* in the Indian Ocean. Bull. Los Ang. Cty. Mus. Nat. Hist., Sci. 5, 79 p.

PARIN, N. V., V. E. BECKER, O. D. BORODULINA, AND V. M. CHUVASSOV.
1973. Bathypelagic fishes of the South-Eastern Pacific and adjacent waters. [In Russ., Engl. summ.] Tr. Akad. Nauk. SSSR Inst. Okeanol. 94:71-172.

PERTSEVA-OSTROUMOVA, T. A.
1974. New data on laternfish larvae (Myctophidae, Osteichthyes) with oval eyes from the Indian and Pacific Oceans. [In Russ., Engl. summ.] Tr. Akad. Nauk. SSSR Inst. Okeanol. 96:77-142.

QUERO, J. C.
1974. *Cyclothone pseudoacclinidens* sp. nov. Poissons, Clupeiformes, gonostomatides espèce nouvelle de L'Atlantique. Rev. Trav. Inst. Pêches Marit. 38:449-457.

SCHULTZ, L. P.
1961. Revision of the marine silver hatchetfishes (family Sternoptychidae). Proc. U.S. Natl. Mus. 112:587-649.
1964. *Family* Sternoptychidae. *In* Y. H. Olsen (editor), Fishes of the western North Atlantic, Part four, p. 241-273, Mem. Sears Found. Mar. Res. 1.

STEEDMAN, H. F.
1974. Laboratory methods in the study of marine zooplankton. A summary report on the results of the Joint Working Group 23 of SCOR and UNESCO 1968-1972. J. Cons. 35:351-358.

WEITZMAN, S. H.
1974. Osteology and evolutionary relationships of the Sternoptychidae with a new classification of stomiatoid families. Bull. Am. Mus. Nat. Hist. 153:329-478.

APPENDIX TABLE 1.—Materials and their sources of *Sternoptyx* spp.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
S. pseudodiaphana	1	BMNH	H.M.S. *Challenger*	159	47°25' S, 130°22' E	BMNH 87.12.7.151
	1			218	02°33' S, 144°04' E	BMNH 87.12.7.157
	6		RRS *Discovery II*	81	32°45' S, 08°47' W	BMNH 1930.1.12.43035
	1			85	33°08' S, 04°30' E	BMNH 1930.1.12.441
	3			86	33°25' S, 06°39' E	BMNH 1930.1.12.552-5
	2			256	34°14' S, 06°49' E	BMNH 1930.1.12.411-12
	4			269	15°55' S, 10°35' E	BMNH 1930.1.12.413-15
	15		RRS *Discovery* (45)	7824	11°01' N, 20°11' W	BMNH 1977.6.14.1-15
	1	IFS	*Walther Herwig*	30/68	36°37' S, 43°30' W	
	8			427/71	33°00' S, 07°50' E	
	50	IOS	RRS *Discovery* (31)	6662	10°58' N, 20°00' W	
	18			7089	17°50' N, 25°25' W	
	22			7803	17°50' N, 25°00' W	
	48			7824	10°50' N, 20°00' W	
	21	LACM	*Eltannin*	1781	39°42' S, 130°11' W	
	41			1812	36°36' S, 87°09' W	
	27			1835	42°23' S, 160°14' E	
	1	MCZ	*Anton Bruun* (3)	160	40°53' S, 60°01' E	
	1		(6)	7351	40°51' S, 64°49' E	
	1		(13)	5	34°26' S, 73°28' W	
	11			6	32°57' S, 74°57' W	
	3			10	33°32' S, 77°56' W	
	3			16	33°36' S, 79°32' W	
	2			20	34°01' S, 84°58' W	
	2			41	33°31' S, 77°29' W	
	1		*Chain* (35)	962	05°24' N, 39°55' W	

APPENDIX TABLE 1.—Continued.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
	2	USNM	*Eltanin* (21)	3	34 00' S, 80 36' W	207241
	19			5	33 06' S, 83 57' W	207243
	18			6	33 04' S, 85 49' W	207234,207235
	5			8	33 00' S, 89 38' W	207236
	7			11	37 12' S, 94 24' W	207233
	7			11A	38 35' S, 95 39' W	207227
	4			13	39 54' S, 107 36' W	207240
	3			15	44 03' S, 120 17' W	207239
S. diaphana	2	BMNH	H.M.S. *Challenger*	171	28 33' S, 177 50' W	BMNH 87 12 7 152-3
	1			214	04 33' N, 127 06' E	BMNH 87 12 7 155
	1	CAS	*Te Vega*	548	35 39' N, 131 53' W	
	13	IOS	RRS *Discovery* (21)	6662	10 58' N, 20 22' W	
	18		RRS *Discovery* (45)	7803	17 50' N, 25 00' W	
	35			7824	10 55' N, 20 00' W	
	51		RRS *Discovery* (52)	8281	32' N 64 W	
	1	LACM	*Valero*	11360	33 20' N, 118 45' W	
	1	MCZ	*Anton Bruun* (6)	7247	07 56' S, 65 14' E	
	2			7298	22 48' S, 64 55' E	
	2			7305	24 22' S, 64 50' E	
	1			7352	29 45' S, 64 58' E	
	5		(19)	824	19 01' N, 79 02' W	
	2			829	19 21' N, 85 31' W	
	1		*Chain* (26)	505	12 00' N, 65 00' W	
	4		*Delaware* (63-4)	31	NW Atlantic	
	6	MSI	*Bellows* (1)	147	27 00' N 86 00' W	
	3		*Mizar* (3)	166	27 36' N 88 40' W	
S. obscura	1	BMNH	H.M.S. *Challenger*	214	04 33' N, 127 06' E	BMNH 87 12 7 156
	1	CAS	*Te Vega*	532	36 40' N, 122 04' W	
	1			620	32 48' N 118 16' W	
	1	IOS	*Manihine* (226)		W Equatorial Indian Ocean	
	3	LACM	*Eltanin*	34	07 47' S, 81 23' W	10203
	1		*Valero*		33 20' N, 118 45' W	11360
	10	MCZ	*Anton Bruun* (6)	7194	03 27' N, 65 07' E	
	10	UANM	*Eltanin* (31)	7A	10 57' N, 149 19' W	
	20	SIO	*Monsoon*		11 00' N 163 00' E	
	11		*Tethys*		07 00' S, 135 00' W	
	25	ZMUC	*Galathea*		10 24' S, 114 07' E	
S. pseudobscura	1	BMNH	H.M.S. *Challenger*	214	04 33' S, 177 06' E	BMNH 87 12 7 154
	1			235	37 07' N, 138 00' E	BMNH 87 12 7 158
	7	IOS	RRS *Discovery* (21)	6662	10 58' N, 20 00' W	
	5		(45)	7803	17 50' N, 25 00' W	
	20			7824	10 55' N, 20 00' W	
	2		*Manihine* (226)		W Equatorial Indian Ocean	
S. pseudobscura	1	MCZ	*Anton Bruun* (6)	7237	05 55' S 65 10' E	
	5			7303	24 03' S, 64 50' E	
	1		(13)	24	33 48' S, 90 19' W	
	13			829	21 25' N 85 30' W	
	1		*Chain* (35)	978	20 00' S 28 04' W	
	3		*Delaware* (63-4)	15	NW Atlantic	
	17	MSI	*Bellows* (1)	142	27 00' N 86 00' W	
	7	SIO	*Horizon*	51375	31 53' N, 152 21' W	
	6		*Monsoon*	56133	12 40' N, 165 09' W	

[1]BMNH—British Museum of Natural History, London; CAS—California Academy of Sciences, San Francisco; IFS—Institut fur Seefischerei, Hamburg; IOS—Institute of Oceanographic Science, Wormley, Surrey; LACM—Los Angeles County Museum, Los Angeles, Calif.; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MSI—Department of Marine Science, University of South Florida, St. Petersburg, Fla.; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; SIO—Scripps Institute of Oceanography, La Jolla, Calif.; ZMUC—Zoologiske Museum Copenhagen, University of Copenhagen, Copenhagen.

BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*

KENNETH S. NORRIS AND THOMAS P. DOHL[1]

ABSTRACT

The Hawaiian spinner dolphin, *Stenella longirostris*, was recorded from Kure Atoll to the island of Hawaii. It enters atoll lagoons or specific coves or swims over shallow sandy areas, usually near deep water, to rest. Access to nighttime feeding grounds may regulate the location of these rest areas. Rest areas are generally 50 meters or less in depth.

Natural scars and marks allowed study of movements and school structure. Schools are fluid assemblages of variable size and composition. Only small subgroups within schools may have long-term integrity.

Spinner dolphins exhibit several aerial patterns including spinning which is mostly associated with sound production upon reentry, and each is typical of a specific school activity level. Sounds may serve as omnidirectional sound sources maintaining school cohesion beyond the limits of vision.

The daily cycle of spinner dolphins consists of nighttime feeding, morning approach to shore, morning-midday rest, and travel to feeding grounds near dusk. Feeding is upon scattering layer fishes, squid, and shrimp.

Dolphins very commonly show scars from large sharks and from the small squaloid shark, *Isistius brasiliensis*, which scoops disc-shaped pieces of blubber from them. These wounds heal to form dollar-shaped scars.

Most that is known in any depth about the behavior of dolphins has come from observations of captive animals. Yet the environment of captivity, which is at best a pool a few dozen meters in longest dimension and 5 or 10 m deep, can allow only certain aspects of normal behavior to occur. Intragroup relationships may persist, but are usually distorted because relationships seldom remain intact. At best only hints of normal movement and activity patterns can persist where feeding schedules are determined by the workdays of trainers. In nature spinner dolphins, at least, travel constantly, even during rest. Dolphins of many species dive and feed in very deep water.

Thus, however difficult it might be, the naturalist who would study dolphin behavior feels the need to study them in nature. It is usually no simple task. They are wary and travel many kilometers in a day. The presence of the observer almost inevitably causes bias. Dolphins hear exceedingly well, and dolphin schools may be aware of an approaching ship a kilometer or more away.

Our first 2-yr effort (1968-69), with a spotted, or "kiko," dolphin, *Stenella attenuata*, school which we knew to frequent the area within a few kilometers of Kaena Point, Oahu, Hawaii, was abandoned for the reasons mentioned above. It simply proved too expensive in time, money, and effort to work with the animals. Our work was never free from observer bias. Reports of a school of the spinner dolphin, *Stenella longirostris*, (Schlegel 1841), living permanently in Kealakekua Bay, on the Kona or lee coast of the island of Hawaii, caused us to visit the area to see if work was feasible. We found an unusual situation in which several vexing observational problems were ameliorated.

Spinner dolphins do occur in Kealakekua Bay frequently (our figures indicate occupancy about 74% of the time). The bay itself is remarkably good for observation. The Kona coast is normally quite calm, especially in morning hours. Lateral visability is usually 20 m or more. The local people seldom disturb the dolphins. Only cruise boats, which seek out the schools and run through them, are a predictable disturbance. An abrupt 150 m lava cliff backs the bay. Schools sometimes came close to the cliff base at places where our visibility was blocked and could not be seen from the clifftop. But, most of the time we could watch wholly undisturbed schools at reasonably close range, although the distance proved too long for individual identification, and the lack of contrast between animal

[1]Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064

Manuscript accepted June 1979.
FISHERY BULLETIN: VOL. 77, NO. 4, 1980

and background defeated good photography. Finally, the bay is relatively small, 3.2 km across its mouth and indented about 2.5 km deep. Its entire area was visible from the clifftop, and usually visibility was good enough that one could see schools well beyond its confines (Figure 1).

These unusual circumstances allowed us to gather new information about spinner dolphin behavior, especially about the diurnal cycle and patterns of movement, though some difficult observational problems remain.

Spinner dolphins proved exceptionally interesting, observational subjects. Not only do they "spin" or leap from the water and revolve rapidly around their longitudinal axis, but they also perform other aerial behavior that can be observed from a considerable distance. These bits of aerial behavior and the sequence in which they occurred proved to be a key to what one might call the emotional or activity level of the school. This level in turn is closely correlated with a number of features of dolphin life, especially the regular sequence of activities during a daily cycle. Aerial behavior, once understood, becomes a predicator of daily activity patterns.

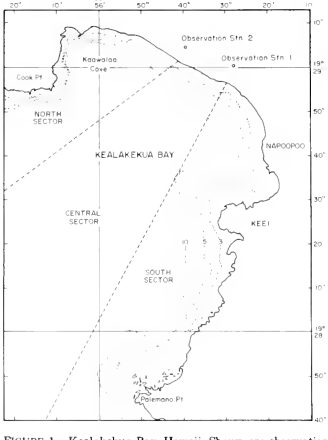


FIGURE 1.—Kealakekua Bay, Hawaii. Shown are observation posts on cliff that backs the bay, shallow-water areas (in meters), and approximate areas frequented by resting schools of spinner dolphins. Also indicated are arbitrary bay sectors used in analysis of arrival and departure directions.

This work, performed in 1970-73, represents a beginning analysis of natural spinner dolphin behavior, a field still in its infancy. Previous reports of the behavior of wild dolphin schools have been mostly single or very fragmentary observations (see Norris and Dohl in press for a review). A few detailed studies exist and allow comparison with this work, such as the work performed by Saayman and Tayler (1971); Saayman, Bower, and Tayler (1972); Tayler and Saayman (1972); and Saayman, Tayler, and Bower (1973), and more recently by Würsig and Würsig (1977); Shane (1977); Würsig (1978); Wells et al. (in press). Saayman and Tayler have analyzed the daily movements of the bottlenose dolphin, *Tursiops aduncus*, and the Indopacific humpback dolphin, *Sousa teuszii*, and their feeding formations and strategies for fish crowding and capture. Würsigs' studies concentrated on Argentinian populations of *Lagenorhynchus obscurus* and *T. truncatus*, while Wells et al. work dealt with *T. truncatus* in Florida.

There are parallels in these works with the behavior patterns described here. The recent work by the Würsigs on the group size, composition, and stability of bottlenose dolphin schools bears similarity. Like ours, much of this work was performed from clifftop observation posts using natural scars and marks to identify individuals. Shane's study, also on bottlenose dolphins, utilized natural scars and marks. Wells et al. carried out extensive tagging studies on Florida bottlenose dolphins. All of these studies and that reported here show remarkable fluidity in school composition and size over short periods of time. The dolphin populations that have been studied, it seems, are not composed of discrete schools of modest size but instead of highly fluid groups that may range considerable distances and may be found associated in very variable combinations of individual animals.

Morphology

Hawaiian spinner dolphins are moderate-sized, slim-bodied, and long-beaked odontocete cetaceans. Adults reach at least 2 m TL (total length), and about 55-62 kg (Perrin 1975). They are handsomely marked animals with a dark gray cape over the dorsal surface, a light gray lateral field (using the terminology of Perrin 1972) sharply demarcated from the cape above, and the white

belly below. The white of the belly extends up the flanks to about the level of the eye. The beak, or rostrum, is dark gray, tipped prominently with black; the lip margins are dark; and the ventral surface of the beak is white. The pectoral fins are dark gray, and a dark flipper band connects its anterior insertion to the eye, which is surrounded by a black eyepatch. Flukes and dorsal fin are dark gray. These color pattern components have been described in more detail by Perrin (1972), and they have been compared with the patterns of geographical forms of spinner dolphins living in the eastern tropical Pacific. In nature, against the blue or turquoise backdrop of tropical water, the dark pattern components of spinner dolphins appear in shades of brown, but the effect is usually lost when the animals are removed from the water. The white and other pattern marks are often suffused with pink, from superficial blood flow in the blubber, which may also contribute to the overall brownish cast of pattern components in living spinners.

Systematics

In recent years a worldwide picture of the distribution and systematics of tropical odontocetes has begun to emerge. Well-documented collections, often with measurements and photographs, have been made from all oceans, especially where dolphins are involved in fishery operations (Kasuya et al. 1974; Perrin 1975). A special beneficiary of this work has been the once chaotic genus *Stenella*. It now seems reasonably clear that the genus is composed largely of three major species or species complexes: the spinner dolphins, allied to *S. longirostris* of the Hawaiian Islands; the striped dolphin, *S. coeruleoalba;* and the spotted dolphins, allied to *S. attenuata* of the Hawaiian Islands. All are tropical or subtropical. All are often found far offshore or near islands.

In the eastern and central Pacific, Perrin (1975) discerned four geographical forms of spinner dolphins: 1) a Costa Rican long-snouted form occurring close to the Central American coast, 2) an eastern form occupying the open sea from the American coast out to long. 115°W, 3) a whitebelly form occupying the open ocean both south and west of the eastern form (and overlapping with it to some extent) to about long. 145° W and nearly to lat. 5° S, and 4) an Hawaiian form localized around the Hawaiian island chain. Perrin (1975) stated that Hawaiian spinner dolphins are most closely related to the adjacent whitebelly form, differing from them by being somewhat more robust, by having a larger area of white belly coloration, and by lacking the speckled margins of the white belly field. He places the complex tentatively in the species *S. longirostris*.

Most of the races of spinner dolphins from around the world are quite similar to the Hawaiian form. Only the Costa Rican and eastern forms are strikingly different, being nearly uniform gray, with faint hints of pattern components found in other races. These aberrant forms also show remarkable sexual dimorphism, which is otherwise rather subtle throughout the species. Fully adult males of these two races often possess a dorsal fin that is canted sharply forward, "like it was stuck on backward," and a very heavy postanal protuberance. The fin of Hawaiian spinner dolphins is either triangular or very slightly falcate, and only a subtle postanal protuberance can be noted in adult males.

METHODS

A camp was established on the Greenwell Ranch at the edge of the cliff overlooking Kealakekua Bay (Figure 1). Two observation sites were used for recording and observation by telescopic means. Observer teams kept regular watches during daylight hours.

Several vessels were used for observations at sea, or to provide an anchored platform in the bay, including the brigantine *Westward* and the motor sailers RV *Hikino* and the RV *Imua*. A trip through the northwest Hawaiian chain was made on the U.S. Coast Guard buoy tender *Buttonwood*.

Fourteen spotting flights were made throughout the main Hawaiian chain, mostly from small fixed wing aircraft.

Underwater observations were made in a specially built underwater observation vehicle or mobile observation chamber (MOC) 6 m long, which looked like a small submarine (Figure 2) but did not submerge. It consisted of a float made from an auxiliary aircraft gasoline tank and a central observation chamber. The viewer in this chamber below water obtained ventilation from a squirrel cage blower and was surrounded by a band of Plexiglas[2] windows at eye height. Controls for turning or tilting the craft were at hand, and a

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

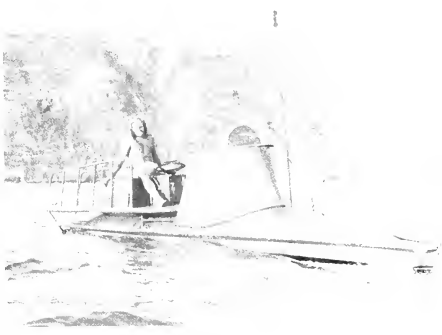


FIGURE 2.—Mobile observation chamber (MOC) at Kealakekua Bay. The hatch is open to a cylindrical observation chamber that projects 1.5 m below the hull. The observer views through a 360° band of Plexiglas windows. The operator steers and operates the engine.

tape recorder was connected to a hydrophone[3] mounted amidships and oriented forward.

The craft was run by an outboard engine set in a well aft. Stability was maintained by 900 kg of lead blocks in a compartment below the observers feet.

Other underwater observations were made with scuba, or by putting an observer with snorkle or scuba below the bow of a slowly moving skiff, holding onto a bow painter. In this way the observers could sometimes be towed among the animals and even be jostled by them. A field station was established at the village of Napoopoo on Kealakekua Bay.

Feeding was observed from skiffs and larger vessels. Dip net samples were taken in the region of feeding, and stomach analysis of such specimens as became available to us were collected. The squid and crustaceans in stomach samples were identified by Richard Young of the Department of Oceanography, University of Hawaii. Fish otolith collections were lost through improper preservation.

Recordings were made with a hydrophone deployed from a stationary skiff located near a school of animals or from the MOC. Monitoring was by use of headphones. During our studies we were fortunate to have William Schevill and William Watkins of the Woods Hole Oceanographic Institution establish a four-hydrophone array deep in Kealakekua Bay. With this apparatus, three-dimensional tracks of passing dolphins were obtained that were of greater range and fidelity than allowed by our simple gear. The experimental arrangement of this array and recording characteristics are described in Watkins and Schevill (1974).

Dolphin radiotracking used dolphin dorsal fin radios (see Evans 1974) and a hand-held direction finder. Dolphins were captured by a standard head net.

Throughout this paper we use the term "school" to indicate all animals in a discrete area that move together. Such schools are often composed of recognizable, discrete "groups" of animals clustered together and moving and diving more or less in unison. For instance, while the direction of movement of larger schools may be the same for all its parts, diving synchrony for all animals may be quite extended and ragged, being composed of a number of synchronously diving groups. Within such groups one can sometimes recognize small "subgroups" of a few (2 to perhaps 12) animals that are often seen together, regardless of the group or school composition around them.

DISTRIBUTION

Marine mammal collectors of the Sea Life Park, an Hawaiian oceanarium, suggested that spinner dolphins occur habitually at certain areas along the island shores, while they are largely or wholly

[3]An Atlantic Research Corporation LC 32 hydrophone, a Hewlett-Packard 466A preampifier, and a Uher 4000s ¼-in tape recorder composed the recording gear. The upper frequency response of this system was approximately 20 kHz at 7½ ips.

absent from others. This led us to collect sighting and capture locations for the entire Hawaiian chain. The same collectors reported that after collection of animals from a given school, the school as a whole might become shy of the boat for an indefinite period, and suggested that it occupied a given area of coast and the school might have integrity through time.

We found that spinner dolphins occur throughout the Hawaiian chain, from its northwesternmost limit at Kure Atoll (lat. 25°40′ N, long. 175°38′ W) to its southernmost limit at South Point, or Ka Lae, on the island of Hawaii (lat. 18°49′ N, long. 155°41′ W). Occurrence is not random, but spinner dolphins are gathered in small to moderate schools (6 to about 250 animals) near all major islands and shoal areas and can be found with some regularity near certain shoals or coves. Only near small islands that drop abruptly without having significant shoals, such as at Nihoa Island, have we not found spinner dolphins. The following is a synopsis of known spinner distribution. Unless otherwise specified, all sightings were by the authors. Specific records are shown in Figure 3.

Kure Atoll. On 3 September, 1971, Norris visited Kure Atoll. The commanding officer, Lt. (j.g.) Joel Greenberg, reported having seen a school of 20-30 spinner dolphins enter a west pass into the atoll lagoon. Without prompting he described their spinning behavior.

Midway Island. On the midafternoon of 3 September 1971, a school of approximately 35 spinner dolphins was noted in shallow water at the edge of the channel inside of Eastern Island. The regular daytime occurrence of animals in the shallow atoll lagoon was reported to us by residents of Midway.

French Frigate Shoals. On 12 September 1971, at 0830 h, 30 animals were noted just off Shark Island, spinning and leaping.

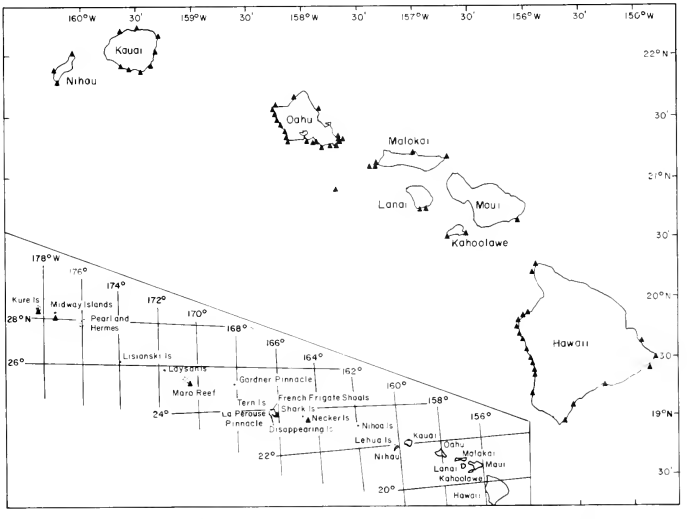


FIGURE 3.—Sightings of spinner dolphin schools by the authors (triangles) in the Hawaiian Island chain.

Pearl and Hermes Reef. Edward Shallenberger reported seeing a spinner dolphin school at this location in the fall of 1978, entering the central lagoon during the day.

Necker Island. On 13 September 1971, 10.2 mi east-southeast of Necker Island at 1600 h, a school of about 30 spinner dolphins was seen.

The following localities in the northwest Hawaiian chain were visited without seeing spinner dolphins; Salmon Bank, Lisianski Island, Laysan Island, Gardner Pinnacles, and Nihoa Island. Five to 10 animals that may have been spinner dolphins were seen 18.5 mi, 134° T from the wreck at Maro Reef, by Ens. Albert Sarra, U.S. Coast Guard, on 9 September 1971.

Niihau Island. Spinner dolphins have been sighted at Kaumuhonu Bay (60 + animals) at the southwest tip of the island, between Lehua Island and Kikepa Point (20 + animals); smaller schools (15 + each) have been noted along the southeast shore near Pueo Point and on the northwest shore at Nonopapa. The Nonopapa record was of a traveling school that moved close to shore along perhaps half of the northwestern coast.

Kauai Island. Spinner dolphin schools were found around Kauai Island at 3-16 km intervals, except along its western coast. The largest schools were estimated at 150 animals on the Napali coast, a 70-80 animal school just north of Kahala Point, and an estimated 60 animal school between Hanapepe and Kaumakani. Smaller schools, scattered along the south and east coasts, averaged about 15-30 animals. The only obvious difference between the vacant coast and the occupied areas is that vacant areas have much narrower, shallow water shelves devoid of deep indentations in the coastline.

Oahu Island. Records from the various sources over 14 yr (1962-76) show that two broad areas of the coast are nearly always occupied by spinner dolphin schools during the day. First, along the Waianae coast between Barber's Point and the vicinity of Kaena Point (the west or Kona shore), schools estimated between 30 and 100 animals can nearly always be found close to shore during the day. Second, an apparently larger school or schools is often seen in the coastal area between about Pearl Harbor and Makapuu Point. Schools of animals seen in this area have been estimated to number from 40 to 250 individuals. Small schools have been seen near Kahana Bay and Waimea Bay. Because this is the windward coast, subject to almost constant tradewinds, little collecting effort has been expended there and dolphins may be more common than our records indicate. A relatively narrow shelf (1.6 km) exists along the Waianae coast except at Kaena and Barber's Points where it broadens considerably. The shelf around the remainder of the island is much broader, averaging about 4 km, and is marked on the northwest and northeastern coasts by a fringing reef.

Molokai-Lanai-Kahoolawe-Maui. Geologically this four-island complex has resulted from one series of volcanic eruptions, producing islands with interconnnecting shallow areas and channels. Spinner schools have been seen at several locations around the margins of this complex, but seem rather seldom to travel to inshore locations over extensive shallow areas such as that at Lahaina Roads (Auau Channel) or over the flats between Molokai and Lanai Islands (Kalohi Channel). Dolphin schools in such areas would have to travel 11 km or more from deep water to reach these shorelines.

Large spinner schools have been seen over Penguin Bank (between western Molokai and Lanai Islands), the south coast of Lanai, especially near Manele Bay (40-100 animals), and along the south shore of Kahoolawe, especially near Halona Point; small schools were seen on the north Molokai shore at Kalaupapa and Cape Halawa, along the Hana coast of Maui, and at Lipoa Point on the northwest end of Maui. Two records of spinner dolphins accompanying humpback whales near Lahaina were reported to us. The bottlenose dolphin, *Tursiops* sp., has often been seen with these whales.

Hawaii Island. Spinner dolphin schools have been found at scattered locations around the entire periphery of the island except for the northeast shore, though there are some shorter stretches of coast where we have never seen schools. It is not surprising, in view of the large size of this island, that there are more localities of regular occupancy by porpoise schools than for any other island. We found seven areas of regular occupancy and four localities with more transient occupancy.

On the lee side of Hawaii, the largest school was centered at Keahole Point, ranging along about 23 km of coast, from Honokohau Harbor to Kiholo Bay. In all, there are estimated to be about 200-250 animals generally occurring in this area, and they may be found in a single school at times or fragmented into two or three smaller schools, separated by a few kilometers of coastline. Here, the dolphins do not seem to occupy any of the small coves consistently, but to congregate over the rather extensive area of shallow water, moving back and forth. Not uncommonly, parts of this aggregation moved during the day beyond the limits listed above and may move as far as Kailua-Kona or beyond, though the constant sea traffic in that harbor seems to prevent normal daily quiescence (defined below). We have termed these animals collectively the "North Kona School." Twenty-eight kilometers to the south, at Kealakekua Bay, a school ranging from 2 to 70 animals (average 25 animals over 73 observations) was found. In our observations, dolphins occurred in this bay on 74% of 113 observation days. They most commonly occupied the deeply indented bay but sometimes were found on the shallow area north of the bay to Keauhou or occasionally nearly to Kailua-Kona. Less commonly they were found to the south in or near the very small bays at Honaunau (City of Refuge) or Hookena.

The entire 56 km stretch from Hookena to South Point seems not to harbor spinner dolphin schools on a regular basis, though it should be noted that a military air closure zone prevented our flying over the Milolii area regularly. We have a single record of a 20 animal school at Milolii. This precipitous coast drops abruptly into deep water, without shallow areas alongshore. Much of the coast is composed of relatively new lava flows from nearby Mauna Loa volcano.

Small schools, estimated generally at about 20 animals, were seen, usually in very rough water, at South Point, between Ka Lae and Honuapo, over the modestly developed shallow area there, or occasionally in the deep cove at Kaalualu.

At Keauhou Cove, directly below Kilauea Crater, a small school (20-25 animals) was consistently found. The dolphins came into very shallow water there in an area protected by Keaoi Islet and flanking coral heads, which produce a small area of calm water along an otherwise rough water coast.

Cape Kumukahi, the easternmost point on the island, hosted a population of about 30 animals. Several small irregular bays along the southern edge of the cape form the "home bay" in this area, with animals being noted at times as far as Opilukao Cove.

The largest school on the windward shore (ca. 100 animals) was often found at Kaloli Point, 18 km south of Hilo Bay. This location seemed also to be the northernmost area of occupancy on this side of the island. The dolphins were typically found in the bay protected by the point and fringing coral reefs. The rather shallow bay (maximum depth 20 m) is close to deep water to the south.

The 112 km stretch of coast from Kaloli Point to the north end of the island (Upolu Point) seemed devoid of resident spinner dolphin schools. It is also the site of the major sugar cane processing plants on the island. Effluent from these plants seems to produce murky waters along the coast and clearly contributes to the long drift lines of flotsam from processed sugar cane. Whether the absence of animals and this activity are related is unknown.

At the north tip of Hawaii we occasionally saw or heard of small schools of spinner dolphins (10-30 animals) in the area between Kawaihae Bay and Honoipu, though more often the entire stretch of coast was found to be without animals from the Kiholo Bay to the north tip at Upolu Point. This circumstance is anomalous, in that well-developed, shallow-water areas occur along this shore, where schools might come during the day, and where the sea is generally calm.

REST AREAS

Three features of the distribution of spinner dolphins in the Hawaiian chain stand out. First, the distribution is discontinous. Some coasts may have several areas where dolphins congregate, and others may have stretches of many kilometers in extent where no amimals are seen. Second, certain coves or shallow areas are clearly regular aggregation sites, while others seem to be used much more infrequently. Third, some areas consistently carry more animals than others. As we will demonstrate, spinner dolphins come inshore during daylight hours to enter a quiescent period of some hours duration, and we think of these congregation sites alongshore as "rest areas."

What typifies such rest areas? First, all rest areas are shallow sandy areas with <50 m depth over part of their extent. They are usually com-

posed of a mixture of open sandy bottom dotted with coral formations. Coves may or may not be present. All rest areas are close to deep water. Usually water >500 m depth can be reached within a few kilometers. Some schools, such as those in the Waikiki (Oahu) or Manele Bay (Lanai) areas, have access to considerably shallower water than others. Schools living there may be restricted to waters no deeper than about 600 m since our observations on the Kona coast of Hawaii indicate that schools do not move more than a few kilometers from shore at night. Other schools, such as at Keahole Point (Hawaii) regularly move into water >2,000 m depth. Of course, the observations we have made on the island of Hawaii may not hold elsewhere.

Apparently spinner dolphins only occasionally travel onto extensive shallow areas like that at Lahaina Roads (Auau Channel), which is about 24 km long. Instead they typically congregate along its margins, along the south shore of Lanai Island and Kahoolawe Island, where deep water is nearby. The areas most closely studied here are Kealakakua Bay and Keahole Point, both have deep water accessible within 1.5-2.5 km of shore. The inference is that rest areas are chosen by dolphins not only for physical characteristics such as depth, bottom type, and perhaps calm water but also for their accessibility to nighttime feeding areas.

Spinner dolphin schools also rest in atoll lagoons. At Kwajalein Atoll, on 10 September 1973, at 1630, a school of about 40 spinner dolphins was noted about 1 km inside Bigej Pass. The school was moving toward the pass, presumably on its way out to sea. A local resident told us that the school was regularly in this pass and not found in other nearby passes into the central lagoon. Similar observations have been made at Kure Atoll, Midway Atoll, and near Shark Island at French Frigate Shoals. The animals (approximately 35), resting quietly in a shallow channel not far inside Eastern Island at Midway, were sighted from a helicopter. Probably wherever atolls and spinner dolphins occur together the animals use the atoll lagoons for rest.

In the eastern tropical Pacific a large spinner dolphin population occupies oceanic areas far from land. In view of the use of shore situations elsewhere in the range of the species, one wonders what, if any, substitution is made. Norris and Dohl (in press) have speculated that the frequently observed association between spinner and spotted dolphins in the eastern tropical Pacific (this association does not occur in Hawaii) may hold the answer. Spinner dolphins may seek the schools of spotted dolphins for refuge during rest in the open sea. We believe this may be true because spotted dolphins feed during the day, while spinners are nocturnal feeders, and spinner dolphin schools have been observed to join spotted dolphin schools in the morning (Norris et al.[4]). If such rest association occurs, the spinner dolphins are associating with alert animals in this oceanic area. Related to this the yellowfin tuna seine fishermen chase and encircle dolphins to catch tuna, most fish apparently follow the spotted dolphins. Since the association between tuna and dolphin is probably food based, the tuna may be following the dolphin species that is actively searching for food. That is, like the tuna, the spinner dolphin may follow active dolphin schools.

Spinner dolphins resting along shores maintain a continuous but slow locomotion, and it seems likely that the searching or feeding activities of spotted dolphins would not greatly change these requirements for rest.

MARKED ANIMAL STUDIES

Dolphin schools are seen frequently at the same localities while other areas never seem to harbor them. Are these schools of resident animals, or are they composed of transients that for some reason choose certain regions of the coast for rest? The frequent observation of dolphin collectors that a given school will avoid their vessel after animals have been collected from it (Norris and Prescott 1961) indicates possible residency. On the other hand, dolphin schools are not always in these rest localities, and the number of animals using a given cove may vary widely from day to day. This indicates fluidity in school structure and variability of school movement. Such fluidity has been noted for other porpoise schools by Würsig and Würsig (1977) and Saayman and Tayler (1979).

Because we were concerned that the spinner dolphins of the Kona coast of Hawaii should not fear our vessel, we sought to recognize individuals by natural scars and marks rather than by placement of tags. Ultimately we were able to catalog 50 recognizable individuals and resight-

[4]Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna industry-preliminary studies. Natl. Tech. Inf. Serv., Final Rep. No. MMC76/12 PB 283-970, xi + 86 p.

ings provided a partial picture of the school and individual movements. Our shipboard work with dolphin schools was restricted almost wholly to Kealakekua Bay through most of 1970. Only toward the end of that year and during 1971 and to a limited extent later, much sea time was spent in other areas. Hence a large proportion of our sightings do not bear on the question of dispersal distances or rates by individual dolphins. We gathered no information on possible interisland movements.

By far the most useful scars and marks were those of the dorsal fin. Twelve of our animals were in this category (Figure 4). These animals could be resighted from shipboard, and sometimes from considerable distances. It is not surprising that 49, (64%) of our 76 resightings were of these animals.

Many marked animals had scars or pattern peculiarities. Such marks could only be sighted on dolphins at the bow of the observation vessel, or from our MOC. The MOC was used sparingly because it was noisy and disturbed dolphin schools and because it was safe only in calm seas. Thus, information on repeated social associations within schools is limited to two sets of sightings and journal notes over 14 days, all within Kealakekua Bay. In any school only a few individuals swam at the bow of a vessel, while others stayed well clear, thus reducing the chances of sighting many animals. Of 38 animals cataloged with body scars or marks, there were 27 resightings. The final marked animal recorded was an individual with a vertical white stripe on its dorsal fin (Figure 4).

Our store of recognizable animals built up slowly over the entire period of the study, thus making interpretation of movements difficult; nonetheless, some important ideas emerge: 1) No resident school permanently and regularly uses a given cove or local region of shoreline. Instead, each cove or resting spot may harbor a given subgroup of dolphins for a matter of days or weeks. 2) Schools are labile mixtures of groups and subgroups. 3) Individual movements may span the entire Kona coast, or even beyond (true ranges of movement remain unknown). A few "marked" individuals have been seen over rather long periods, but other equally recognizable animals have been seen only briefly, or never again

FIGURE 4.—Spinner dolphin with vertical white stripe on both sides of its dorsal fin. We suspect that this animal had shed a radio pack after the pin had migrated out of the fin.

after an initial sighting, suggesting either rapid population turnover or high levels of intermixing between the various schools of the area.

Two pale animals were seen. They were very different visually from their associates. This was especially evident from the air. They were seen along the entire southern Kona coast from Keahole Point to Kamilo Point east of Ka Lae (South Point) and over the longest time span for any "marked" animals (1,220 days out of the total 1,246-day recording period). These pale animals were seen either alone or on occasion together in the same school. These data are suggestive only, because such pale coloration cannot be assigned definitely to a given animal since it is a recurrent condition in the species. For example, such a pale animal was captured near Oahu, and for some years was an exhibit animal at the oceanarium, Sea Life Park. The animal, called "haole" for "white person", gradually grew darker during captivity but always remained slightly pale. Perrin (1972) described a pale animal from the eastern tropical Pacific, as "albinistic."

Let us examine each of our conclusions in turn. First, is the question of residency. Taking only those animals recognizable from the surface, we find that 7 of 12 animals were seen in both the large Keahole Point schools and in the smaller Kealakekua Bay schools. The pale animals were seen both in Kealakekua Bay and Keahole Point schools and far to the south at Kamilo Point. There were long periods when a given animal was not seen at one or another locality. This information cannot be usefully quantified because schools were sometimes large and all animals could not be examined and because our records are not the result of concerted attempts to check each animal in a given school. Instead, the records reflect opportunistic sightings during the pursuit of other activities.

Animals clearly moved back and forth between the Keahole Point and Kealakekua Bay assemblages. Of the 12 animals, 6 were seen at more than one locality and then returned to the first locality of sighting at least once. Three animals were seen at a single locality only, but this may reflect low sighting frequency rather than lack of movement.

Finally, three animals were seen at two or more localities but did not return to the locality of first sighting. For these reasons we reject the idea of a given cove having a definable resident school (Table 1).

TABLE 1.—Movement of Hawaiian spinner dolphins that were identified by natural scars and marks.

Dolphin number	Total time observed (days)	Maximum distance travelled (km)	Number of sightings
1	293	18	3
23	183	0	3
24	1,096	36	14
30	342	36	11
32	246	0	3
39	236	36	3
40	275	36	4
44	170	36	6
45	1,220	113	7
46	862	10	3
49	39	36	2
50	1	0	1

Reversals = 6
One location = 3
Two or more sequential locations = 3

Our data are too incomplete to show how long a given animal might spend at a single locality, or how often it switches between rest localities. Only the number of consecutive days during which a given surface-visible marked animal was seen at a single locality vs. the number of days of consecutive observation during the sighting period is indicative. Considering the animals for which most resightings are available: numbers 24 and 30, during four separate continous periods of observation of 9, 8, 9, and 10 days, animal 24 was seen 2, 2, and 3 days consecutively (Table 2). Animal 30 was seen only once, 2 days in a row, during consecutive observation periods of 7, 10, and 10 observation days. Animal number 13 (a large calf traveling with its mother) was seen three consecutive days during a 16-day observation period at Kealakekua Bay. During consecutive observation periods in which the observer moved from Kealakekua Bay to Keahole Point, certain animals were noted on consecutive days at the two localities, indicating a switch in a single night from one to the other. These data indicate that movements are frequent, at least between the Kealakekua Bay and Keahole Point rest areas.

As for the conclusion that dolphin schools consist of labile aggregations of groups and subgroups, the best information comes from fluctuations in school sizes with which a given marked animal was associated. The results reflect almost

TABLE 2.—Occurrence of a single spinner dolphin (No. 24) and the size of schools in which it was seen at Kealakekua Bay, Hawaii, 1970.

Dates of observation	Estimated school sizes	Number of times seen
28 Apr -6 May	15-30	3 days of 9
23 June-30 June	15-40	2 days of 8
10 Sept -18 Sept	25-36	3 days of 9
28 Oct -6 Nov	7-120	3 days of 10

the entire range of school sizes observed. For example, at various times number 24 was found in schools varying from 7-10 to 120 animals, and number 30 covered about the same school size range, from 6 to 150 animals. Observations from the MOC showed that on one occasion the same subgroup, with the same general internal arrangement of animals, persisted for at least 3 days. Many times, during three consecutive observation days (25-27 March 1970) the same subgroup of five animals came to the bow of the MOC. This sort of asssociation is well known in captive schools and persists for long periods of time (McBride and Hebb 1948; Tavolga and Essapian 1957; and Bateson[5]). Such groups in captivity may be constructed of related or nonrelated animals or even of animals of different species (Bateson see footnote 5). Thus, while our observations of wild schools do not provide proof, we expect that some subgroup structure may persist over long periods and that familial lineages may be important, as has been observed in captivity (Tavolga and Essapian 1957).

The role of subgroups in larger dolphin schools is apparently not simple. Such schools are not simply composed of groups and subgroups that themselves have cohesion. Instead, there are also some assemblages that seem typical only of large schools. For example, in large schools, groups are often segregated. Groups of juvenile animals or of mother-young pairs may be seen. Large schools differ from one another by the presence or absence of such groups. Some schools were composed only of adults, while others had a high proportion of young animals. Subgroups may move between schools. Some social ordering, largely related to growth and reproduction, may take place in schools regardless of the origins of their constituent parts. A major force in such ordering within large schools may be the aggression of certain large adults, that may be either male or female, who herd vulnerable groups to central locations within the school (McBride and Hebb 1948). Such patterns have been proposed for *S. coeruleoalba* by Kasuya (1972) and for *S. attenuata* by Kasuya et al. (1974).

AERIAL BEHAVIOR PATTERNS

An experienced observer of spinner dolphins can quickly judge the activity state of a school by watching its aerial patterns. It is possible to judge the alertness of school members by checking the kind and frequency of aerial patterns. In fact, such analysis soon makes it obvious that the entire sequence of changing behavior patterns through any 24-h cycle is related to the level of activity, or "emotional state," as indicated by aerial patterns.

Spinner dolphins not only "spin" but perform several other clearly recognizable aerial patterns. These include leaps, tail-over-head leaps, backslaps, headslaps, noseouts, and tailslaps, or a combination of these patterns—each performed with variable vigor and frequency at various times of day.

The spin. The spinner dolphin rushes to the surface as if about to make an arcing leap, and at the last instant, when most of its body is out of water, tips its flukes slightly and flexes its tail stock, causing the airborn animal to spin about its longitudinal axis. As many as four revolutions may be made in the course of such a leap (Hester et al. 1963). The dolphin may literally appear to flicker as flippers, flukes, and the dorsal fin flash by. The animal falls back into the water, usually partly on its side, and its rapidly rotating body scoops out a hollow of water around the sinking animal. The hollow then collapses producing a welter of spray (Figure 5) and a discernible clap of sound. The spin is enhanced in air by postural movements, in addition to the momentum initially imparted when leaving the water. Just as a gymnast flexes his or her body or as a skater moves elbows in a spin, the spinning dolphin flexes its head and tail and moves its flippers toward or away from its body (Figure 6).

Spins are usually performed in a series of descending intensity (as are other aerial patterns). A given animal may spin as many as a dozen times in succession, each successive spin generally being of somewhat reduced intensity compared with the last. The first leap may reach an apex perhaps 3 m above the surface, while in the last of a series the animal may not clear the water at all. Most spin series are short, being composed of three or four spins.

All age-classes spin. It is not uncommon to see small calves spinning repeatedly in moving schools. In one case a young animal leaped into a spin while in a feeding school, landing a dozen meters off our bow. Each successive spin brought the animal closer to us, as it was seemingly oblivi-

[5]Bateson, G. 1965. The cetacean community in Whaler's Cove-Sea Life Park.

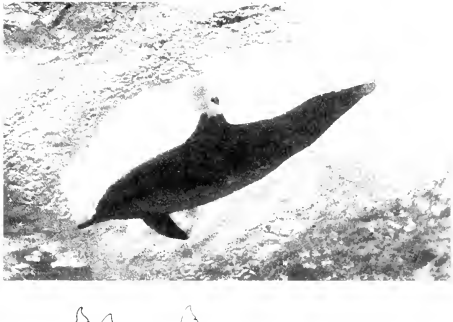


FIGURE 5.—Spinner dolphin reentering the water after a spin, seen from below. Note the longitudinal hollow of water scooped out by the rotating animal. Photo by Henry Groskinsky, courtesy Time, Inc.

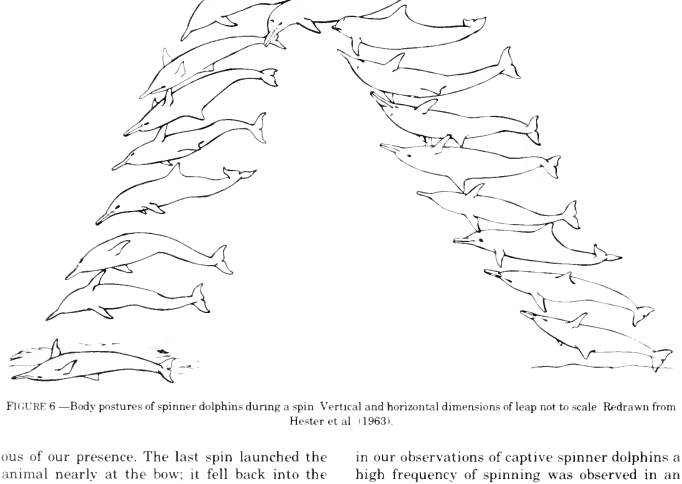


FIGURE 6.—Body postures of spinner dolphins during a spin. Vertical and horizontal dimensions of leap not to scale. Redrawn from Hester et al. (1963).

ous of our presence. The last spin launched the animal nearly at the bow; it fell back into the ship's bow wave, startled, and swam rapidly away below the surface.

Spins may be seen in all parts of a school. Leadership or dominance do not seem to be the obvious factors in spinning behavior. In fact, the opposite could be true since very young animals spin, and in our observations of captive spinner dolphins a high frequency of spinning was observed in an animal that had not been socially accepted into the resident captive school. The best correlation of frequency of spinning and the condition of a school seem to relate to alertness, or activity level of the animals involved, the greater the alertness the more frequent the spins. The more spread out a

school the more frequent spins seem to be. In feeding schools, which are the most dispersed of all school formations, spinning and other high energy aerial behavior occur almost continously.

The leap. The most common aerial behavior in which spinner dolphins actually leave the water is the leap. Spinner dolphins perform leaps by bursting from the water at about a 30° angle, rising a meter or two above the surface, and falling back into the water on the belly or side in a welter of foam. Less frequently, reentry may be made cleanly, snout first.

Tail-over-head leap. The most active and perhaps physically demanding aerial behavior pattern is the tail-over-head leap and its variant, the tail-over-head leap with spin. These aerial patterns are seen only when the Spinner dolphin school is most active. In this pattern the animal bursts from the water at a rather high angle, slings its tail over its head in a wide arc, usually trailing a spiral of spray and enters tail first, often slapping its flukes against the water with a loud "thwack" in the process (Figure 7). On occasion this may be accompanied by one or two revolutions of a spin at the same time.

Backslap. The animal leaps about half or a little more of its length out of water at about a 30°-45° angle, upside down. As it falls back, it arches its body sharply, giving the water a sharp slap with the dorsal surface of its head and beak (Figure 8). Backslaps are often performed in slowly moving schools

FIGURE 8.—A typical backslap of a spinner dolphin. As the school moves slowly the dolphin emerges in the direction of swimming, belly up, and arches its back at the last instant and slaps its back against the water

Headslap. The reverse of the backslap. The animal emerges in the normal position, once again at about 30°-45° angle to the water surface, and then flexes its head sharply downward, slapping its chin and lower beak against the water (Figure 9). It is one of the most common patterns seen in moving schools.

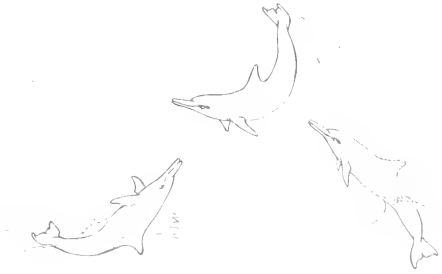


FIGURE 7.—The tail-over-head leap of a spinner dolphin. This may at times be combined with a spin

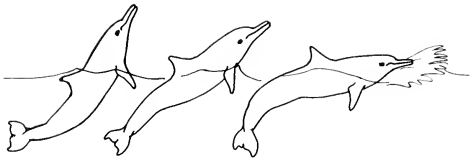


FIGURE 9.—A headslap. The spinner dolphin emerges belly down in the direction of swimming and flexes its body forward sharply at reentry.

Noseout. The least active aerial behavior. The spinner dolphin simply arches its back as it swims to the surface, raising its snout into the air. It is sometimes seen briefly when a resting school is disturbed, or in schools where other, more active behavior is occuring. It is often the first aerial behavior seen in an awakening school.

Tailslap. This pattern may be performed in either the normal or the inverted position. With the dolphin at the surface the tail is arched, bringing the flukes above the surface. The flukes are then brought down smartly against the water producing a clearly audible sound. In the inverted position an animal may sometimes scull along making repeated and rapid tail slaps in a behavior we have called "motorboating," because it not only leaves a continous wake, but makes a "pop pop pop" sound. An animal may slap 10 to 20 or more times in succession in this way (Figure 10). A whaler's term, "lobtailing," describes the same behavior, but seems less descriptive than "tailslap," a term now widely used by porpoise trainers.

What are the functions of aerial behavior? A key point, we feel, is that each pattern, with the possible exception of the noseout, clearly makes noise and, in fact, seems primarily structured to make noise. For example, in a headslap the last component of the pattern is a rapid flexure of the trunk and neck causing the chin and throat to slap against the water. The tail-over-head leap effectively slaps the flukes against the water with great force. The spin scoops a cavity from the sea surface whose walls collapse and thus produce a sound we have heard both above and below the water. Other aerial patterns are similarly structured. Such sounds probably radiate in all directions. Dolphin sound generation and beaming apparatus, on the other hand, transmits sound in a structured beam, directed forward (Schevill and Watkins 1966; Norris and Evans 1967; Evans 1973). This beaming is better known for clicks than whistles or burst pulse signals, though apparently also true of the latter, at least in the killer whale, *Orcinus orca* (Schevill and Watkins 1966). The directionality of clicks has been discussed for *S. longirostris* by Watkins and Schevill (1974). Thus, while vocal signals are directed almost wholly in certain sectors, the sounds of aerial behavior are likely to approach omnidirectionality. Our recordings indicate that none of the signals of aerial behavior propagate long distances. Tail slaps may be the loudest.

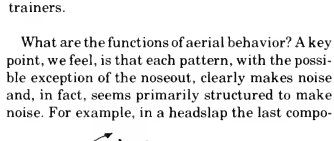


FIGURE 10.—An inverted tailslap by a spinner dolphin. Tailslaps also may be made in normal body posture. Often a series of a dozen or more slaps may be made at a single time, which has been termed "motorboating" because of the white wake and the sound produced.

Aerial behavior is most frequent in fully active schools in which the animals are dispersed, sometimes rather widely. In tight resting schools (see below) sounds of all kinds except for desultory clicking are nearly absent. Conversely, our observations of a captive spinner dolphin school held in a community tank at the Oceanic Institute, Oahu, Hawaii, showed that aerial behavior continued through the night and, in fact, was most frequent in the dark. Thus, high frequencies of aerial behavior seem correlated with conditions in which many animals in the spread school cannot see each other.

Finally, these patterns are stereotyped by species, and a trained observer can often visually identify the genera or species of dolphins by their aerial patterns, sometimes from long distances.

Perhaps the dolphins can make such identifications underwater by sound.

What can the use be of such sound signals? The following possibilities seem apparent: 1) If we can gage the activity state of a school by its aerial behavior, it is likely that the dolphins can do so too, and probably in a more refined way than we can; 2) such sound signals may be used where vision is useless; 3) school cohesiveness in the dark, or when animals are spread beyond the limits of vision, may be promoted by repeated short-range omnidirectional sound signals from all parts of a school. The incidence of aerial behavior is correlated with times when such signals would be most useful. This seems to us to be the most likely function.

We considered, and rejected the idea, that the spin might be a pattern relating to dominance or courtship in the school. This seems refuted because animals of all age classes and both sexes spin and because captive observations have shown that even animals that have been rejected from the social structure of a school spin.

Another possibility is that spinning is related to removal of ectoparasites such as remoras and copepods. While it might be useful occasionally in detaching such creatures, we have never seen a case in which this seemed to be occurring, and essentially every animal observed to spin was apparently without parasites. Captives spin regularly even though free of parasites.

THE DAILY ACTIVITY CYCLE

Observations of spinner dolphin schools along the Kona coast of the island of Hawaii, and to a minor extent elsewhere in the Hawaiian chain, show a regular sequence of activities during each 24-h period. Broadly, this consists of nighttime feeding, about which we know little, morning coastward movement that brings the animals into coves and sheltered coastline areas, rest, awakening, zigzag swimming, and then departure to the feeding grounds. Each of these activities will be discussed in turn.

Feeding

Feeding is upon scattering-layer organisms (Table 3) and seems to be performed during synchronous or subsynchronous dives of large and dispersed schools. What we take to be feeding dives start as early as dusk, before most of the scattering layer approaches the surface, and such evidence as we have (mainly from a single radiotracking, from chance encounters with schools at night, and from schools that we have followed to the feeding grounds) suggests that the schools patrol along the breaks in the submarine island slope and toward morning gradually make their way into shallow water over the shelf. A radiotracked animal, caught over approximately 140 m of water at Keahole Point just before dusk (at 1650 h) on 1 March 1971, moved back and forth along the shore between a point near Kailua-Kona and Kiholo Point. A detailed radiotrack was made during the night of 1-2 April (Figure 11). The animal stayed with a large school that moved slowly offshore and by 2000 was over the island slope. The group then patrolled back and forth over the slope within a stretch of coast approximately 20 km in length and over water that varied from about 360

TABLE 3.—Squid and shrimp in the diet of Hawaiian spinner dolphins.

Sample and date	Capture locality	Squid	Shrimp
0170-42 Sept 24, 1970	1 km off Ala Wai, Oahu	28 mantles (mantle length 25-52 mm, mean 38 9 mm) 5 *Abralia astrosticta* 14 *Abralia trigonura* 67 squid beaks, probably of the same species	11 pasiphaeids (to 17 8 mm carapace length) 1 small 4 abdominal portions 1 caridean cephalothorax Probable euphausid fragments
0170-35 Mar 25, 1970	Off Waikiki, Oahu	2 *Abralia astrosticta* 7 *Abralia trigonura* 152 squid beaks of the above species 49 macerated squid	No identifiable remains
0171-1 Jan 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 *Abralia astrosticta* 6 *Abralia trigonura* 204 squid beaks, probably of the above species 1 *Histioteuthis* sp	20 *Sergia fulgens* (12 5-15 5 mm carapace length, mean 14 6 mm)
0171-2 Jan 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 *Abralia astrosticta* 8 *Abralia trigonura* 310 squid beaks of the above species	1 *Acanthephyra* sp 1 *Pasiphaea* sp 2 *Pasiphaea* sp 15 *Sergia fulgens* (12-14 5 mm mean 13 6 mm Some of the above may be of undetermined species) 1 *Oplophorus grimaldii* (identification probable) 3 *Acanthephyra* sp (identification probable)

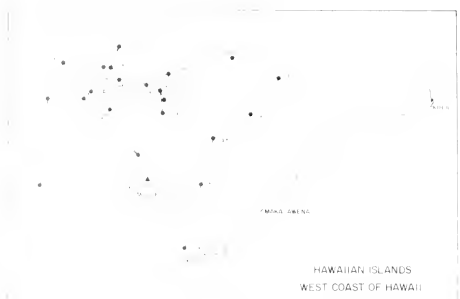


FIGURE 11.—Radiotrack chart of a marked spinner dolphin 31 March–2 April 1971. Dolphin stayed in moving school of 100 animals presumably feeding over the island's submarine slopes.

to 2,600 m deep. By 0300 the school and the radiotagged animal had moved closer to shore and continued to move in ever shallower water until dawn.

Feeding schools were observed on three occasions at dusk. Each was composed of widely scattered groups, covering as much as 3 km in widest dimension, moving together. Diving was subsynchronous. Before a dive occurred, groups were evident and there was much aerial behavior across the entire width of the school. Then groups of the school dove individually, all following within approximately a minute or two. Dives were long, averaging 3.5 min according to our records. Surfacing was approximately as coordinated as diving, that is, the various groups straggled to the surface over a minute or two.

It was striking to see these very broad diffuse schools reverse their course in relative synchrony (within a minute or two), even at dusk, indicating a communication mechanism, probably acoustic, that could pass information rather quickly across the school.

Stomach contents were obtained from four spinner dolphins caught early in the day (before noon), while three animals taken in the afternoon had empty stomachs. This same pattern seems to occur in the oceanic spinner dolphins of the tropical Pacific, and a high percentage (65.3%) of empty stomachs not segregated according to time of day) of 49 spinner dolphins taken from the eastern tropical Pacific were empty (Perrin et al. 1973). A time-stratified sample would probably show some food in the stomachs in the morning before digestion of the night's catch is complete, with empty stomachs in the afternoon. If spinner dolphins were diurnal feeders, one would expect few empty stomachs during the day at any time. The observed morning defecation period also fits this scheme. We conclude from our own observational data that the spinner dolphin in the open eastern tropical Pacific and around the Hawaiian Islands feeds at night. Our evidence, and that from other studies, suggests that it feeds upon scattering-layer organisms found at considerable depth. Fitch and Brownell (1968) reach a similar conclusion from otolith studies of stomach contents of five spinner dolphins taken from the yellowfin tuna grounds; they stated: "We feel certain that three of the cetaceans we investigated (*Kogia simus*, *Stenella longirostris*, and *Lissodephis borealis*) had been feeding 800 ft (250 m) or more beneath the surface . . ." Perrin et al. (1973) similarly concluded that spinner dolphins are feeding mostly on mesopelagic fish and squid, with a small increment of epipelagic squid species in their diet. Our results (Table 3) confirm these earlier works, but show a considerable component of sergestid crustaceans in the diet of the Hawaiian spinner dolphin. Epipelagic squid were absent, though common in Hawaiian waters, while such relatively deepwater forms as *Abraha astrosticta*

and *A. trigonura* were common in the stomach samples but rare in collections of squid from Hawaiian waters. Richard Young[6] described *A. trigonura* as being uncommonly taken in Hawaii, but being a vertical migrant occuring from 500 m depth during the day to the upper 100 m at night. This species made up the majority of our samples. As for *A. astrosticta*, Young stated that it is known in Hawaii from only a few captures, and that most were taken on the bottom in trawls, while small individuals were sometimes taken in midwater. Our samples were adults. Young commented as follows: "It is a displaced midwater faunal element, or an animal having the distinctive adaptations of a midwater animal but which seems to migrate along the bottom. The *Histioteuthis* is also a vertical migrator that stays below about 150 meters." (See Table 3). John Walters (see footnote 6) commented that the shrimp *Sergia fulgens* is an enigmatic form known only in the adult form (ours were adults) from night tows.

Morning Shoreward Movement

After nighttime feeding, spinner dolphin schools turn toward shore, ultimately congregate in certain sheltered locations where the schools subside into the rest pattern. In the case of the radiotracked animal, this movement toward shore seemed to begin at about 0300 and to consist of a gradual movement that zigzagged ever closer to shore.

The directions from which schools come into Kealakekua Bay suggest that the movement toward the coast may be a general one and not necessarily pointed precisely at a rest cove. Some entering schools first swim along the coast, round Palemano Point at the south tip of the bay, and enter the bay over the shallows near Keei and Napoopoo (Figure 1), while others enter the bay directly from the open sea, coming in at various angles to the trend of the coast. Still others enter from the north, once again after a traverse of unknown length along the shore to the north of the bay. More schools enter along the southern limb of the bay than from the north or center. The true figure for south entry may be even higher than the figures indicate (58% for south entry vs. 14.5% for north entry; 27.5% entered in the middle sector), since some first sightings were made close to the cliffs at the back of Kealakekua Bay and, because of their location, were placed in the second sector records. It is likely that some of the schools entered from the south or north prior to the beginning of observation.

These congregation patterns suggest that the bays and coves used for rest periods may not necessarily be the direct target of daily inshore movement. The bays seem simply to collect schools that accumulate along the coast after a night's feeding. The fact that more schools arrive from the south than from the north may reflect the nearby presence of adequate resting areas over the rather extensive shallow-water areas immediately north of the bay between Keikiwaha Point and Keauhou. Waters to the south of Kealakekua Bay are deep close to shore and only very modest sized shallow coves exist at Honaunau and Hookena. Farther south, along the 20 km stretch of coast between Hookena and Milolii, no spinner dolphins were seen although both flights and ship searches were made. Nonetheless, data from marked animals show movement between the populations on each side of this gap. Unless rest areas are encountered, dolphin schools remain transient. This does not preclude the possibility that the animals may be familiar with the various rest coves or actively seek them when nearby.

Arrival times (Figure 12) concentrated between 0600 and 0950 h, though some schools arrived much later in the day. The early arrivals typically subsided into rest and spent the majority of the day in the bay. Later arrivals (those entering between 1100 and 1700 h) tended not to form resting schools and often moved out of the bay after a brief stay. The late afternoon arrivals may have completed a rest period elsewhere and then entered the bay as part of a longshore movement prior to going to the feeding grounds. Dolphins engaged in such longshore movements have been followed out to sea. In one such case a school rested, left the bay to the south, traveled slowly very close to shore until the small cove at Honaunau was encountered, and then turned out to sea as dusk approached.

Not all dolphin schools encountering Kealakekua Bay enter it. We occasionally saw schools crossing the bay mouth and swimming on in either direction. Our impression is that this occurred when other schools were deep in the bay, but unfortunately, adequate records to document

[6]Richard Young (Professor of Oceanography, University of Hawaii) examined and identified stomach samples from our Hawaiian spinner porpoise in 1973 and provided notes on the occurrence of squids in the samples, while John Walters (University of Hawaii) provided identifications of shrimps.

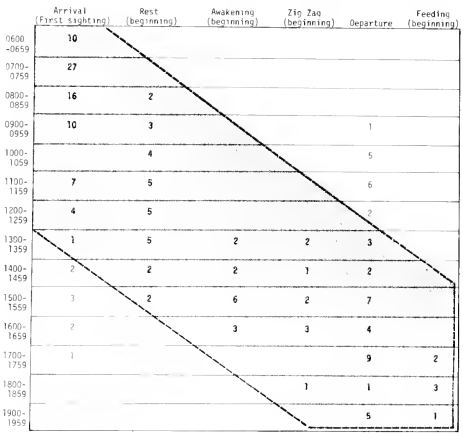


FIGURE 12—Cumulative record of time of first sighting, onset of rest, wakening, etc.

the point were not kept. Our efforts at listening to dolphins in Kealakekua Bay showed that dolphins at the mouth of the bay can easily hear those in its deepest recesses, so the effect may be one of exclusion of the passing school by occupants. The point needs further study.

Small schools often seemed to coalesce upon arrival in the bay. This first became apparent when our estimates of school size during an arrival sequence increased sharply, or even doubled, between the time the animals were at the bay entrance and when they were deeper in the bay. In other records such obvious increase in school size occurred after the animals were deep in the bay. The arrival of such supplementary schools was occasionally observed and their coalescence into a single school noted.

School structure during entry was best observed in those that entered in the central sector, without the visual interference of headlands or the swells and breakers that sometimes obscured sightings close to shore. Such schools were sometimes first seen as far as 4 km beyond the bay and could be watched during the entire entry traverse. These schools typically swam in a ragged rank composed of quite discrete groups. The dolphins were often quite active, and their passage was accompanied by spins and other aerial behavior. Often, by the time the bay mouth was reached aerial behavior had subsided considerably, though it often persisted to some degree for as long as 2 h after initial entry. In small schools of approximately 6-15 animals, entry was often quite unobtrusive. In spite of a conscientious watch from the clifftop during early morning hours such small schools were sometimes seen first deep in the bay. Large schools typically exhibited more aerial activity than small ones, and it appeared to persist for a longer period.

Arriving dolphin schools often come to the bows of vessels where they engage in assisted locomotion or "bowriding" (Norris and Prescott 1961). Even so, if a vessel pursued such schools, repeatedly making passes through their ranks or changing speeds upon approach, the school usually edged toward deep water, and if the harassment continued, the school left the bay. Observers on shipboard usually failed to note the effect on the school as a whole, since their attention was focused on the bowriding animals. But an observer on the cliff above the bay, watching the entire school, could quickly discern this retreat. This effect nearly always occurred, even if the intruding vessel moved very carefully. Later, when the school had subsided into quiescence, it was much

more difficult to disturb the animals sufficiently to cause them to flee the bay. Even persistent attempts to enter their ranks merely caused avoidance and often a transitory flurry of aerial activity (Figure 13).

Defecation was a common feature of arriving schools, prior to subsidence into rest. From the underwater viewing vehicle the olive colored trails of semiliquid fecal material were often seen streaming from the dolphins. Three or four animals sometimes defecated simultaneously within the field of view of the vehicle. A rate for one 40-animal school was calculated at one defecation every 15 s. Presumably this rather short defecation period is related to nighttime feeding and early morning digestion. The trailing animals of a school swam through the dispersed clouds of feces with no evident reaction.

Subsidence Into Rest

Once a spinner dolphin school arrives deep in Kealakekua Bay, it normally subsides slowly into rest, a process sometimes requiring 2 h or more. This process is so gradual and so affected by features such as school size and the time of day, that its precise onset was difficult to assign (Figure 13), and an arbitrary definition was necessary. Because rest involves the cessation of aerial behavior by all school members, we defined rest as occurring when a 10-min observation of the school revealed no aerial behavior. Occasionally, even this criterion was confounded because aerial behavior is, to some extent, "infectious," and a school subsiding into rest may sometimes exhibit 10-min periods without aerial behavior followed by periods in which some aerial activity occurs in several animals. But, generally, once a school was quiet for 10 min, little or no aerial activity occurred until arousal. Typically arriving schools were in ranked form, with group structure evident. Such schools often moved quickly (5-8 km/h) and swam resolutely, with considerable aerial behavior. Little time was spent below the surface. Dives were brief (Figure 14). Once such a school arrived at the back of the bay, under the lava cliffs,

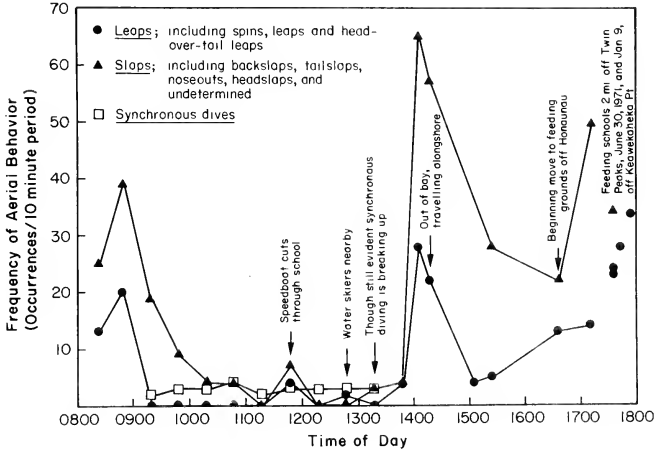


FIGURE 13.—Aerial behavior per 10-min interval for a spinner dolphin school of approximately 40 animals, 30 June 1971, Kealakekua Bay, Hawaii. Synchronous dives define the rest period, broken briefly by the speedboat. See text.

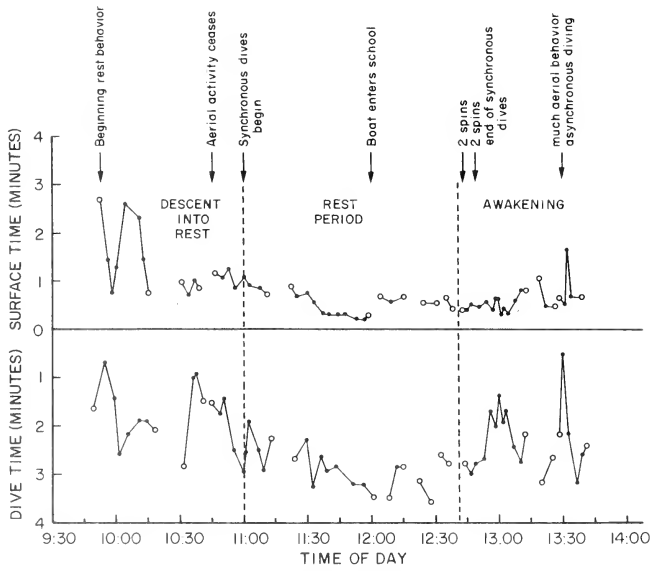


FIGURE 14.—Trends in diving and surface times in a 40 animal school of spinner dolphins, Kealakekua Bay, Hawaii, 2 May 1970. Breaks in record represent loss of the school by the observer, when a surfacing and descent was apparently missed.

it moved back and forth across the width of the bay. Its traverses sometimes took it nearly to Kaawaloa on the north and to Keei on the south (Figure 1). The various classes of aerial behavior slowly disappeared in a rough graded series: the most athletic patterns such as spins and tail-over-head leaps first, then head- and backslaps, then tailslaps, and finally all but an occasional noseout was gone.

School size and shape gradually changed at the same time. The ranked school shifted into a sub-discoidal shape and tightened markedly. For instance a school of 30 animals that once formed a spread rank over 75 m of water might become concentrated in a 20 m diameter disc. Movements became leisurely; in fact, the surface excursions of the schools became almost surreptitious as the animals rose quietly from the depths, breathed once or twice, and descended again. It became very easy to overlook them, and two or three observers were needed to produce a complete record of their dive sequences. During rest most time was spent underwater (Figure 14).

Vocalization was at a high level in arriving schools and subsided as the rest period approached. Arriving schools made a variety of noises including click trains, burst pulse signals such as squawks or barks, and pure-tone whistles or squeals. All but clicks ceased during rest.

Rest

During rest, quiet spinner dolphin schools moved slowly back and forth, deep in the bay.

Their excursions were entirely confined to shallow water (about 3-50 m). Only when disturbed or when rest was over did the schools begin to edge into deeper water. For instance, resting schools seldom ventured into the deep channel that entered the bay at Kaawaloa, but instead moved mostly back and forth between our observation station #1 and Napoopoo (Figure 1), an area of shallow sandy bottom dotted here and there with isolated coral heads.

Resting schools often changed direction underwater, which made it difficult to predict where they would surface. Interindividual and intergroup distances gradually decreased as rest deepened, until many animals were very close to or actually touching one another, while the arriving school showed evident group structure and independence of both movement and diving time within the school; the resting school swam in much closer synchrony. Arrival of synchronous diving by an entire school provided a good, if arbitrary, indicator of the onset of rest.

On a few occasions we were able to watch synchronous dives from the MOC. The underwater vantage point allowed the observer to see subgroups of animals in the school as a whole. Tight, uniformly oriented groups dove slowly, with measured tail beats, toward the sand bottom below; leveled out a few body lengths above the bottom and moved slowly along, schooled tightly; and swam largely without individual exploratory movements. Occasionally an animal descended to the bottom and beat boils of sand up into the water with its flukes. At the end of a dive the animals rose rather steeply to the surface, not as a single tightly integrated group, but more or less seriatum, as a column of subgroups. Often after rising, the animals spread outward from this rising column a short distance before turning to define the compact confines of the surface school, like the petals of a flower opening. Once on the surface, group structure could be seen, but the animals seemed much more regularly spaced than is the case in active schools. Diving, too, was steeper and slower than in travelling groups. While individuals in resting schools seemed less alert than animals in feeding or travelling schools, the resting school itself was very wary of strange features of its environment. Any strange object placed in a rest cove, such as a buoy, boat, or line was avoided for a matter of days before a school seemed to habituate to its presence. It was striking that they reacted to foreign objects in much the same way as we have come to expect from fish schools, and not with typical dolphin individuality. For instance, when a resting school cruised inshore of us near the cliffs, we waited in a quietly rocking skiff some 75 m offshore, and the school approached slowly as a discoidal group, thinned as it reached a point directly inshore of us, streamed betweeen the skiff and the cliff as a long line of quietly moving animals, and reformed its discoidal group once past us. We found that our skiff or our anchored workboat could deform such discoidal groups from some distance, causing the side nearest the skiff to become dented or malformed as the entire school reacted to our presence. When a four-hydrophone array capable of sound triangulation was placed near the path of such resting schools, it was assiduously avoided and no animals were known to pass through it for 6 days after its placement (Watkins and Schevill 1974). A line stretched across the surface of the water was capable of deflecting such schools. In such cases, even though the animals moved slowly and other evidence of alertness, such as complex phonation or aerial behavior, was nearly absent, the school as a whole remained alert. We suppose this is due to sensory integration by the closely packed school, that is, by the reception of environmental information by some members of a school and transmission of its occurrence to all or most of them. It was usually possible to cruise among alert schools, and many individuals might station at the bow within a few feet of an observer, but resting animals very seldom came to a vessel.

A graphic demonstration of spinner dolphin's fear of strange objects was given by our attempts to encircle quiescent spinner dolphin schools with a modified Hawaiian "hukilau[7]."

Our hope was that this fear might be utilized to assist in their release from tuna seines, since at the time large numbers were being killed per year in the yellowfin tuna fishery. We conceived that light weight gear of this sort could be deployed in a tuna net to crowd the captive animals, and thus assist in their release. Our tests, run in August 1973 in Kealakekua Bay, used a hukilau composed of 450 m polyporpylene cork line ($\frac{1}{2}$ in; 1.27 cm) from which were hung every 2 m, thin poly-

[7]A hukilau is a Hawaiian "net" made of a cork line with palm fronds woven through it at intervals, which is towed across coral areas, chasing fish in front of it. Because a mesh net is not involved, it does not entangle on the rough bottom but still serves to concentrate the fish, which are then netted from inside the hukilau over sandy bottom.

prophylene lines (¼ in; 0.6 cm) 18 m long (Figure 15). With this insubstantial barrier we were able to encircle whole schools of spinner dolphins in 20-40 m of water and to crowd them severely. In one case when the hukilau was reduced to a surface area of 6 × 10 m, a school of 40-60 animals refused to leave through the wide openings but continued to mill inside (Figure 15). Even when two of the thin vertical lines were removed, leaving a "door" 6 m wide, the school continued to circle, "eyeing" the opening but not passing through it. Only when the area was further reduced did the majority of the animals pass through the wide opening. They had been held captive for 3 h 50 min in this fashion.

Although large and small schools may become quiescent, sporadic low intensity aerial behavior may continue. The impression given is that very small schools (ca. 6-12 animals) maintain a degree of individual wariness, perhaps related to the uncertain protective effectiveness of their few members, while very large schools may always contain some alert animals. For instance, based on a small number of observations in the large (100-150 animals) schools seen at Keahole Point, we have never noted deep quiescence. It is as if the members of the small school were afraid, and that some activity always occurred somewhere in the larger schools. Only schools of about 20-40 animals seem to achieve the most complete quiescence.

Even though aspects of diurnal behavior sequences were recorded on 83 days, complete sequences were recorded on only 13 days. Based on these observations, rest periods ranged from 41 min to 6 h (mean = 3.62 h).

Once quiescent, resting schools are rather difficult to disrupt. Several times cruise boats or water skiers went through resting schools during our observations. The usual result was a brief flurry of low-level aerial behavior, for example, a desultory headslap, an imperfect spin, and then the school would subside into complete quiescence again (Figure 13).

Arousal

Arousal, unlike descent into rest, is abrupt, both in terms of school dispersion and aerial activity. In a completely quiescent spinner dolphin school, arousal was marked by sudden active aerial behavior—a complete spin or headslap, for instance. Within 10 min of such initial aerial activity the school was often fully alert, with aerial activity high throughout the school. In fact, the highest levels of aerial activity recorded occurred at arousal, and later, during feeding (Figure 13).

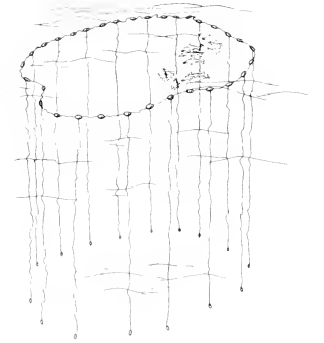


FIGURE 15.—An Hawaiian "hukilau" composed of a cork line and hanging vertical weighted lines, showing a school of spinner dolphins held inside. Vertical lines are 3 m apart and 20 m long. See text.

Zigzag Swimming

At arousal the pace of the spinner school quickens. Group structure suddenly becomes obvious again. At arousal the school moved back and forth across the bay, or sometimes in and out from the bay center to the cliff base. In either case the school often began to traverse deep water. Typically, it swam toward the bay mouth beginning with a flurry of activity and speed, often with animals rushing through the water, creating spray and small bow waves as they raced along. As the bay mouth was approached, usually the school gradually slowed and finally began to mill then turned back into the bay. Sometimes the school then subsided into further rest, or accelerated again, often toward the opposite side of the bay. This entire pattern is what we have termed "zigzag" swimming. These patterns, we suspect, are, to some extent, influenced by the topography of Kealakekua Bay, and may take somewhat different expressions elsewhere.

Spinner dolphins were observed moving in zigzag fashion at Kealakekua Bay, in and out and from headland to headland. The longest bout of

this behavior took 2.75 h. Typically zigzag swimming ended with fast swimming that took the school beyond the confines of the bay altogether. It was as if one had been rocking a blob of mercury in a bowl, and a final strong motion sent the blob flying, completely free of the bowl.

If the animals left the bay early in the day, the school usually traveled close to the shoreline, either to the north or south, and later in the day, turned toward deep water offshore. When a school left the bay near dusk, it usually headed directly out to sea.

As exodus from the rest location began, schools traveled either as ranked schools (wider than long) or in straggling lines arranged in more or less linear fashion. As the school moved offshore, it spread. It sometimes coalesced with other schools moving in the same general direction. By the time feeding grounds were reached, usually near dusk, a school that, during rest, had formed a 25 m diameter disc might have expanded until its groups were scattered over a kilometer or more of sea. As noted earlier, we have estimated some feeding schools as 3 km in breadth.

Social behavior, including mating, aerial behavior, sexual play, and aggressive chases, becomes especially evident in spinner dolphin schools moving toward the feeding grounds. Once there subsynchronus feeding dives begin.

Dive Patterns

An example of the daily cycle of dive patterns is shown in Figure 14. As animals entered the rest area, the pattern was one of short dives, with most time spent on the surface. Then this pattern gradually shifted as dives became longer and surface times shorter. When the school was near or over the shallow area where rest occurs, dives become synchronous, or nearly so. During arrival the groups of a school, especially if it was a large one, often dive out of synchrony with one another. During rest, as shown in Figure 14, the duration of dives continued to increase until the longest dives were approximately 3.5 min duration; surfacings at that time were brief, between 10 and 30 s duration. Throughout the rest period, the school, if it is small or moderate in size, dives in synchrony. During the arousal period, surface times gradually increase while dives tend to become much more variable in length than during rest. Finally, as the school travels out to sea, individualism reaches its peak, with animals scattered in pairs or small subgroups, or even alone, within the envelope of the school as a whole. Synchronous diving is lost as movement is at or close to the surface and directed into horizontal travel. Then, on the feeding grounds, when the school is at its most dispersed, the scattered school slows and begins synchronized diving again, presumably to feed. Internal factors, such as the return to equilibrium after a dive might play an important role in determining diving patterns. As for mediating signals, the cessation of aerial behavior in an area of the school that has dived could signal adjacent school segments that diving is occurring; or, vocal signals could mediate it, and thus a wave of information about a dive in progress could travel across the school. The high incidence of aerial behavior in feeding schools and the lack of precise synchrony in feeding dives support such a speculation.

Social Behavior

Social behavior in wild spinner dolphin schools has thus far proved all but impossible to observe in an orderly fashion. Glimpses of individual animals or subgroups are fleeting, and the opportunity to identify individuals or their sex is sporadic. Hence, the observations that follow are highly fragmentary.

Mother-Young Behavior

Very small calves are always seen in the company of adults. However, young spinner dolphins of quite small size (about 1.2-1.7 m TL) may form groups within a school with no evident adults in close attendance. Newborn calves with adults have been seen at all seasons of the year (Figure 16), as have groups of unattended larger calves.

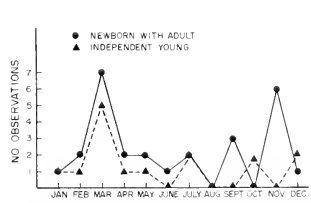


FIGURE 16.—Annual occurrence of newborn in spinner dolphin schools off Hawaii (1968-72). Only sightings of newborn with evident fetal folds are included

Nursing has seldom been seen in nature. In one clifftop observation, a 60-animal school swam below, containing a group of adult-calf pairs. One of these pairs engaged in nursing. The adult turned slightly on her side as the young dolphin positioned itself obliquely alongside with its beak pressing against her at the mammary slits. The behavior persisted for a few seconds before the animals dove. The posture was like that reported in captive dolphins (Dohl et al. 1974).

For 33 days in February-March 1970, a female pair was seen in Kealakekua Bay and nearby Keauhou. Unlike most such pairs, the two often swam near our observation vehicle. The calf had the distal 5-6 cm of its rostrum broken through and bent to the side with some ragged flesh exposed. In spited of this apparently grievous wound the calf appeared active and well nourished. Contact was very frequent between mother and calf. Both the adult and calf used their flukes, flippers, and dorsal fin to achieve this contact. On two occasions the young animal touched its dorsal fin to the adult's flank, laid its flukes up under and touching hers, and held this position as their combined tail beat propelled them both along. The young animal rode both above and below the adult, sometimes directly beneath her midbelly, occasionally sliding backward until the moving flukes of the adult tapped against its dorsal fin. In our observations we never noted true assisted locomotion as described by Norris and Prescott (1961), though swimming speed was generally so slow that it might not be expected.

A common posture was for the baby to swim below and a little to the side of the big female, at which time she placed her flipper against the young animal's back, just anterior to its dorsal fin. Much of the time the pair in this position swam in synchrony, turning and diving together.

On occasion the young animal swung away from the adult for a few meters but soon turned, increased speed, and rushed back to her. Once, during a particularly long sortie, the adult pursued the calf, slapped its back with her flukes, and then the pair dove together.

Sexual Associations

At times, both on a given day and over several days time, specific subgroups of 2-6 spinner dolphins whose members could be individually recognized, were seen together from the viewing capsule. It was possible to determine the sex of some of the animals. Sexually related behavior was exhibited between male and male and male and female pairs. It takes several forms. What Bateson (see footnote 5) called "beak propulsion" was noted (Figure 17). In it one animal swam up from below another and inserted the tip of its rostrum into the genital slit of the upper animal, apparently pushing the passive animal along. Both the dorsal fin and the flippers are commonly used to stroke or

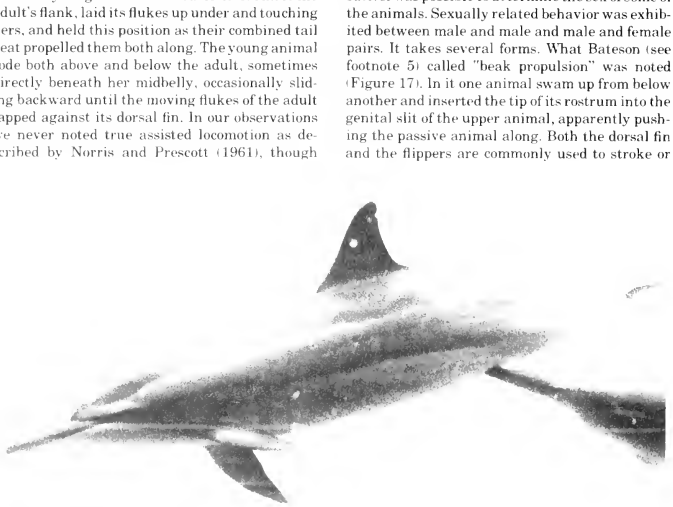


FIGURE 17.—Beak propulsion by a captive pair of spinner dolphins at Sea Life Park, Hawaii. An adult female is pushing an adult male

probe the genital area of another animal, and the upper animal sometimes rode along with the dorsal fin of the lower animal pressed into its genital area. Mating postures were commonly seen, most often in alert schools early in the morning or near dusk. On one occasion (in captivity) we were able to determine that both partners in such a pair were males, even though females were present in the tank. We were able to confirm heterosexual contact in some pairs in nature. Typically, one animal swam in the normal upright orientation while another swam upside down, with the genital areas of the two pressed together. Either sex could be above or below. Intromission was usually difficult to see, but was noted on occasion. Contact was sometimes maintained for several seconds. In some observations the upper partner was relatively quiescent and propelled itself with fluke strokes of much reduced amplitude compared with those of normal swimming. One mating chase was noted as a school moved onto the feeding grounds off Keauhou, the pair raced by the bow of our vessel as we travelled at an estimated 4 kn. They dove and spiralled swiftly together. The coupling and synchrony of movement of the pair was so perfect that the two animals were not evident until the pair turned on its side. Together they veered away from the bow, diving about 20 m down and remaining in the coupled position for several seconds. We heard whistling with the unaided ear when such coupled animals were near the ship.

A particularly complete observation of mating was made from the MOC on 26 July 1970, at Kealakekua Bay. A male-female pair swam directly in front of the viewing capsule, and the female swung under the male until their ventral surfaces were in contact. The penis of the male was seen to enter the female, though no thrusts were noted as the position was held for 3-5 s, while the animals glided without fluke strokes, and then the animals parted. Shortly, the female again moved under the male, but no further intromission appeared to take place. Instead, the male accelerated with a few fluke strokes, and the pair cruised off, side by side.

Competition for partners was occasionally observed. On 29 March 1970 at Kealakekua Bay, the MOC entered a school of 12-13 animals, and 2 were noted swimming upside down. Both pursued and came up under a single adult above them. Later, three inverted animals pursued two in the normal swimming posture. At that moment another large adult swam rapidly to the moving group and forcefully inserted itself between one inverted animal and the one above it. The upper animal then dove away from the group, with the intruder following. The two inverted animals moved quietly, maintaining their upside-down orientation, toward another nearby animal swimming in normal orientation.

Observations of captive spinner dolphins show that much social interaction is sexually related and that it may occur between animals of all age classes and combinations of both sexes. As has been found in the Atlantic bottlenose dolphin, *Tursiops truncatus*, sexual behavior and social communication are interwoven to such an extent that it is often impossible to separate true courtship and mating behavior from communicative behavior of other sorts. For example, Caldwell and Caldwell (1967) reported a 2-day-old male Atlantic bottlenose dolphin having an erection when brushed by its mother. Sexual maturity is not reached in the spinner dolphin until a minimum of 3.7 yr (Perrin et al.[5]) and even later in the bottlenose dolphin, and thus one must view this precocious use of sexual patterns as part of the development of communication concerning relationship. Such communicative use of sexual patterns has been reported for mixed schools of captive spinner and spotted dolphins (Bateson see footnote 5).

Other Social Patterns

Contact, not necessarily sexual in context, is common between members of dolphin schools. When groups of animals swam near the viewing capsule, one could often see animals touching one another with the tips of pectoral fins, the dorsal fins, or fluke tips. Jostling or pushing of animals near the capsule often occurred and was accompanied by sound emissions. Such jostling can be seen commonly in other bowriding groups. Because a few animals from a given school seem to do most of the riding and some seem to occupy specific places at the bow, one gains the impression that hierarchical relations in the school are involved.

The release of air may correlate with social signals in spinner schools. Commonly, long streams

[5]Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Growth and reproduction of the eastern spinner dolphin. A geographical form of *Stenella longirostris* in the eastern tropical Pacific. U.S. Dep. Commer., NOAA Natl. Mar. Fish. Serv., Admin. Rep. LJ-76-13, 84 p.

of air were noted issuing from the blowhole corners in spinners near the capsule. Whistles and chirps could often be heard concurrently. Sometimes, during active chases one or more animals would release a large bubble of air underwater, which boiled upward to the surface. Pryor (1973) has correlated such behavior in captive animals with frustration.

Spinner dolphins change school swimming patterns in relation to weather. In rough seas, groups of dolphins appear to ride the swells and breaking waves that sweep toward the Kona coast. On one such occasion, while we "hove to" in a rough sea, perhaps 100 spinners passed us. They were divided into small groups of less than a dozen animals. These groups swam tightly together and often could be seen racing down the foreslope of the waves, sometimes breaking the water together and sometimes staying wholly within the wave. Such behavior is commonly seen in other cetacean species (Norris and Dohl in press).

Sound Emmissions

A detailed study of spinner dolphin sound emissions will be presented in a future paper. A few observations are appropriate here.

There is a marked diurnal fluctuation in the kind and amount of spinner dolphin vocalization (Powell 1967). Alert schools produce an array of sound types such as clicks, pure-tone whistles or "squeals," and a variety of burst pulse signals that can be described by such terms as barks, moos, chirps, etc. The clicks are of considerably lower intensity than either the whistles or the burst signals (Watkins and Schevill 1974), and the clicks may be more tightly focused.

Resting schools are nearly silent, emitting almost entirely clicks and even these are sporadic. Simultaneous with arousal, vocalizations rise in variety and abundance. Whistles and burst pulse signals can be heard quite long distances underwater. With Watkins and Schevill, we were able to station ourselves outside Kealakekua Bay and hear whistles and various burst pulse signals from a group of spinners swimming close to the cliff, approximately 2 km distant. Thus, a school of dolphins swimming outside Kealakekua Bay during longshore movement would be able to detect animals deep in the bay without entering it. It is possible that the schools we have seen passing the bay when others occupied it may have been excluded by acoustic signals.

No context-specific sound signals have been identified by us, except that it seemed clear that clicks were emitted concurrent with the inspection of the environment. The likelihood of context-specific acoustic signaling in the daily events in the school, however, seemed high. For example, synchronous diving in very widely dispersed schools, or simultaneous turning of an entire school at dusk, are unlikely to be visually cued (though it is not impossible). The sounds produced by aerial behavior have, in a few instances, been picked up by our listening gear. Tailslaps are especially loud, while spins (which we have recorded in captive situations) produced a lower intensity signal quite different in character.

Predators

Hawaiian spinner dolphins seem to be attacked with some frequency by sharks. Several of the scarred animals we cataloged had obviously been wounded by large sharks. Lunate rows of tooth marks, especially on the tail region, some apparently from sharks with a 12-15 in (31-38 cm) gape were noted. In one case it seemed that the entire tailstock had once been in a shark's mouth. Nicked or tattered dorsal fins may also have been produced by shark bite.

Subcircular scars somewhat larger than a silver dollar commonly seen on tropical and subtropical cetaceans are common on spinner dolphins. Jones (1971) suggested that these scars are produced by the small squaloid shark *Isistius brasiliensis*. This small shark occurs with scattering layer organisms, is bioluminescent over its entire body, and is thought to be a squid mimic. Feeding dolphins may be attracted to it, and when close, the shark may swim to the dolphin, attach itself, and then scoop out a disc of blubber and flesh with its peculiar dental and branchiostegal apparatus. The shark has erect cutting teeth only in the lower jaw and a jaw apparatus that allows it to attach and push the teeth through the flesh of its prey like a cookie cutter. The shark may bite while facing the tail of the porpoise and be swung around in the current, cutting as it goes. Discs of dolphin blubber have been found in the stomachs of this shark (Jones 1971). We have seen fresh wounds of this shape and size several times, including some completely through the blubber to the flesh beneath. Nearly every adult dolphin bears some scars of this sort, on some part of its body. We have never seen such scars on the appendages or head, though

they are common on the throat, flanks, and especially on the belly and the region between the flippers.

DISCUSSION

Instead of finding tightly knit schools of constant size that habitually occupied a given cove, as we had expected we found coves occupied by schools of highly variable numbers and composition. These variable schools often merged with other schools to form large feeding groups offshore, and school members moved back and forth between resting areas many kilometers apart in what seemed a completely free fashion. Rather than finding dolphins occupying a "home cove" the tendency to gather in shallow waters near shore seems to be related to a combination of topographic factors including the presence of adequate areas of shallow water and the proximity to nearby deepwater feeding grounds. Further, the population occupying such a cove during the daily rest period seems limited in some fashion by this same topography. Kealakekua Bay seems able to hold only about 60-70 animals, and even this number seems so large that rest may be inhibited. Deep rest, without aerial behavior, seems only to occur when relatively few animals, about 30-40 or less, are in the cove. In contrast, Keahole Point regularly holds >100 animals during daily rest.

Instead of finding schools headed directly for rest areas in the morning, we found schools moving toward the coast in the morning in a much more general fashion, encountering the coast, swimming alongshore, entering coves, sometimes coalescing with schools already in occupancy, or apparently sometimes passing by a cove filled with animals, to move on toward other less occupied rest areas. The entry and exit patterns of schools relative to coves also suggests such opportunistic use. At Kealakekua Bay, schools entered primarily from the south perhaps because rest areas south of this bay are very restricted while much more extensive areas exist to the north and in effect this inhospitable shore "collects" but does not hold incoming schools, Exit, on the other hand, is primarily to the north, as if schools came into the cove rested for a time, and continued on their way toward offshore feeding grounds. The primary feeding grounds seem to be to the north and west of Kealakekua Bay, off the shallows of the island, though our observations are sparse. To the north of Kealakekua Bay are other rest areas, while to the south deep water adjoins the shore. Thus occupancy or lack of same of a given rest cove and arrival direction to it may be related to nighttime feeding movements which leave animals offshore at various locations after the scattering layer descends with dawn. None of this, of course, indicates that dolphins do not know where available rest areas are, or know the features of them.

What, then, is the true dolphin school? Are the large offshore aggregations, formed of a coalescence of smaller resting groups, such a cohesive unit? Or, should we focus our attention on school subgroups of a few animals, which may habitually swim together (though our evidence is inconclusive in this respect), in the search for structure, regarding the large groups as opportunistic assemblages? Or, can both be properly considered as schools?

The large offshore feeding assemblages have clear structure in some respects. Such schools often dive and surface more or less together, and much social behavior is evident at times in them. These schools swim in a common direction and sometimes change course in a coordinated fashion. We often noted age-related subgroups within them; mothers and calves, or juveniles swimming together. But, if such schools are followed, they will sometimes split into parts that move in different directions, and clearly, they fragment during the day when smaller schools enter coves or shallows to rest.

Smaller schools exhibit most of the same behavior, though many times not all age classes will be represented in them. Schools of less than about 30 animals are seldom split for long by a vessel. These groupings we call schools, preferring to recognize that such schools change in size from time to time.

Clearly, from our marked animal information, individuals utilize a rather extensive area of coast for feeding, moving from group to group, and thus, in aggregate the population of a given portion of coast is a functional unit, in relation to its trophic relations with the immediate environment. The degree of discreteness of such populations from those adjacent remains wholly unknown, as does any possible intermixing between islands.

Considering this high degree of fluidity, how is directed movement of a school achieved and how does the structure of schools come about? No leader seems to exist in the standard sense of an animal determining direction of movement by

swimming at the head of a group. Yet directed movement does occur in cetacean schools. Killer whales arrive off sea lion and sea elephant rookeries at the proper time to catch pups (Norris and Prescott 1961), and pilot whales arrive at specific feeding grounds when squid come to spawn or when capelin arrive in large schools (Sergeant and Fisher 1957). Such patterns presumably have a learned component, and similar patterns of dolphins opportunistically using human activities to locate and capture food must be largely or wholly learned. For instance, bottlenose dolphins follow trawlers in the Gulf of Mexico (Leatherwood 1975) and in the Gulf of California (Norris and Prescott 1961) and obtain fish and other food items stirred up by the trawl or cast over the side during sorting of the catch.

Tavolga and Essapian (1957) described adult male bottlenose dolphins harassing newborn calves and their mothers, and dominance by adult females is also discussed. We have noted strong aggressive behavior in captive male spinner dolphins at Sea Life Park oceanarium in Hawaii. In the wild dolphin school, similar actions probably serve to order the structure of the school. Females and newborn young may be herded to their normal position in the interior of the school. We expect that such aggression combined with experience may serve to regulate the direction of school movement from various locations in a school. For instance, adult male killer whales usually occupy a position in travelling schools far out on the wings of the moving group, and from this position directional signals may be communicated to the school as a whole (Norris and Dohl in press).

The tendency of spinner dolphins to rest over shallow sandy areas is most probably a protective adaption allowing the quiescent school to place a protective bottom close beneath it and a shore nearby on one flank. The chances of attack from those directions by large deepwater sharks are correspondingly reduced. With much individual behavioral flexibility suppressed in resting schools, collective wariness rises, we presume through sensory integration by the school. Thus, the use by spinner dolphins of alert daytime-feeding spotted dolphin schools in the open eastern tropical Pacific Ocean, we feel, may account for the otherwise unusual daytime association between these two species.

We regard this study as preliminary, allowing glimpses into the life of one wild dolphin species and focusing our attention on important problem areas such as acoustic signalling, school structure, energetics, and social relationships.

ACKNOWLEDGMENTS

The assistance we have been given in this study has been great. We thank our vessel captains, Dan Camacho, Frank Cunningham, Georges Gilbert, Roger Gray, George Hanawahini, and Vern Hanson, and also our observers, Larry Hobbs and David Bryant.

We thank also Wilham Arbeit, George Barlow, Marlee Breese, Gregory Bateson, Paul Breese, Robert Elsner, William Evans, Sheri Gish, Sharon Gwinn, Ted Hobson, Ingrid Kang, William McFarland, Fred Munz, Karen Pryor, Scott Rutherford, William Schevill, Robert Shallenberger, Edward Shallenberger, and William Watkins for other field assistance.

The discussions we have had with George Barlow, Gregory Bateson, William Perrin, William Rogers, and Karen Pryor have helped a good deal to clarify our ideas of what these often elusive and hard-to-see animals were doing.

Sherwood Greenwell went far out of his way helping with our observation posts on his land. Bob Haws and Don Brandy, especially, helped with the flying. Tap Pryor assisted us many times with ships and support. The MOC grew from the hands and mind of Jimmy Okudara.

Richard Young and John Walter of the University of Hawaii identified the cephalopod and shrimp remains in stomach contents.

Nothing could have been accomplished without patient programmatic support, most of which came from the Biological Branch of the Office of Naval Research, through the continuing interest of Deane Holt, Helen Hayes, Charles Woodhouse, and Ron Tipper. Other support (for the hukilau work) came from the National Marine Fisheries Service and from the Oceanic Institute.

Finally, our thanks to Bob Leslie, native of Kealakekua Bay, and some of his fishermen associates, such as "Only LeRoy," we learned much about our animals and the place where they lived.

LITERATURE CITED

CALDWELL, M. C., AND D. K. CALDWELL.
1967. Dolphin community life. Los Ang. Cty. Mus., Q. 5(4): 12-15.

DOHL, T. P., K. S. NORRIS, AND I. KANG.
1974. A porpoise hybrid, *Tursiops* × *Steno*. J. Mammal. 55:217-221.

EVANS, W. E.
1973. Echolocation by marine delphinids and one species of fresh-water dolphin. J. Acoust. Soc. Am. 54:191-199.
1974. Radio-telemetric studies of two species of small odontocete cetaceans. *In* W. E. Schevill (editor), The whale problem: A status report, p. 385-394. Harv. Univ Press, Camb. Mass.

FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25:2561-2574.

HESTER, F. J., J. R. HUNTER, AND R. R. WHITNEY.
1963. Jumping and spinning behavior in the spinner porpoise. J. Mammal. 44:586-588.

JONES, E. C.
1971. *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull., U.S. 69:791-798.

KASUYA, T.
1972. Growth and reproduction of *Stenella caeruleoalba* based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst. (Tokyo) 24:57-79.

KASUYA, T., N. MIYAZAKI, AND W. H. DAWBIN.
1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. (Tokyo) 26:157-226.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottle-nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off Southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.

MCBRIDE, A. F., AND D. O. HEBB.
1948. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. J. Comp. Physiol. Psychol. 41:111-123.

NORRIS, K. S., AND T. P. DOHL.
In press. The structure and functions of cetacean schools. *In* L. Herman (editor), The behavior of marine mammals. Wiley Interscience.

NORRIS, K. S., AND W. E. EVANS.
1967. Directionality of echolocation clicks in the rough-tooth porpoise *Steno bredanensis* (Lesson). *In* W. N. Tavolga (editor), Marine bio-acoustics, p. 305-316.

NORRIS, K. S., AND J. H. PRESCOTT
1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool. 63:291-402.

PERRIN, W. F
1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish. Bull., U.S. 70:983-1003.
1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr., Univ. Calif. 21, 206 p.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71 1077-1092.

POWELL, B. A.
1976. Periodicity of vocal activity of captive Atlantic bottlenose dolphins: *Tursiops truncatus*. Nav. Ord. Test Stn. Tech. Publ. 4302:237-244

PRYOR, K. W.
1973. Behavior and learning in porpoises and whales. Naturwissenschaften 60:412-420.

SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER
1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. Koedoe 15:1-24.

SAAYMAN, G. S., AND C. K. TAYLER.
1971 Responses of man to captive and free-ranging cetaceans. Baralogia; Proc. 1st and 2d South African Symposium for Underwater Sciences. Univ. Pretoria, p. 1-9
1979. The socioecology of humpback dolphins (*Sousa* sp.). *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals, Vol. 3: Cetaceans, p. 165-226. Plenum Press, N.Y.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenburg). Behavior 44:212-233.

SCHEVILL, W. E., AND W. A. WATKINS.
1966. Sound structure and directionality in *Orcinus* (killer whale). Zoologica (N.Y.) 51:71-76.

SCHLEGEL, H.
1841. Abhandlungen aus dem Gebiete der Zoologie und vergleichenden Anatomie. 1. Heft. A. Arnz and Comp., Leiden, 44 p.

SERGEANT, D. E., AND H. D. FISHER.
1957. The smaller cetacea of eastern Canadian waters. J. Fish. Res. Board Can. 14:83-115.

SHANE, S. H.
1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. Thesis, Texas A&M Univ., College Station, 239 p.

TAVOLGA, M. C., AND F. S. ESSAPIAN.
1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zoologica (N.Y.) 42:11-31.

TAYLER, C. K., AND G. S. SAAYMAN
1972. The social organisation and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Ann. Cape Prov. Mus Nat. Hist. 9.11-49.

WATKINS, W. A., AND W. E. SCHEVILL.
1974. Listening to Hawaiian spinner porpoises, *Stenella* cf. *Longirostris*, with a three-dimensional hydrophone array. J. Mammal. 55:319-328.

WELLS, R. S., B. IRVINE, AND M. D. SCOTT.
In press. The social ecology of inshore odontocetes. *In* L. Herman (editor), Cetacean behavior. Wiley Interscience, N.Y.

WURSIG, B.
1978. On the behavior and ecology of bottlenose and dusky porpoises in the South Atlantic. Ph.D. Thesis, State Univ. New York, Stony Brook, 334 p.

WURSIG, B., AND M. WURSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.

LARVAL DEVELOPMENT OF *HYPOCONCHA SABULOSA* (DECAPODA: DROMIIDAE)[1]

WILLIAM H. LANG[2] AND ALAN M. YOUNG[3]

ABSTRACT

Larval development of the dromiid crab, *Hypoconcha sabulosa*, consists of three zoeal stages and one megalopa. The zoea exhibit numerous characteristics normally associated with anomuran larvae.

Hypoconcha sabulosa (Herbst) is a relatively uncommon inhabitant of coastal waters from North Carolina to the coast of Texas. Another member of the genus, *H. arcuata* Stimpson, coexists throughout much of the range (Williams 1965). These crabs are frequently overlooked owing to their habit of carrying an empty clam shell on their back. Kircher (1970) described the laboratory-reared larval stages of *H. arcuata* the larval stages of *H. sabulosa* are undescribed.

The family Dromiidae is an enigmatic group which has remained a point of contention in the phylogeny of the Decapoda. It has often been suggested that the brachyurans are a monophyletic group and that the dromiids represent a primitive true crab (Balss and Gruner 1961; Glaessner 1969; Stevcic 1974; Warner 1977). However, it is also strongly argued that the brachyurans are polyphyletic and that the dromiids are more closely related to anomuran or thalassinid groups (Gurney 1942; Williamson 1974).

METHODS

On 14 June 1976, a single gravid *H. sabulosa* female was collected by dredging in the North Inlet estuary, near Georgetown, S.C. Water temperature at the time of collection was 24° C; salinity was 27‰. The female was returned to the Baruch Laboratory, Columbia, S.C., and placed in a 9 cm Carolina culture dish containing filtered natural seawater of 25‰ salinity and maintained at 25° C under a 14L:10D light schedule. On 21 June, the brood began hatching and 22 active larvae were placed individually in 6 cm dishes containing 15 ml filtered seawater (25‰) and maintained as described for the adult. Water was changed daily and freshly hatched brine shrimp nauplii (San Francisco Bay Brand[4]) were added as food following each water change. Additional larvae hatching during the following day were reared in a 1 l shallow glass dish under similar conditions. These larvae were sacrificed during development to provide replicate material for descriptions.

Records were kept for each of the 22 larvae individually cultured to determine the number and duration of larval stages. Exuviae and larvae were preserved in 70% ethyl alcohol. Drawings were made from preserved larvae using a Zeiss drawing tube. Measurements of preserved larvae were made with an ocular micrometer; total length and carapace length are as defined by Pike and Williamson (1960a). Abbreviations and setal types mentioned are as in Johns and Lang (1977). Descriptions and sizes are based on at least five apparently healthy larvae sacrificed at each stage.

RESULTS

Development

Three zoeal stages and a megalopa were obtained through laboratory rearing; no variability in the number of larval molts was observed. Larvae were easily reared in both mass culture and individual chambers. Of larvae not sacrificed, 72% survived to megalopa and 75% of the megalopae successfully molted to first crab (Table 1).

[1]Contribution No. 287 from Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, SC 29208.

[2]Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, S.C.; present address: U.S. Environmental Protection Agency, Environmental Research Laboratory, South Ferry Road, Narragansett, RI 02882.

[3]Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, S.C.; present address: Biology Department, Nasson College, Springvale, ME 04083.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted June 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980

TABLE 1.—Survival, development time, and duration of the larval stages of *Hypoconcha sabulosa* reared in the laboratory.

Item	Zoea I	Zoea II	Zoea III	Megalopa	1st crab
Percent survival from first zoeal stage to successive stages (% based on original 22 minus those sacrificed for figures)		86	76	72	53
Percent survival within each stage (% of stage not sacrificed to reach subsequent stage)	86	89	93	75	
Days from hatching to reach each stage mean (range)		3 6 (3-6)	7 2 (6-9)	10 5 (9-13)	20 9 (17-25)
Duration of each stage in days mean (range)	3 6 (3-6)	3 9 (3-4)	3 4 (3-4)	10 6 (8-14)	

At 25° C, 25‰ salinity, development to first crab averaged 21 days (Table 1). Mean duration of each zoeal stage was 3 or 4 days while the megalopa lasted approximately 10 or 11 days. Mean sizes and ranges for five larvae at each stage are given in Table 2.

TABLE 2.—Size of *Hypoconcha subulosa* larvae stages, based on five larvae at each stage.

Stage	Carapace length (mm)		Carapace width (mm)		Total length (mm)	
	Mean	Range	Mean	Range	Mean	Range
Zoea I	1 30	1 20-1 37	0 72	0 66-0 74	2 39	2 21-2 50
Zoea II	1 49	1 40-1 55	0 81	0 73-0 88	2 51	2 33-2 70
Zoea III	1 62	1 51-1 70	0 90	0 85-0 93	2 90	2 81-2 92
Megalopa	1 60	1 54-1 64	1 20	1 11 1 24	—	—

Larval Description

Live *H. sabulosa* zoeae are strong, active swimmers which readily capture *Artemia salina* nauplii. At first sight they generally look like large, proportionally short and bulky pagurid zoeae. The zoeae have a generally reddish-brown color and are most noted by the distinctive line of chromatophores along the ventral and posterior carapace margin (Figure 1).

Figures of the larval stages show the most common arrangement of setal numbers observed. For the most part, the figures should be self-explanatory; the descriptive text is intended to note significant morphological features and outline setal numbers with observed variations.

Zoea I

Carapace (Figure 1A, a) without dorsal and lateral spines, rostrum directed anteriorly, ventrolateral carapace margin smooth. Carapace striated with crisscrossing fine ridges giving a textured "skinlike" appearance. At least one pair of transverse grooves evident, eyes sessile.

Abdomen (Figure 1A, a) without spines or distinct projections, somite six and telson fused, small pleopod buds may be present.

Telson (Figure 2A) triangular with distinct median notch; setation 7 + 7 with outer fixed spine, hairlike plumose seta, and five large plumose setae.

AN1 (Figure 3A) — Single segment; terminal setation of three aesthetascs and two simple setae; subterminal setation of two plumose setae.

AN2 (Figure 3E) — With 10 plumose setae on scale and 4 plumose setae on endopodite.

MN (Figure 4A, a) — With concave median surface and lateral serrate rim. Ventroposterior region with asymmetric group of teeth.

MAX1 (Figure 5A) — With two-segmented endopodite, distal segment with six setae, proximal segment with two setae; basal endite with three cuspidate and two plumodenticulate setae; coxal endite with four stout multidenticulate setae, three plumodenticulate setae, and one simple seta.

MAX2 (Figure 6A) — With indistinctly segmented endopodite, 2 or 3 setae; bilobed basal endite, distal lobe with 5 setae, proximal lobe with 5 setae, bilobed coxal endite, distal lobe with 5 setae, proximal lobe with 9 setae, scaphognathite with 17 or 18 marginal plumose setae. All setae plumose, plumodenticulate, or simple.

MXP1 (Figure 7A) — Exopodite with four plumose setae; endopodite five-segmented with numerous median margin setae and one lateral margin seta on distal segment.

MXP2 (Figure 7E) — Exopodite with four plumose setae; endopodite four-segmented with indicated pattern of median margin setae and one lateral margin seta on distal segment.

MXP3 — Limited to undeveloped bud.

P1 (Figure 7L) — Unsegmented biramous appendage with up to two plumose setae.

Zoea II

Carapace (Figure 1B, b) with same basic features as stage I but with two distinct pairs of transverse grooves; eyes stalked.

Abdominal somites (Figure 1B) with pleopod buds; somite six and telson partially fused.

FIGURE 1.—*Hypoconcha sabulosa* Lateral and dorsal view of zoeal stages I (A, a), II (B, b), and III (C, c).

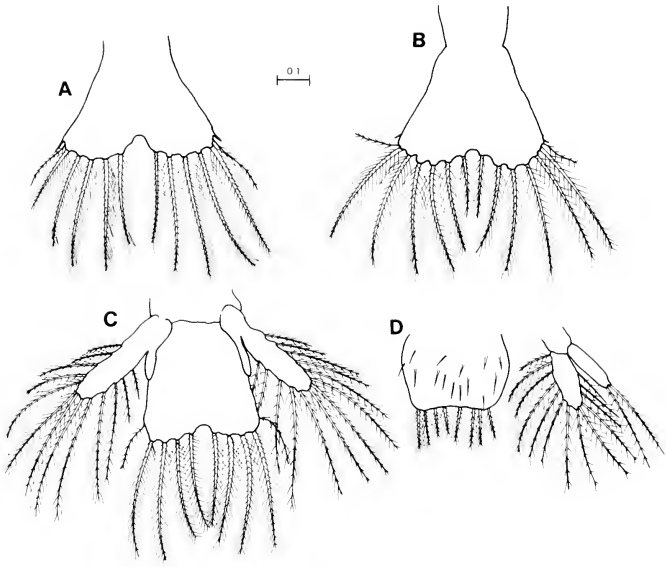


FIGURE 2.—*Hypoconcha sabulosa*: telson of zoeal stages I (A), II (B), and III (C), and megalopa (D). Only one disarticulated uropod is shown for megalopa.

Telson (Figure 2B) with reduced median notch; setation 8 + 8 with small outer fixed spine, hair-like plumose seta, and six large plumose setae.

AN1 (Figure 3B) — Indistinctly segmented; terminal setation of five aesthetascs and three fine simple processes; subterminal setation of two large plumose setae and two or three short plumose setae; additional one or two short setae may be present along basal margin.

AN2 (Figure 3F) — Similar to stage I with 19 plumose setae on scale and 3 plumose setae on endopodite.

MN — Similar to stage I; no palp.

MAX1 (Figure 5B) — With major features as in stage I, basal endite (7 setae) and coxal endite (10 or 11 setae) with additional fine setae as indicated.

MAX2 (Figure 6B) — With two-segmented endopodite, 5 setae distal, 3 setae proximal; bilobed basal endite with 5 or 6 setae distal, 6 setae proximal; bilobed coxal endite with 4 setae distal, 11 setae proximal; and scaphognathite with 21-23 plumose setae. Setal types a mixture of simple, plumose, and plumodenticulate.

MXP1 (Figure 7B) — Exopodite with six plumose setae; endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP2 (Figure 7F) — Exopodite with five plumose setae, endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP3 (Figure 7I) — Exopodite with five plumose setae; endopodite indistinctly segmented with two to three plumose setae.

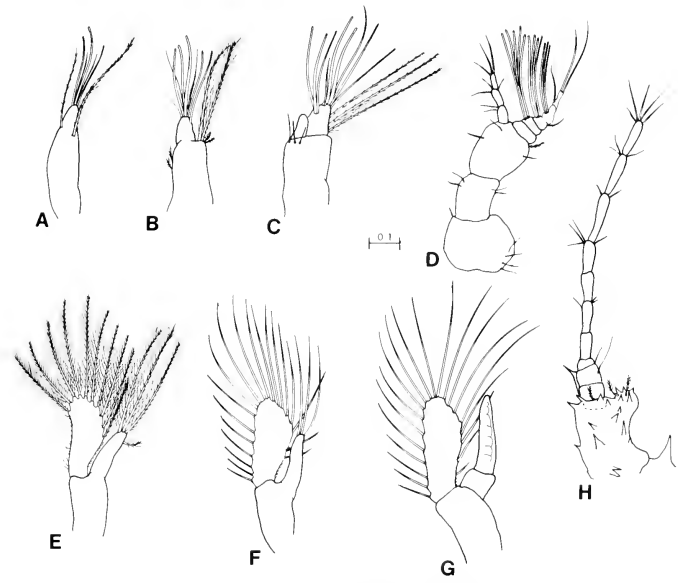


FIGURE 3:—*Hypoconcha sabulosa*: antennule of zoeal stages I (A), II (B), III (C), and megalopa (D); antenna of zoeal stages I (E), II (F), and II (G), and megalopa (H).

P1 to P5 (Figure 1B) — Conspicuous buds, first pereiopod distinctly biramous, four plumose setae on rudimentary exopodite (Figure 7M).

Zoea III

Carapace (Figure 1C, c) similar to stage II, a small blunt lateral spine near ventral carapace margin and posterior to second transverse groove present in some individuals; eyestalk with anterodorsal papilla.

Abdominal somites (Figure 1c) with elongated pleopod buds; sixth somite and telson distinctly segmented.

Telson (Figure 2C) normally 6 + 6 with very small outer spine, hairlike plumose seta, and 4 plumose setae; 2 zoeae 7 + 7 with 5 plumose setae, uropods with simple endopodite lobe and 13 or 14 setae on exopodite.

AN1 (Figure 3C) — Two-segmented; inner ramus a simple lobe; outer ramus with three terminal stout aesthetascs, three or four terminal fine processes (either simple setae or aesthetascs), three or four subterminal aesthetascs; basal segment with three stout plumose setae and three or four short plumose setae, also two short plumose setae (not figured) or proximal margin.

AN2 (Figure 3G) — With simple two-segmented endopodite and 18-21 plumose setae on scale.

MN (Figure 4B) — With simple palp.

MAX1 (Figure 5C) — With two-segmented endopodite, distal segment with two or three termi-

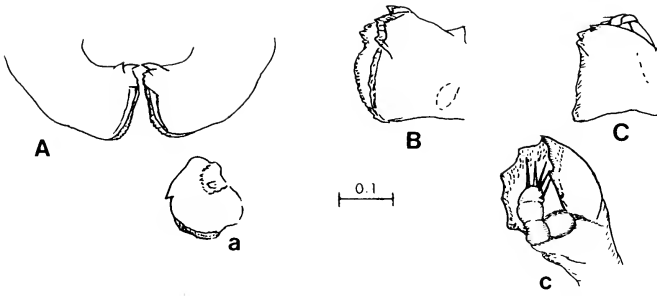


FIGURE 4.—*Hypoconcha sabulosa*: ventral view (A) and outline of biting survace (a) of stage zoeal I mandible: ventral view of zoeal stage III mandible (B); ventral view (C) and dorsal view (c) of megalopa mandible.

nal setae and two pairs of subterminal setae, proximal segment with two setae; basal endite with four or five stout cuspidate setae and five to seven finer plumose or plumodenticulate setae; coxal endite with six or seven stout multidenticulate setae and seven to nine finer setae.

MAX2 (Figure 6C) — With two-segmented endopodite, 5 setae on terminal segment, 3 or 4 setae on proximal segment; bilobed basal endite with 6 setae each lobe; bilobed coxal endite with 4 or 5 setae distal lobe, 14-17 setae in three rows proximal lobe (3 subterminal setae on opposite surface not figured); scaphognathite with 25-28 plumose setae.

MXP1 (Figure 7C) — Same as stage II but with one additional seta on endopodite lateral margin.

MXP2 (Figure 7G) — Exopodite with six or seven plumose setae; endopodite as in stage II but with additional seta on lateral margin.

MXP3 (Figure 7J) — Exopodite with six or seven plumose setae; endopodite with two distinct segments, four setae on terminal segment, one or two setae on proximal segment.

P1 to P5 (Figure 1C) — With pronounced extension beyond carapace; first pereiopod (Figure 7N) biramus, exopodite with six terminal setae; remaining pereiopods uniramus with segmentation evident and some simple setae or hairs.

Megalopa

Carapace (Figure 8A) dorsoventrally flattened with circular anterior margin and concave posterior margin; hepatic carapace margin with seven to nine distinct spines on each side, median anterior region depressed leading to short tapered rostrum; ventroposterior margins with short plumose setae; surface generally covered with numerous hairs, spinules, and plumose setae; eyestalk with distinct anterodorsal spine.

Abdominal segments with distinct lateral spines on segments two to six; dorsal surface with numerous hairs and spinules.

Telson (Figure 2D) nearly square, covered with hairs; anterior margin straight to slightly concave with 8 plumose setae; articulated uropods, endopodite with 2 plumose setae, exopodite with 13 or 14 plumose setae.

AN1 (Figure 3D) — With three basal segments; outer ramus with five segments, setation from tip to base, three simple setae, three or four aesthetascs, four aesthetascs, no setae; inner ramus with three segments with 2-3-2 setae.

AN2 (Figure 3H) — Basipodite with palp, numerous spines and three or four plumose setae; endopodite with 10 segments.

MN (Figure 4C, c) — With outer cutting edge and depressed center; palp three-segmented with five processes on distal segment.

MAX1 (Figure 5D) — With three-segmented endopodite, setation reduced to 6 setae as shown; basal endite with 7 cuspidate setae, 8 or 9 plumodenticulate setae, and 3 plumose setae on

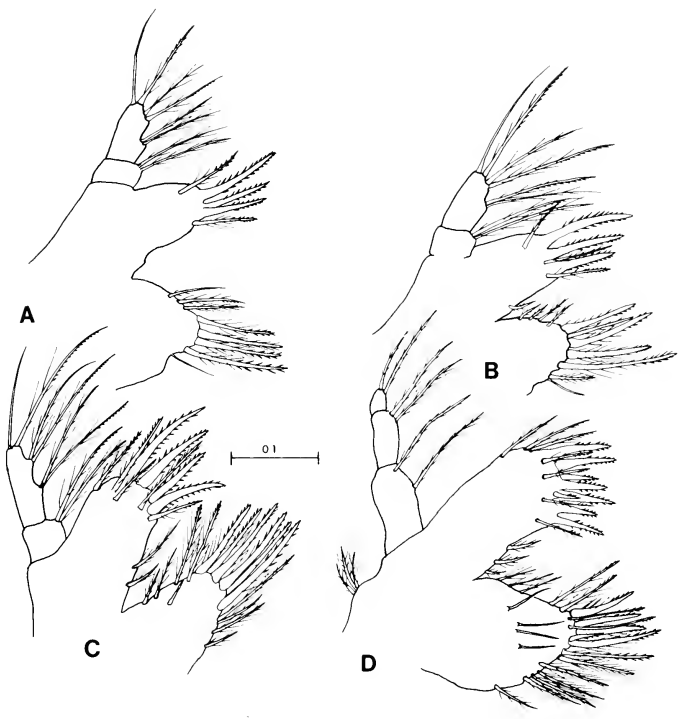


FIGURE 5.—*Hypoconcha sabulosa*: maxillule of zoeal stages I (A), II (B), and III (C), and megalopa (D).

proximal margin; coxal endite with 5 or 6 stout multidenticulate setae and 18-20 finer setae.

MAX2 (Figure 6D) — With two-segmented endopodite, 5 setae on terminal segment, 1 or 2 setae on proximal segment; bilobed basal endite with 9 setae distal lobe, 8-10 setae proximal lobe, bilobed coxal endite with 7-9 setae distal lobe, 20-22 setae proximal lobe; scaphognathite with 37-40 plumose setae.

MXP1 (Figure 7D) — Exopodite with 2 or 3 terminal and 2 or 3 subterminal plumose setae; endopodite indistinctly segmented with 8 setae; basipodite with 24-28 setae; coxapodite with about 15 setae.

MXP2 (Figure 7H) — Exopodite with 5-7 terminal and 2 subterminal plumose setae; endopodite five-segmented, 5 or 6 terminal setae and 8-10 setae subterminal.

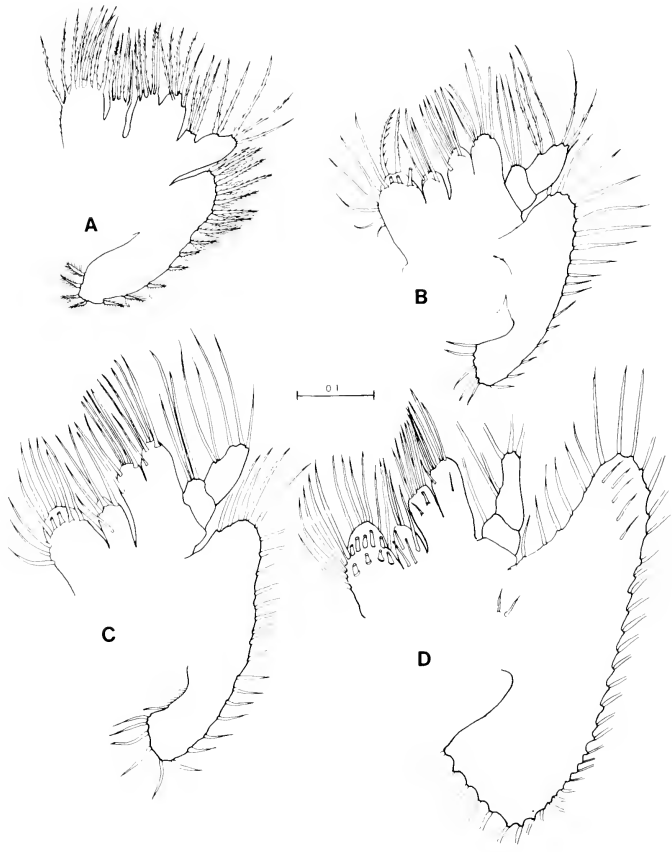


FIGURE 6.—*Hypoconcha sabulosa* maxilla of zoeal stages I (A), II (B), and III (C), and megalopa (D). Setules have been omitted from B-D for graphic clarity

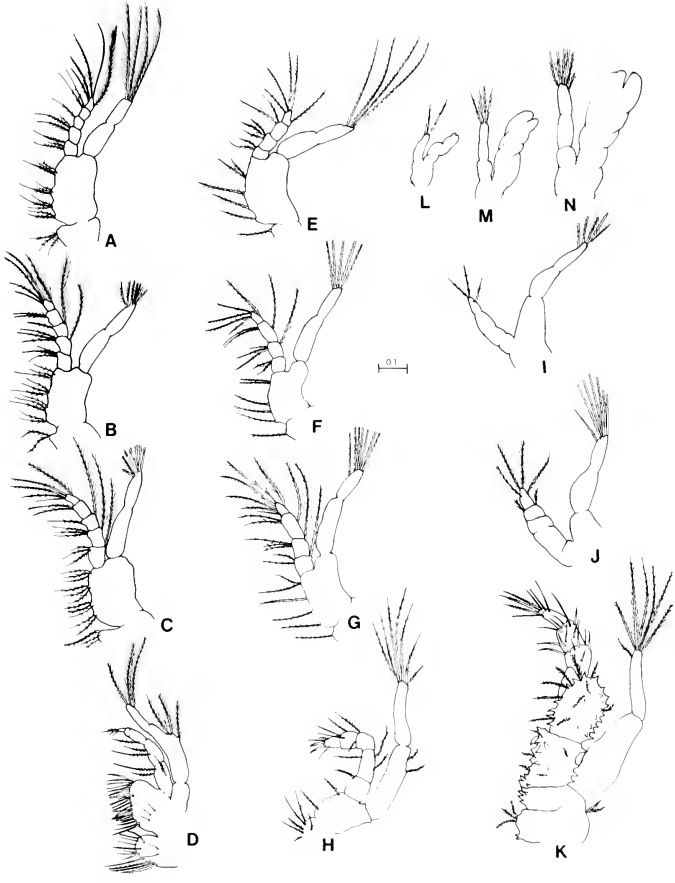


FIGURE 7.—*Hypoconcha sabulosa*: first maxilliped of zoeal stage I-megalopa (A-D); second maxilliped of zoeal stage I-megalopa (E-H); third maxilliped of zoeal stage II-megalopa (I-K); and first pereiopod of zoeal stage I-III (L-N).

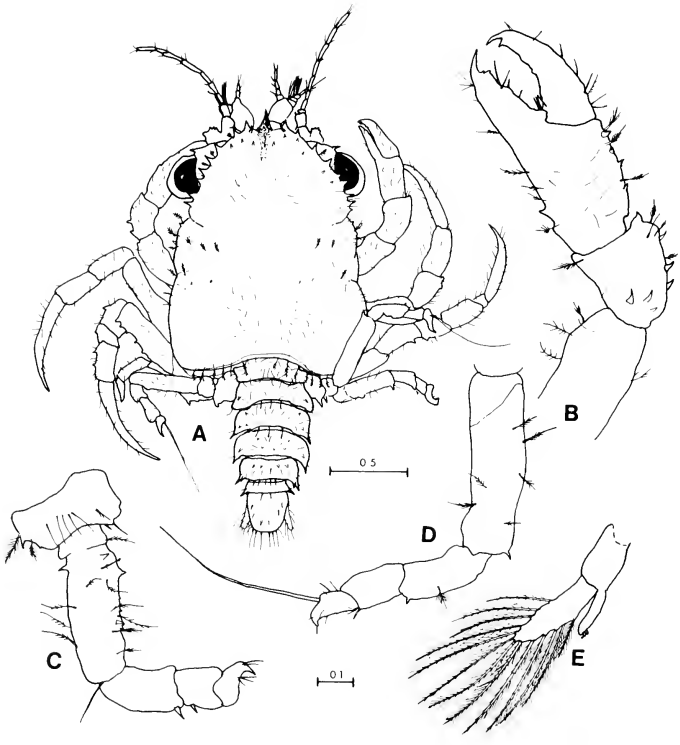


FIGURE 8.—*Hypoconcha sabulosa* dorsal view of megalopa (A) and details of appendages; cheliped (B), fourth pereiopod (C), fifth pereiopod (D), and second pleopod (E).

MXP3 (Figure 7K) — Exopodite with 6 or 7 plumose setae; endopodite five-segmented, setation tip to base, 6 or 7, 6-8, 6, 10-12, 5-8, numerous spines on two lower segments.

P1 to P5 (Figure 8A-D) — Uniramous with numerous hairs and short plumose setae. First pereiopod (Figure 8B) with equal-sized claws; second and third pereiopod similar, dactylpods with simple tapered tip; fourth pereiopod (Figure 8C) shorter, dactylpod hooked; fifth pereiopod (Figure 8D) carried high and over carapace, dactylpod hooked with long stiff simple process.

DISCUSSION

Hypoconcha Species Distinction

Both *H. arcuata* and *H. sabulosa* have similar ranges and habitats along the southeastern United States coast (Hay and Shore 1918; Williams 1965) and adult morphology is quite similar (Rathbun 1937; Williams 1965). The source of larvae for this study was a small (carapace 17 × 17 mm) female with characteristics dorsal carapace, color, and marginal spines (Williams 1965). However, the ventral carapace ridges were weakly developed and the three characteristic tubercles (Rathbun 1937) were not evident (one small tubercle was present). This may be characteristic of young specimens or it may indicate hybridization of the two species. The distinction of species for these two forms should perhaps be reinvestigated.

Not surprisingly, the differences between the larval morphology of *H. arcuata* given by Kircher (1970) and *H. sabulosa* are slight. The differences we observed overlap the ranges of variation reported for setation or represent fine points open to interpretation. Based on present published information, a reliable means to distinguish corresponding zoeal stages between the two species is absent. *Hypochoncha sabulosa* megalopae have spines on the eyestalk and abdominal segments, features not noted for *H. arcuata*. However, these may be points of omission by Kircher (1970) and represent only tentative differences. A detailed direct comparison of larvae is needed to determine if these species can be identified during ontogeny.

Characteristics of Dromiidae Larvae

Knowledge of dromiid larvae is limited to five genera within the family Dromiidae (Table 3). The larvae of *H. sabulosa* demonstrate most general features of dromiid larval development; some features, however, such as carapace armature are surprisingly diverse. Larval development ranges from six zoeal stages in *Dromidia antillensis* to two zoeal stages in *Conchoecetes artifiosus*. Four of ten documented species have abbreviated development (Table 3).

The dromiid zoeal carapace is elongated with a large, anteriorly directed rostrum, transverse grooves, and, in most cases, a textured surface of fine ridges. The carapace may lack armature (*Hypoconcha*, *Conchoecetes*), have posterolateral spines (*Dromia*), have supraorbital spines (*Dromidia*), or have a dorsal spine and lateral "wings" (*Petalomera*). Carapace margins are either smooth or denticulate. All zoeae are richly pigmented with a general orange-red color.

The antennal morphology is unique to the group. The endopodite has 3 or 4 plumose setae in stage I larvae. The exopodite is a flat scale and after stage I has setae on its outer margin.

The mandibular palp generally does not develop until the terminal zoeal stage while the maxilla endopodite is well developed and often distinctly segmented. The endopodites of the first and second maxillipeds are five- and four-segmented respectively. The third maxilliped is usually biramous and rudimentary in stage I but well developed with a basally situated endopodite by stage II.

TABLE 3.—Principal studies on the postembryonic development in taxa of the family Dromiidae.

Taxon	Author	Material
Dromiidae	Gurney (1924) Gurney (1942)	Plankton sample with unknown parents
Conchoecetes artifiosus	Sankolli and Shenoy (1968)	Laboratory—all stages
Cryptodromia octodentata	Hale (1925)	Abbreviated development
Dromia personata	Cano[1] (1893) Williamson[1] (1915) Lebour[1] (1934) Pike and Williamson[2] (1960b)	Plankton—I, IV, megalopa Plankton—I, IV, megalopa Plankton—I,II,IV, megalopa Plankton—I,II,III
	Rice et al (1970)	Laboratory—all stages
Dromidia antillensis	Rice and Provenzano (1966)	Laboratory—all stages
Dromidia australis	Hale (1927)	Abbreviated development
Epipedodromia thomsoni	Hale (1925)	Abbreviated development
Hypoconcha arcuata	Kircher (1970)	Laboratory—all stages
Hypoconcha sabulosa	Present paper	Laboratory—all stages
Petalomera lateralis	Montgomery (1922) Hale (1925)	Abbreviated development
Petalomera wilsoni	Wear (1970) Wear (1977)	Plankton—I, II Plankton—megalopa

[1]Described as *Dromia vulgaris*.
[2]Described as *Dromia personatus*

The pereiopods may be uniramous (*Conchoecetes*, *Petalomera*) or biramous (*Dromidia*). Only the first pereiopod is biramous in *Dromidia* and *Hypoconcha*. Uropods are well developed in late zoeae of *Dromia*, *Dromidia*, and *Hypoconcha* but are reduced in *Conchoectes* and *Petalomera*.

Systematic Position of the Dromiidae

The classification and phylogeny of the Dromiidae and other decapod groups rests princi-

pally on three lines of evidence: comparative morphology, fossil records, and larval development (Stevcic 1971). Based primarily on comparative morphology of adult crabs and sparse fossil records, the family Dromiidae has usually been considered primative but true brachyurans (Balss and Grunner 1961; Burkenroad 1963; Glaessner 1969; Hartnoll 1975; Warner 1977).

In contrast to these findings, the larval development of dromiids is, in many aspects, typically anomuran. Gurney (1924) found all larvae of *Dromia* to be "definitely Anomuran." Brachyuran and anomuran larvae have since been well characterized in several comprehensive studies (Gurney 1942; Pike and Williamson 1960a; Williamson 1974); the findings of Gurney (1924) have been consistently substantiated. The megalopa is not so easily characterized and appears to more closely resemble its parents than both postlarval anomurans and nondromiid brachyurans (Wear 1977). A detailed account of the classification of the Brachyura and a proposed new system has recently been published by Guinot (1978).

The Brachyura are characterized not only by the advanced organizational level of adults but also by a consistant larval form. The evolutionary path should include "brachyurization" to both a crab body (Stevcic 1971) and a "brachygnath zoea" (Williamson 1974). A key to better understanding the dromiids is to find larval types which appear to lead toward a brachygnath form. If, like the Dromiidae, the Dynomenidae and Homolodromidae are found to have larvae showing no tendency to develop brachygnath features, the Dromiacea (Guinot 1978) may have progressed toward a crablike form independent of lines leading toward the true brachyurans.

The combination of adult and larval characteristics exhibited by the Dromiidae has not been satisfactorily explained. In view of obvious contradictions and the relative importance of adult morphology in decapod classification, removal of the Dromiidae from the Brachyura based solely on known larval features (Gurney 1924, 1942; Kircher 1970; Williamson 1974) is not warranted. Placement of the Dromiidae within the Brachyura, is by no means "of little doubt" as claimed by Warner (1977) but represents more a matter of convenience (Guinot 1978); their position is tenuous at best. Hopefully additional material (larval, morphological, or fossil) will lead to a comprehensive account of the Dromiidae and related families.

ACKNOWLEDGMENTS

This study was initiated by the authors while at the University of South Carolina. The authors express their appreciation to the Belle W. Baruch Institute for support. Aid for completion of this project was provided by the EPA Environmental Research Laboratory at Narragansett, R.I., particularly through the cooperation of Don C. Miller and Donald K. Phelps. Akella N. Sastry, Graduate School of Oceanography, University of Rhode Island, generously allowed use of his microscope. We would also like to thank Daniele Guinot, Richard G. Hartnoll, Anthony L. Rice, and Zdravko Stevcic for providing publications and useful information.

LITERATURE CITED

BALSS, H., AND H. E. GRUNNER
1961. Decapoda, XI. Stammesgeschichte. *In* Dr. H. G. Bronn's (editor), Klassen und Ordnungen des Tierreichs, Bd. 5, Abt. 1, Buch 7, Lief. 14, p. 1797-1821. Geest and Portig, Leipz.

BURKENROAD, M. D.
1963. The evolution of the Eucarida, (Crustacea, Eumalacostraca), in relation to the fossil record. Tulane Stud. Geol. 2:1-21.

CANO, G.
1893. Svillupo dei Dromidei. Atti. Accad. Sci. Fis. Nat., Napoli, Ser. 2, 6:1-23.

GLAESSNER, M. F.
1969. Decapoda. *In* R. C. Moore (editor), Treatise on invertebrate paleontology, Pt. R, Arthropoda 4,2:R390-R533. Geol. Soc. Am., Boulder.

GUINOT, D.
1978. Principes d'une classification evolutive des Crustaces Decapodes Brachyoures. Bull. Biol. Fr. Belg. 112:211-292.

GURNEY, R.
1924. Crustacea. Part IX. — Decapod larvae. Nat. Hist. Rep. Br. Antarct. "Terra Nova" Exped., Zool. 8:37-202.
1942. Larvae of decapod Crustacea. Ray Soc. (Lond.) Publ. 129, 306 p.

HALE, H. M.
1925. The development of two Australian sponge crabs. Proc. Linn. Soc. N. S. W. 4:405-413.
1927. The Crustaceans of South Australia 1. Gov. Print., Adelaide, Aust., 201 p.

HARTNOLL, R. G.
1975. Copulatory structure and function in the Dromiacea, and their bearing on the evolution of the Brachyura. Publ. Stn. Zool. Napoli 39 (Suppl.):657-676.

HAY, W. P., AND C. A. SHORE
1918. The decapod crustaceans of Beaufort, N.C., and the surrounding region. Bull. U.S. Bur. Fish 35:369-475.

JOHNS, D. M., AND W. H. LANG
1977. Larval development of the spider crab, *Libinia emarginata* (Majidae). Fish. Bull., U.S. 75:831-841.

KIRCHER, A. B.
1970. The zoeal stages and glaucothoe of *Hypoconcha ar-*

cuata Stimpson (Decapoda:Dromiidae) reared in the laboratory. Bull. Mar. Sci. 20:769-792.

LEBOUR, M. V.
1934. The life-history of *Dromia vulgaris*. Proc. Zool. Soc. Lond. 1934:241-249.

MONTGOMERY, S. K.
1922. Direct development in a dromiid crab. Proc. Zool. Soc. Lond. 1922:193-196.

PIKE, R. B., AND D. I. WILLIAMSON
1960a. Larvae of decapod Crustacea of the families Diogenidae and Paguridae from the Bay of Naples. Publ. Stn. Zool. Napoli 31:493-552.
1960b. Larvae of decapod Crustacea of the families Dromiidae and Homolidae from the Bay of Naples. Publ. Stn. Zool. Napoli 31:553-563.

RATHBUN, M. J.
1937. The oxystomatus and allied crabs of America. U.S. Natl. Mus. Bull. 166:1-278.

RICE, A. L., R. W. INGLE, AND E. ALLEN
1970. The larval development of the sponge crab, *Dromia personata* (L.) (Crustacea, Decapoda, Dromidea), reared in the laboratory. Vie Milieu, Sér. A, Biol. Mar. 21:223-240.

RICE, A. L., AND A. J. PROVENZANO, JR.
1966. The larval development of the West Indian sponge crab *Dromidia antillensis* (Decapoda:Dromiidae). J. Zool. (Lond.) 149:297-319.

SANKOLLI, K. N., AND S. SHENOY
1968. Larval development of a dromiid crab, *Conchoecetes artificiosus* (Fabr.) (Decapoda, Crustacea) in the laboratory. J. Mar. Biol. Assoc. India 9:96-110.

STEVCIC, Z.
1971. The main features of brachyuran evolution. Syst. Zool. 20:331-340.
1974. La structure cephalique et la classification des decapodes brachyoures. Biol. Vestn. 22:241-250.

WARNER, G. F.
1977. The biology of crabs. Van Nostrand Reinhold Comp., N.Y., 202 p.

WEAR, R. G.
1970. Some larval stages of *Petalomera wilsoni* (Fulton & Grant, 1902) (Decapoda, Dromiidae). Crustaceana 18:1-12.
1977. A large megalopa attributed to *Petalomera wilsoni* (Fulton and Grant, 1902) (Decapoda, Dromiidae). Bull. Mar. Sci. 27:572-577.

WILLIAMS, A. B.
1965. Marine decapod crustaceans of the Carolinas. U.S. Fish Wildl. Serv., Fish. Bull. 65:1-298.

WILLIAMSON, D. I.
1974. Larval characters and the origin of crabs (Crustacea, Decapoda, Brachyura). Thalassia Jugosl. 10:401-414.

WILLIAMSON, H. C.
1915. Decapoden, I. Teil (Larven). Nord. Plankton Lief. 18, Abt. 6:315-588.

BLACK ROCKFISH, *SEBASTES MELANOPS*: CHANGES IN PHYSICAL, CHEMICAL, AND SENSORY PROPERTIES WHEN HELD IN ICE AND IN CARBON DIOXIDE MODIFIED REFRIGERATED SEAWATER

JEFF COLLINS, KERMIT D. REPPOND, AND FERN A. BULLARD[1]

ABSTRACT

The purpose of this study was to determine changes in various properties of fillets, minced flesh, and washed minced flesh from black rockfish, *Sebastes melanops*, as affected by time of holding in ice or carbon dioxide modified refrigerated seawater and frozen storage at -18°C. Fish were held up to 14 days in the holding mediums and removed periodically and analyzed for changes in physical, chemical, and sensory properties. The yield of fillets calculated from the initial whole weight was unaffected by time of holding in either system. Subjective observations made during the holding periods indicated that fillets of good quality could be prepared from rockfish held for 10 days in either system. These observations were confirmed in a later series by sensory evaluation of cooked portions from the frozen blocks of fillets prepared at intervals during an 11-day holding period. The chemical analyses for trimethylamine, total volatile acid, and total volatile base were of no use to measure spoilage. Washing the minced flesh resulted in a reduction of solids, trimethylamine oxide, and salt and a reduction in yield when expressed on a salt-free constant, 18% solids basis. The extractable protein nitrogen of minced flesh decreased with time of frozen storage at -18°C and was strongly influenced by the length of holding period for the fresh whole fish.

Several papers have been published on the fresh or frozen characteristics of fillets or minced flesh from rockfishes. Different species of rockfishes gave products having different fresh acceptability and frozen storage life (Miyauchi and Stansby 1952). Stansby and Dassow (1949) found that the frozen storage quality of fillets from yellowtail rockfish, *Sebastes flavidus*, could be improved by removing part of the dark flesh along the lateral line. Barnett et al. (1971) compared yellowtail rockfish held in refrigerated seawater (RSW) and RSW modified with the addition of CO_2 (MRSW). The fresh storage life was extended 1 wk in MRSW over RSW. Teeny and Miyauchi (1972) increased the frozen life of minced flesh of yellowtail rockfish and silvergray rockfish, *S. brevispinis*, by using various additives. Additional improvements in storage life were obtained by washing the minced muscle of black, silvergray, and yellowtail rockfishes (Miyauchi et al. 1975.)

The objectives of this study were generally to characterize and compare the changes that occur in black rockfish with time of holding in ice and in MRSW, to determine sensory properties of fillets as affected by fresh holding time, and to determine the changes in amine content and extractable protein nitrogen with time of frozen storage of washed and unwashed minced flesh.

EXPERIMENTAL PROCEDURES

Sampling

Two groups of fish were used in this study. Lot 1 was used to determine physical and chemical properties and Lot 2 was used for formal sensory evaluation. The fish were caught over a 2-h period with hook and line, with or without bait. These fish are found locally on exposed, highly sloped rocky shores with strong currents where trawling gear cannot be used. A sporadic local fishery has employed the same fishing technique. Lot 1 fish (154 fish, 265 kg, 0.2 kg SD) were captured 2 July 1977 at the Triplets, 20 mi northwest of Kodiak, Alaska, and delivered to the laboratory about 2 h later. The fish were individually tagged and weighed before placing in the previously described ice and MRSW holding systems (Bullard and Collins 1978). The raw fish handling and sample preparation were similar to that previously reported for walleye pollock (Reppond et al. 1979), and are briefly described here. Fish were sampled according to weight classes to give an average of

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

Manuscript accepted April 1979.
FISHERY BULLETIN: VOL. 77, NO. 4, 1980.

1.8 kg/fish for an 11-fish sample at holding periods of 0, 4, 6, 8, 10, 12, and 14 days. When removed from the holding systems, the fish were washed briefly to remove slime or ice, drained on a rack for 5 min, and individually weighed. The fish were filleted by hand and the fillets were rinsed briefly, drained on an inclined screen for 5 min, and weighed. Notes were made on the appearance of the round fish and the condition of the gills, viscera, and fillets. The fillets were ground using the coarse blade of an Oster[2] food grinder, and a portion was washed with cold water (1 part flesh: 2 parts water) for 15 min on a reciprocating shaker. The flesh was drained for 30 min on an inclined 16-mesh plastic screen then weighed. Composite portions of both washed and unwashed meats were frozen at -34° C for chemical tests. Other portions were sealed in polylaminated pouches and stored at -18° C for 2, 4, 6, and 9 mo.

Sensory

Lot 2 fish (184 fish, 258 kg) were used for formal sensory testing and were caught in the same location 1 mo later, on 26 August. These fish were held in ice and in MRSW in the same manner as Lot 1 and at 0, 3, 6, 8, and 11 days were filleted. The fillets were packed into blocks and held at -34° C for sensory evaluation several months later. The blocks were sawed into portions measuring 80 × 50 × 12 mm and thawed at room temperature. The control sample and samples from fish held in ice were salted by immersion in a 5% solution for 1.5 min to minimize differences in salt content with samples from fish held in MRSW. The portions were cooked in individual sealed aluminum pans at 232° C for 20 min in a commercial oven. Because of the difficulty in equalizing the salt content, samples from the two holding systems were not directly compared. The results of the sensory test were evaluated by analysis of variance. If analysis of variance indicated a change had occurred with time of holding, the Student-Newman-Keuls test was used to determine which samples were different.

Analyses

The frozen samples for chemical tests (Lot 1) were tempered overnight in a refrigerator at 3° C and ground twice using the fine blade of an Oster food grinder. Analyses were carried out for total nitrogen, total solids, chloride (Horwitz 1975: 15, 309, 310), total volatile acid (TVA, Friedemann and Brook 1938), total volatile base (TVB, Stansby et al. 1944), and extractable protein nitrogen (EPN, Dyer et al. 1950). Analyses for trimethylamine oxide (TMAO, Bystedt et al. 1959), nonprotein nitrogen (NPN, Nikkilä and Linko 1954), and trimethylamine (TMA, Tozawa et al. 1971) were carried out on a 5% trichloroacetic acid extract. An aliquot of the extract was neutralized and analyzed for dimethylamine (DMA) by Dowden's method (1938) modified by increasing the time of extraction to 15 min on a mechanical shaker.

RESULTS AND DISCUSSION

Physical Appearance and Yield

At each period of sampling, informal subjective observations were made on the whole fish and their raw fillets. We noted differences in gills, fins, and slime between the two holding systems. In ice, the gills were bright red to day 6 but discolored quickly in MRSW. Cloudiness of the eyes started at day 8 in ice but the eyes were white in a day or two in MRSW. The beginning of off-odors in the fillets, softening of flesh, and gut decompostion was observed in both holding systems at 10 days and worsened thereafter. At day 14, the odor of the fillets was objectionable and mincing intensified the odor. The quality of fillets from the fish held in MRSW were generally judged better than from fish held in ice for the same time. As noted later in this paper, neither formal sensory nor chemical tests detected the changes observed on the 10th day of holding in ice or MRSW. Chemical tests could not confirm the poor raw quality at 12 and 14 days which was so obvious that we would not serve these fillets to a taste panel. Consequently, we concluded that experienced observers could subjectively judge the various stages of raw quality, namely: good quality (0-8 days), onset of spoilage (10 days), and unacceptable quality (12 days).

Whole fish gained weight with time of holding in either system (Table 1). Fish held for 14 days in ice gained half as much weight as those held in MRSW, about 3% and 6%, respectively. The yield of fillets increased slightly with time of holding in ice but was constant with time of holding in MRSW. The average yield of fillets was slightly

[2]Reference to trade names here does not imply endorsement by the National Marine Fisheries Service, NOAA.

higher from fish held in ice than from fish held in MRSW, 31.7% and 30.5%, respectively. When yield data are converted to a salt-free, 18% solids basis however, equal yields of fillets were obtained in both systems (34%). The solids content of the fillets decreased slightly in ice but increased in MRSW because of the increase in salt content (Table 1). The absorption of salt from the MRSW system is not a problem because rockfish have thick flesh and skin.

TABLE 1.—Initial round weight and change in yield, salt, and total solids content of fillets and washed ground flesh from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Round wt[1] (kg)	Gain in wt (%)	Fillets Yield (%)	Salt (%)	Solids (%)	Washed ground flesh Yield[2] (%)	Salt (%)	Solids (%)
			Ice					
0	18 35	0 00	30 7	0 03	20 2	40 5	0 05	15 0
4	19 09	1 15	31 0	0 07	19 2	36 5	0 04	14 6
6	18 88	1 51	31 5	0 09	19 5	38 5	0 06	13 8
8	19 48	2 08	31 8	0 10	19 4	38 9	0 08	13 5
10	19 51	2 15	31 2	0 10	19 3	38 5	0 06	13 3
12	19 66	2 74	32 1	0 09	19 1	39 3	0 04	13 1
14	21 49	2 75	32 7	0 08	19 1	40 0	0 07	13 0
			Modified refrigerated seawater					
0	18 35	0 00	30 7	0 03	20 2	40 5	0 05	15 0
4	19 90	2 56	30 4	0 20	20 2	36 8	0 08	14 2
6	19 35	3 89	30 6	0 28	20 6	34 7	0 11	15 0
8	19 26	4 25	30 0	0 36	20 4	34 0	0 14	14 8
10	18 93	4 40	30 4	0 48	20 7	34 2	0 20	15 3
12	19 48	6 27	30 8	0 57	20 9	33 5	0 22	16 1
14	18 81	5 65	30 6	0 76	20 9	32 9	0 27	16 8

[1]Total round weight of fish that composed the sample
[2]Yield of washed ground flesh if no portion had been reserved for analysis of fillets

Sensory Evaluation

No significant ($P<0.05$) change in flavor, texture, or preference was noted between the zero time control and any sample from either holding system (Table 2). No significant differences in sensory scores occurred among the ice-held samples but the differences in flavor and preference scores between samples held 3 days and 8 days in MRSW were significant. However, these differences were probably circumstantial since neither the 3- nor 8-day MRSW sample differed from any of the other samples from that holding system.

The bland flavor of rockfish flesh was reflected in the preference scores which ranged from "like slightly" to "neither like nor dislike." The sensory data indicate that when held in ice or in MRSW this species of rockfish will maintain its acceptability during commercial holding periods of at least 8 to 10 days.

TABLE 2.—Change in mean sensory analysis scores ± standard deviations for baked portions of blocks of fillets from black rockfish (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW). Panel had 12 judges. Flavor and texture scores were on the following scale: 5-Very good, 4-Good, 3-Fair, 2-Borderline, and 1-Poor. Preference scores were on a 9-point scale: 9-Like extremely, 8-Like very much, 7-Like moderately, 6-Like slightly, 5-Neither like nor dislike, 4-Dislike slightly, 3-Dislike moderately, 2-Dislike very much, and 1-Dislike extremely.

Time of holding (days)	Flavor		Texture		Preference	
	Ice	MRSW	Ice	MRSW	Ice	MRSW
0	3 5±0 7		4 1±0 6		6 3±1 4	
3	3 1±0 4	3 8±0 6	3 9±0 7	4 1±0 3	5 8±0 7	6 4±1 3
6	3 4±0 7	3 6±0 5	4 1±0 5	4 0±0 4	6 3±1 2	6 3±0 9
8	3 6±0 6	2 9±0 8	4 3±0 5	3 8±0 6	6 5±1 0	5 2±1 3
11	3 5±0 8	3 1±0 5	4 0±0 5	3 8±0 6	6 4±1 3	5 4±1 2

Chemical Analyses

The protein content of fillets (Table 3) was unaffected by time of holding but was slightly lower from fish held in ice than in MRSW. The nonprotein nitrogen content decreased slightly with time of holding in both holding systems.

Several chemical tests were performed to measure spoilage. TVA values increased from 0.07 at 8 days in ice to 0.10 meq/100 g at 10 days which may indicate a change in quality at 10 days. No change was noted in fillets from the MRSW system. TVB values were constant and low (about 4 mg N/100 g). As with walleye pollock, TVB data were not useful to indicate spoilage. TMA values increased

TABLE 3.—Change in analytical values of fillets from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice						Modified refrigerated seawater					
	Protein[1] (%)	NPN (%)	TVA (meq H^+ 100g)	TVB (mgN 100 g)	TMA (mg N 100 g)	DMA (mg N 100 g)	Protein[1] (%)	NPN (%)	TVA (meq H^+/100 g)	TVB (mg N 100 g	TMA (mg N 100 g)	DMA (mg N 100 g)
0	18 3	0 34	0 06	3 9	0 20	0 20	18 3	0 34	0 06	3 9	0 20	0 20
4	18 5	0 33	0 06	3 6	0 41	0 30	18 8	0 32	0 06	3 3	0 37	0 23
6	18 8	0 31	0 06	—	0 41	0 24	19 0	0 31	0 07	—	0 43	0 23
8	18 3	0 31	0 07	—	0 49	0 27	19 0	0 30	0 06	2 8	0 49	0 29
10	18 4	0 31	0 10	—	0 59	0 29	19 2	0 30	0 06	—	0 56	0 18
12	18 2	0 30	0 11	—	0 62	0 30	19 1	0 30	0 07	2 9	0 67	0 37
14	18 4	0 30	0 10	3 9	0 82	0 24	19 0	0 27	0 08	—	0 69	0 29

[1]6 25 N

in an equal, gradual and linear manner with time of holding in both systems. DMA values did not change with time of holding or system (0.3 mg DMA-N/100 g).

Effects of Washing Minced Flesh

Washing the minced flesh of black rockfish resulted in a reduction in salt and solids content (Table 1), in slightly lower EPN values (Table 4), and a big drop in TMAO content (Table 5). Washing increased the apparent yield of minced fillets from 32 to 38% (ice) and from 32 to 33% (MRSW). When yield data of fillets and minced, washed flesh are placed on a comparable basis by converting to a salt-free, constant 18% solids basis however, the washing procedure reduced the yield in both systems from 34 to 28%.

Frozen Storage

A number of research papers have been published on the general subject of toughness of fish flesh and the relationship (or not) of free fatty acids, formaldehyde, and EPN (Mills 1975). The tough texture that develops in frozen fish is always accompanied by a decrease in EPN (Castell et al. 1973) but texture and EPN are not necessarily equated. It is generally accepted that reduced EPN occurs with increased fatty acid content and formaldehyde content (sometimes indirectly measured as DMA). The extractable protein nitrogen (Table 4) of minced flesh from ice-held fish decreased slightly at 2 and 4 mo of frozen storage, decreased to about 50% at 6 mo, and decreased to about 35% at 9 mo. The same general trend was observed with MRSW-held fish except EPN values

TABLE 4.—Change in extractable protein nitrogen content (percent) of minced flesh (unwashed and washed) from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice					Modified refrigerated seawater				
	Months of frozen storage at -18 C					Months of frozen storage at -18 C				
	0	2	4	6	9	0	2	4	6	9
	Minced flesh					Minced flesh				
0	85	87	70	60	32	85	87	70	60	32
4	83	83	68	64	42	85	—	73	70	31
6	80	72	78	46	42	80	63	64	59	24
8	87	74	73	54	37	86	53	73	42	26
10	78	70	77	53	34	78	56	65	38	30
12	82	69	72	33	35	73	56	60	49	24
14	86	73	64	48	27	74	48	39	26	22
	Washed minced flesh					Washed minced flesh				
0	90	79	63	56	30	90	79	63	56	30
4	77	79	75	59	33	78	61	58	57	32
6	83	76	74	62	29	75	65	63	42	28
8	81	69	70	38	34	79	71	60	28	26
10	77	75	62	49	34	83	45	54	27	19
12	83	77	66	31	26	67	44	44	23	21
14	74	70	63	42	26	68	40	47	23	15

TABLE 5.—Change in trimethylamine oxide content (milligrams TMAO-N/100 g) of minced flesh (unwashed and washed) from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice					Modified refrigerated seawater				
	Months of frozen storage at -18 C					Months of frozen storage at -18 C				
	0	2	4	6	9	0	2	4	6	9
	Minced flesh					Minced flesh				
0	136	100	68	69	74	136	100	68	69	74
4	130	97	56	66	70	145	98	70	67	69
6	128	96	66	65	66	140	93	68	63	66
8	129	92	66	60	64	127	86	63	66	62
10	125	86	64	60	66	126	85	63	58	62
12	143	84	64	60	66	121	83	62	58	59
14	143	86	63	63	61	120	83	59	61	56
	Washed minced flesh					Washed minced flesh				
0	36	—	37	36	39	36	—	37	36	39
4	30	—	29	28	29	27	—	30	25	27
6	28	—	26	28	26	24	—	25	23	23
8	25	—	26	25	26	25	—	26	24	26
10	26	—	27	24	26	24	—	25	23	24
12	24	—	26	26	24	22	—	25	26	23
14	22	—	25	25	23	20	—	23	22	22

were slightly lower. Although EPN did not change significantly with time of fresh holding in ice and only slightly in MRSW, the effect of the length of time of fresh holding on EPN became apparent in samples held at -18° C for 6 to 9 mo. If EPN is related to the texture of black rockfish, the data in Table 4 suggest that 6 mo of frozen storage at -18° C was too long for minced flesh at any level of fresh quality and that various periods of frozen storage would give acceptable texture depending on the level of fresh quality when frozen.

The TMAO content of the unwashed minced flesh was unaffected by time of holding in ice but decreased slightly in MRSW (Table 5). Although not expected to change with the frozen storage of this non-gadoid fish, amine data were obtained since no data on TMA and DMA and only one value for TMAO (93 mg N/100 g, Dyer 1952) have been reported in the literature for *S. melanops*. There was a strong reduction in TMAO content of the unwashed minced flesh with time of frozen storage to 4 mo with little change thereafter. TMA and DMA values were not affected by frozen storage (data not included in tables). Consequently, the substantial reduction in EPN was not caused by formaldehyde. We cannot explain either the observed loss of TMAO without a concomitant increase in either TMA or DMA content or the lack of change in TMAO content with time of frozen storage of the unwashed minced flesh.

SUMMARY

Black rockfish was held in the round in ice or MRSW to 14 days. The yield of fillets was not affected by time of holding but fish held in ice gave slightly higher yields than fish held in MRSW, 32 and 31%, respectively. The usual chemical spoilage tests (TMA, TVA, TVB) were of little or no use as indicators of spoilage. Observations of the beginning of off-odors, softness of flesh, and decomposition of viscera at 10 days were not confirmed by sensory evaluation of the cooked portions. For this species, early changes in quality were best judged subjectively on the raw, whole fish and fillets. Formal sensory evaluation was less sensitive than informal evaluation to change in quality, and chemical spoilage tests were not sensitive to obviously advanced spoilage. Washing the minced flesh resulted in a reduction in salt, solids, and TMAO content. The yield increased with washing because of increased water content but when calculated on a salt-free, constant 18% solids basis, the yield decreased in both systems to 28% when minced and washed. The EPN values of minced flesh from ice-held fish decreased during frozen storage at -18° C from about 80 to 35% after 9 mo and MRSW-held fish gave similar but slightly lower EPN values. The degree of fresh quality strongly influenced EPN values during frozen storage indicating that the time of holding in ice or MRSW should be considerably less than 10 days to maintain good quality for any reasonable period of frozen storage.

LITERATURE CITED

BARNETT, H. J., R. W. NELSON, P. J. HUNTER, S. BAUER, AND H. GRONINGER.
1971. Studies on the use of carbon dioxide dissolved in refrigerated brine for the preservation of whole fish. Fish. Bull., U.S. 69:433-442.

BULLARD, F. A., AND J. COLLINS.
1978. Physical and chemical changes of pink shrimp, *Pandalus borealis*, held in carbon dioxide modified refrigerated seawater compared with pink shrimp held in ice. Fish. Bull., U.S. 76:73-78.

BYSTEDT, J., L. SWENNE, AND H. W. AAS.
1959. Determination of trimethylamine oxide in fish muscle. J. Sci. Food Agric. 10:301-304.

CASTELL, C. H., B SMITH, AND W. J. DYER.
1973. Effects of formaldehyde on salt extractable proteins of gadoid muscle. J. Fish. Res. Board Can. 30:1205-1213.

DOWDEN, H. C.
1938. The determination of small amounts of dimethylamine in biological fluids. Biochem. J. 32:455-459.

DYER, W. J.
1952. Amines in fish muscle. VI. Trimethylamine oxide content of fish and marine invertebrates. J. Fish. Res. Board Can. 8:314-324.

DYER, W. J., H. V. FRENCH, AND J. M. SNOW.
1950. Proteins in fish muscle. I. Extraction of protein fractions in fresh fish. J. Fish. Res. Board Can. 7:585-593.

FRIEDEMANN, T. E., AND T. BROOK.
1938. The identification and quantitative determination of volatile alcohols and acids. J. Biol. Chem. 123:161-184.

HORWITZ, W. (editor).
1975. Official methods of analysis of the Association of Official Analytical Chemists. 12th ed. Assoc. Off. Anal. Chem., Wash., D.C., 1094 p.

MILLS, A.
1975. Measuring changes that occur during frozen storage of fish: a review. J. Food Technol. 10:483-496.

MIYAUCHI, D., M. PATASHNIK, AND G. KUDO.
1975. Frozen storage keeping quality of minced black rockfish (*Sebastes* spp.) improved by cold-water washing and use of fish binder. J. Food Sci. 40:592-594.

MIYAUCHI, D. T., AND M. E. STANSBY.
1952. Freezing and cold storage of Pacific Northwest fish

and shellfish Part I - Storage life of various rockfish fillets. Commer Fish Rev 14(12a):24-28.

NIKKILA, O E., AND R R LINKO
1954. Denaturation of myosin during defrosting of frozen fish. J Food Res 19:200-205.

REPPOND, K D., F A BULLARD, AND J COLLINS.
1979. Walleye pollock, *Theragra chalcogramma*: physical, chemical, and sensory changes when held in ice and in carbon dioxide modified refrigerated seawater. Fish. Bull., U.S. 77:481-488.

STANSBY, M E., AND J. DASSOW.
1949. Storage life of whole and split rockfish fillets. Commer Fish. Rev. 11(7):1-8.

STANSBY, M. E., R W HARRISON, J. DASSOW, AND M. SATER.
1944 Determining volatile bases in fish. Comparison of precision of certain methods. Ind. Eng Chem., Anal. Ed 16:593-596.

TEENY, F M., AND D. MIYAUCHI.
1972. Preparation and utilization of frozen blocks of minced black rockfish muscle. J. Milk Food Technol. 35:414-417.

TOZAWA, H., K ENOKIHARA, AND K. AMANO.
1971 Proposed modification of Dyer's method for trimethylamine determination in cod fish. *In* R Kreuzer (editor), Fish inspection and quality control, p. 187-190. Fishing News (Books) Ltd., Lond.

BEHAVIOR AND ECOLOGY OF THE DUSKY DOLPHIN, *LAGENORHYNCHUS OBSCURUS*, IN THE SOUTH ATLANTIC

BERND WÜRSIG AND MELANY WÜRSIG[1]

ABSTRACT

Dusky dolphins were present in Golfo San Jose, Chubut, Argentina, during most of the year, with a seasonal low in abundance during winter and a high in summer. The presence of the prey species southern anchovy, *Engraulis anchoita*, appeared to affect seasonal movements.

Surface feeding was highly visible and birds also fed on fish schools which dolphins herded to the water surface. Surface feeding occurred mainly in spring and summer in the study area, and in late summer and fall in more oceanic waters near the mouth of the bay. This surface feeding pattern corresponded with the presence of southern anchovy.

Dolphins moved in small groups of about 15 individuals while resting in early morning and while looking for food in late morning. Group sizes increased during surface feeding as groups joined existing feeding activity. Because surface feeding occurred mainly around noon and early afternoon, group sizes increased at those times. Dives were longer before and during feeding, and shorter while resting. During spring, summer, and fall nights, dives were shorter, leading to the possibility that dolphins were resting at those times. The nonsurface feeding period corresponded with nighttime dispersal of southern anchovy schools. Dolphins moved in shallow water while resting and in deeper water while surface feeding. Near shore resting may be a predator-avoidance mechanism.

Most aerial behavior occurred during surface feeding, with behavior before and during surface feeding related to either herding and confining prey or possible communication of neighboring groups. Postfeeding aerial displays were assumed to serve a social function.

Calves were born mainly in the summer.

Recently there has been an increase in the number of studies of movements and migration patterns, behavior, and ecology of dolphins. Most of this work has consisted of long-term observations of the bottlenose dolphin, *Tursiops* sp. (Caldwell et al. 1965; Caldwell and Caldwell 1972; Tayler and Saayman 1972; Irvine and Wells 1972; Saayman et al. 1972, 1973; Saayman and Tayler 1973; Leatherwood 1975; Odell 1975, 1976; Castello and Pinedo 1977; Shane 1977; Würsig and Würsig 1977, 1979; Würsig 1978; Wells et al. in press; Irvine et al.[2]), but other odontocete cetaceans have received attention as well (review to 1974 by Norris and Dohl in press; Saayman and Tayler 1979, on *Sousa* sp.; Evans 1976, on *Delphinus delphis*; Norris and Dohl 1980, on *Stenella longirostris*; Gaskin et al. 1975, on *Phocoena phocoena*; Würsig in press, on *Lagenorhynchus obscurus*). This paper presents data on the yearly and daily occurrence and feeding cycles, movement patterns, general and social behavior, and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in a south Atlantic bay on the coast of Argentina.

Little information on dusky dolphins is available in the published literature. Gaskin (1968) described the distribution of these animals around New Zealand relative to sea-surface temperature, and Gaskin (1972) presented a summary of the literature. Although the genus *Lagenorhynchus* appears worldwide, populations of *L. obscurus* are confined to the Southern Hemisphere, most notably around New Zealand, South Africa, and South America. The exact northern and southern limits of the species are not known. Brownell (1965) states that dusky dolphins are distributed circumpolar to lat. 30° S, but this is disputed by Gaskin (1972). According to Rice (1977), *L. fitzroyi* is synonymous with *L. obscurus*.

More information is available on the Pacific whitesided dolphin, *L. obliquidens*. It has been described by Brown and Norris (1956), Norris and Prescott (1961), and others. A recent review of the status of this species in the eastern North Pacific

[1]State University of New York at Stony Brook, Program for Neurobiology and Behavior; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064.

[2]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Final report for U.S. Marine Mammal Commission, Contracts MM4AC004 and MM5AC0018, 53 p.

Manuscript accepted July 1979.
FISHERY BULLETIN: VOL. 77, NO. 4, 1980.

has been presented by Leatherwood and Reeves (1978).

MATERIALS AND METHODS

Dusky dolphins were observed at Golfo San José (Figure 1) from September 1973 through January 1974 and from July 1974 through March 1976. We made observations from shore and from a 4.5 m rubber Zodiac[3] boat powered by an 18-hp Evinrude outboard motor.

Shore observations were made through binoculars, and movement patterns of dolphin groups, ranging from six to several hundred individuals, were followed with a Kern Model DKM 1 surveyor's theodolite (see Materials and Methods in Würsig and Würsig 1979). This technique allowed us to describe where and how fast the dolphins moved during different times of day.

Observations were made from the boat by moving up to a group of dolphins and then stopping the engine. This allowed us to drift near the dolphins while taking notes on their behavior. We believe that the natural behavior of dolphins was at times affected by the presence of the boat, and therefore made an attempt to confirm all behavior seen from the boat by shore-based observations.

To get some idea of group stability over time, we spaghetti-tagged 24 individuals in conjunction with a radio-tagging study. These tags were color-coded plastic streamers lanced into the thick blubber behind the dorsal fin. For a description of the tags and tagging procedures, as well as radio-track data, see Würsig (in press).

To compare seasonal occurrence data with water temperature, we measured temperature 1 m below the surface 5-10 times per month. For uniformity, these readings were made 0.5-3 km from shore, and in the afternoon. We used a calibrated laboratory thermometer marked every 0.2° C from 5.0° to 30.0° C.

Underwater sounds made by dolphins were recorded through U.S. Navy Sonabuoy hydrophones suspended 5-10 m below the boat. They were recorded on a Sony TC800B reel-to-reel tape recorder. A complete analysis of dolphin vocalizations is not presented in this paper. However, measurements were made of approximate distance of travel before attenuation (sounds no longer picked up by the hydrophones) of certain splash sounds related to aerial behavior. During such measurements, dolphin and boat position were recorded from shore by surveyor's theodolite, thereby providing the distance from the sound source to the hydrophone.

We used standard statistical techniques to test for differences and similarities of observations. These techniques are from Sokal and Rohlf (1969) unless stated otherwise.

RESULTS

Seasonal Occurrence Pattern

On days with winds >20 km/h, it was difficult to see dusky dolphins. Of the 433 days with winds <20km/h, dolphins were seen on 251 days, or 58%. Dolphins were seen from shore during 19 of 21 mo (Figure 2a); June and July 1975 were the only months without sightings. Although the rate of sightings varied from month to month, there was an increase in sightings from late winter (August) to summer (February 1975; December 1975), and a decrease from fall to midwinter (March through June 1975). During both years, dolphins were present on over 50% of days during which observations were made from August through February, with the one exception of · 50% on the days in January 1976.

Could this cycle of dolphin occurrence be related to water temperature? Figure 2b shows average surface temperature per month within 3 km of shore during the same 21-mo period. Although upon superficial examination it appears that dolphins were less often present during the coldest months, this is not strictly true. Thus, although August was the coldest month in both years, dolphins in August were present over 70% of sighting days. The rise in temperature in spring-summer 1975-76, however, occurred earlier than in 1974-75, and temperatures from September to February were 1°-2° C higher per month than in the preceding year. Dolphins were more abundant earlier in 1975-76 than in 1974-75. While "the peak" of dolphin presence occurred in January 1975, it occurred in October 1975 in the next season, with a sharp drop-off to January 1976.

Where were the dolphins during the period from March through July, when they were rarely sighted in the study area? During 19 of 24 (79%) boat trips made throughout the bay in these months, we found them in the western part of Golfo San José, closer to the mouth of the bay and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

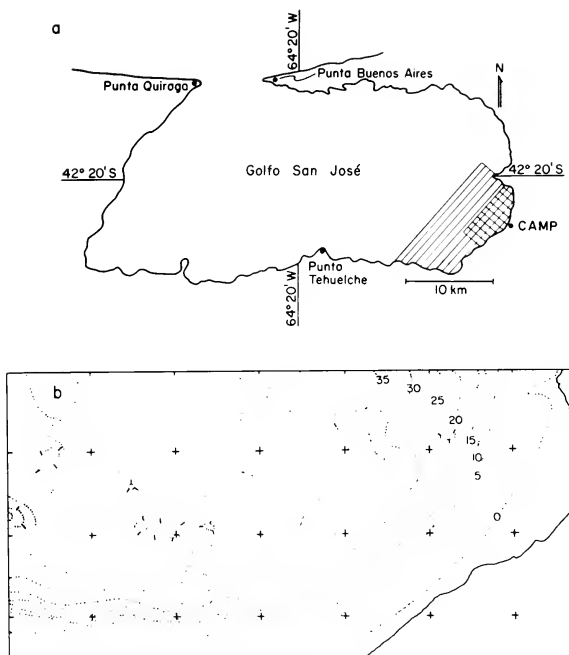


FIGURE 1.—Map of Golfo San José on Peninsula Valdés, Argentina (a). The bay is about 750 km² in area, with a 7 km wide mouth opening to the Atlantic. The lined area in the southeast portion of the bay represents the study area. The crosshatched subsection is shown in detail in b. It is a depth contour map of one-fourth of the study area. Margin numbers represent meter distances relative to a zero location on land. Crosses form 1 km squares. "Cliff Hut" and "Camp" are the locations from which most observations were made. Depth contours are in meters at mean low water (MLW). The usual distance for good observation of a moving dolphin group was at least 3 km. At a normal tide height of 5 m above MLW, water depth of 40 m was 1 km from Cliff Hut, and thus clearly visible. The map is from a larger area map which was by courtesy of Roger Payne, New York Zoological Society; Oliver Brazier, Woods Hole Oceanographic Institute; and Russ Charif, Harvard University.

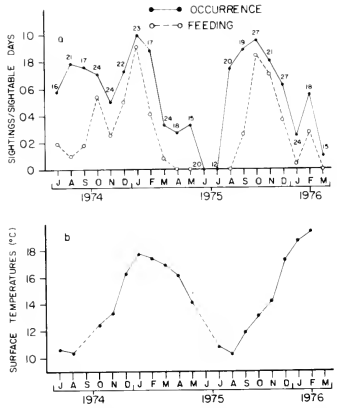


FIGURE 2.—Fraction of possible days per month on which dusky dolphins were sighted, and were seen surface feeding (a). The y-axis represents the ratio of number of days on which dolphins were sighted or were seen feeding divided by the number of days each month with winds <20 km/h (sightable days). During all sightable days, observations were made from dawn to dusk. Numbers above points represent the number of sightable days per corresponding month. Average surface temperatures within 3 km of shore during the same 21-mo period as in Figure 2a(b).

near the open ocean (Figure 1a). A large oceanic mass of water changes temperature less rapidly than nearshore shallow water, and this may have influenced the dolphin's movement, perhaps by a shift in prey location. Dolphins were found near the mouth of the bay from March through July, when temperatures in the study area dropped from 17° to 11° C (Figure 2), and it is likely that near-mouth temperatures decreased more slowly due to the influence of the open ocean water.

Although dolphins were present at the study site most of the year, and were found in Golfo San José the entire year, we did not know whether the animals were part of the same population or herd during all seasons. However, four spaghetti tags inserted in December and January were resighted in August, November, December, and January of subsequent years. This indicated that at least some of the animals were present in different seasons, and thus did not appear to migrate.

Seasonal and Daily Surface Feeding Cycles

Surface feeding of dusky dolphins was often highly visible, with birds flocking above the feeding site, allowing us to estimate from a distance when and where the dolphins were feeding on schooling fish (Figure 2a). Regardless of season, whenever dolphins were seen they were often feeding. However, in August and September 1974 and 1975, dolphins were present much of the time but little surface feeding appeared to take place. Little or no surface feeding took place in low-dolphin months of June and July and in high-dolphin months of August and September. This low in surface feeding corresponded with the lowest temperature period (about 12° C and below) of the year, possibly because fewer food fish were in the area.

When surface feeding bouts occurred, they were observed throughout the day. However, the length of feeding bouts increased as the day advanced. Feeding bouts were longest at 1500 h, then declined as evening approached (Figure 3).

Although feeding lasted longer during the afternoon (to 1500 h), there were nevertheless some long feeding bouts in the morning (Figure 4), with a significant increase in long bouts in the afternoon.

Depth of Water and Speed of Movement

Are dusky dolphins found at certain water depths and does their swimming speed vary with water depth? To answer these and similar questions, we tracked group movements by surveyor's theodolite. Figure 5a shows that they were most often tracked while in water 5-10 m deep. This peak is probably somewhat biased because observations were possible more often within about 1 km from shore, where depths of 0-30 m were found. Nevertheless, since both 0-5 m and 10-30 m depth areas approximated the area at 5-10 m, dolphins appeared to have a clear preference for traveling in water 5-10 m deep while near shore. A small but significant secondary peak also occurred at 35-45 m. Although dolphins traveled in water >65 m, this has not been represented in Figure 5a, since no water within sight was >65 m. For radio tracked movement out of sight of land see Würsig (in press).

The overall average speed was 7.7 km/h. There was a shift in speed depending upon depth of water in which the animals were traveling (Figure 6).

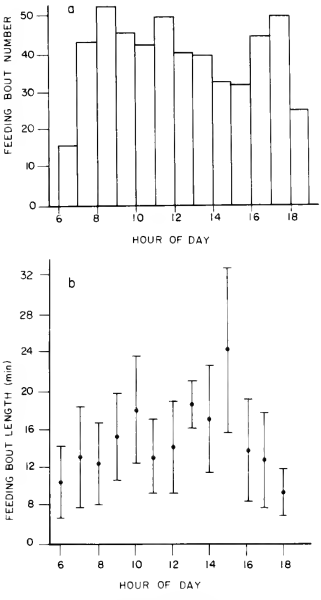


FIGURE 3.—The number (a) and mean lengths (b) of dusky dolphin feeding bouts throughout the day, summed for 21 mo from June 1974 to March 1976. Bars above and below mean feeding lengths enclose 95% confidence intervals for means.

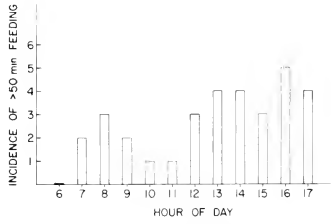


FIGURE 4.—The number of >50-min surface feeding periods of dusky dolphins during different times of day. Significantly longer surface feeding periods occurred in the afternoon (0600-1200 h = 9 or 28%; 1200-1700 h = 23 or 72%; testing equality of percentages, arc sine transformation ofr statistic t_s).

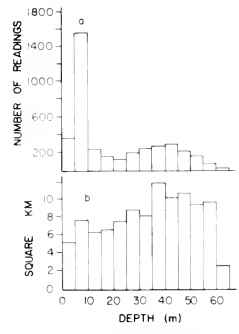


FIGURE 5.—Number of theodolite readings of dusky dolphins over depths from 2 to 65 m (a). Although most readings were at 5-10 m, a smaller peak occurred at 35-45 m which appeared to correlate with feeding activity at that depth (see text). Amount of area available in the study region as a function of water depth, at a mean tide height of 5.0 m above mean low water (b).

Groups moved at about 5 km/h in water 1-10 m, and faster in deeper water (average speed in water 55-60 m was 16 km/h). Furthermore, there was a general movement from shallow to deeper water as the day advanced (Figure 7a), and dolphins moved more rapidly in the afternoon than in the morning (Figure 7b).

Because water depth and dolphin speed were related (Figure 6), it is not surprising that dolphins, on the average, moved faster in those months in which they were in deeper water (compare Figure 8a with b). At the same time there was a strong correlation between depth and speed during different months and the amount of feeding activity during those months (compare Figure 8a with Figure 2a; correlation = 0.77, $P = 0.003$, Kendall coefficient of rank correlation).

Dolphin groups moved into deeper water in the afternoon in each of the 7 mo for which adequate depth versus time of day data exist (Figure 9a). In August and September, when little surface feeding occurred, and when water temperatures were lower than in summer, dolphins stayed in rela-

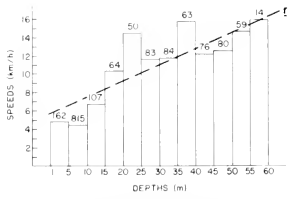


FIGURE 6.—Average speeds with which dusky dolphins traveled at different depths. The least squares regression, fit to the means shown, is statistically significant ($P<0.01$). Numbers over bars represent number of observations in that category.

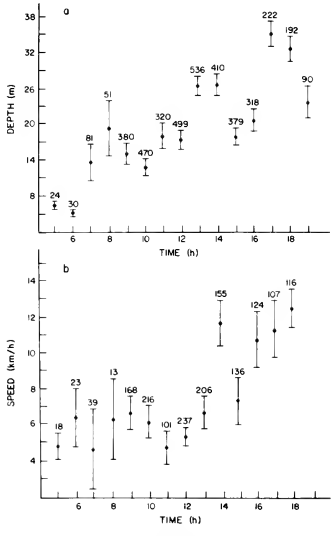


FIGURE 7.—Mean depth of water (a) and mean swimming speed (b) of dusky dolphins as a function of time of day. Bars represent 95% confidence intervals for means and numbers above bars represent the number of theodolite readings per hour interval.

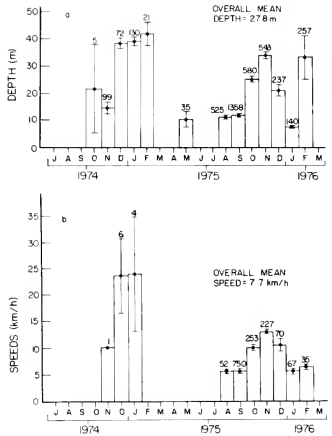


FIGURE 8.—Mean depth of water inhabited by dusky dolphins for different months (a), and mean speed of travel for dolphins for different months (b). Numbers represent number of theodolite readings obtained per month; bars represent 95% confidence intervals for means.

tively shallow water compared with the following months (Mann-Whitney U-test, $P<0.001$).

Dolphins usually moved more rapidly during afternoon than morning (Figure 9b). The increase in rapid movement per month appears related to the amount of surface feeding bouts in that month. Thus, in August 1974 and 1975 few surface feeding bouts occurred, and there was no increase in speed during the day. In September, some feeding took place, and there was a small speed increase. In October, November, December, and January much surface feeding took place during one or both years, and the afternoon speed increase was most dramatic. In February, both surface feeding and afternoon speeds were again down to pre-October levels (August, September, and February afternoon speeds are significantly different from October, November, December, and January afternoon speeds, Mann-Whitney U-test, $P<0.001$).

From these data we concluded that dolphins traveled faster at surface feeding times. This was confirmed by comparing speed data of dolphins as

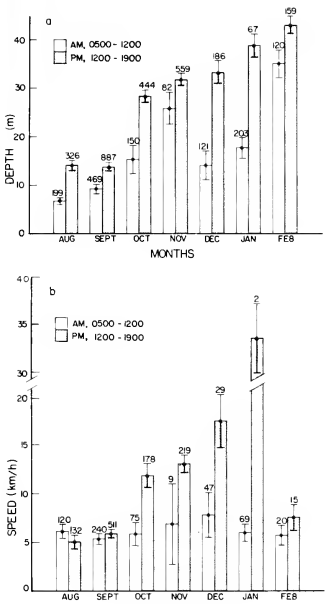


FIGURE 9.—Mean depth of water (a) and mean speed (b) of dusky dolphin travel in mornings versus afternoons, separated into those months for which adequate data are available. The lines above and below bars represent 95% confidence intervals for means, and numbers represent number of theodolite readings. During August and September, dolphins were found in significantly shallower water than during the spring and summer months of October-February (Mann-Whitney U-test, $P < 0.001$). During August and September, dolphins also moved significantly slower than October through January (Mann-Whitney U-test, $P < 0.001$). Almost all speed increases in these months took place in the afternoon.

they moved with no feeding bouts present in the area, and as they moved near feeding bouts (Table 1). The mean speed without feeding bouts was 6.3 km/h, while speeds around feeding bouts averaged about 15 km/h.

Dusky dolphins spent more time in deeper water when surface feeding. Furthermore, the depth of water in which surface feeding occurred increased as the summer season advanced (Figure 10). Thus the mean depth of feeding bouts during September was 21 m, but by February dolphins were surface feeding in waters 41 m deep. Since it is a general rule (and confirmed for Golfo San Jose by Pizzaro (1976), and pers. obs.) that deeper offshore water is cooler than shallow nearshore water in summer,

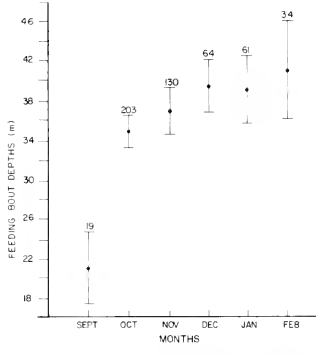


FIGURE 10.—Mean depth of dusky dolphin surface feeding bouts during different months. Bars above and below means represent 95% confidence intervals for means. Numbers above bars represent the number of theodolite readings of feeding bouts per month.

this change in preferred feeding locations may represent a change in movement patterns of fish upon which the dolphins were feeding. We caught fish from schools on which the dolphins were feeding on 15 separate occasions, and identified the species composing such schools in the field about 50 more times. In all cases, the fish were southern anchovy, *Engraulis anchoita*. These fish are found in deeper water during summer in a nearby coastal area, where they are netted by fishermen (Mermoz[4]), and we suspect that they move into deeper water in summer in the present study area as well.

[4]J. Mermoz, research scientist, Museo de Ciencias, Buenos Aires, Argentina, pers. commun 1975.

TABLE 1.—Average speeds of dusky dolphins not associated with feeding, and associated with feeding activity. The difference in speed between no feeding activity seen (row 1) and speed around feeding activity (rows 2, 3, and 4) is significant ($P < 0.001$, t'-test of equality of means when variances are assumed to be heteroscedastic).

Row	Category	Average speed (km/h)	Standard deviation	Theodolite readings (n)
1	No feeding activity seen	6 3	2.35	1,390
2	Dolphins not associated with feeding activity in the area	15 3	3 46	72
3	Movement towards feeding activity	13 7	3 43	88
4	Movement out of feeding activity	15 6	3 52	109

Relationships of Group Sizes, Feeding, and Aerial Behavior

For the purposes of this paper, we defined a group as a number of animals that are swimming together and moving as a unit (but not necessarily all pointed in the same direction). Individuals of a group were usually within visual range and certainly within acoustic range of at least some conspecifics. Group sizes varied from 6 to about 300 individuals. There was a seasonal shift in group sizes. From May through September, groups with <20 animals were more common than at other times of the year (Figure 11). As stated earlier, a low in feeding bouts occurred in the southeast part of Golfo San Jose from March to September (Figure 2a), and we gained the impression from boat trips to the middle and western section of the bay that surface feeding there occurred with high frequency in March and April, but did not often occur anywhere in the bay from May to September. As a result, it appears that smaller groups were most abundant during the nonsurface feeding months of May to September.

There was a direct relationship between size of dolphin group and surface feeding frequency. Thus, groups with <20 individuals were found in feeding bouts only 19% of the times they were spotted, while groups with >20 animals were seen feeding more of the time (Table 2). Because a surface feeding-speed relationship was noted, it is not surprising that speed of group travel increased with increasing group size. While small groups

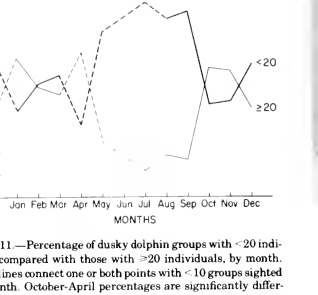


FIGURE 11.—Percentage of dusky dolphin groups with <20 individuals compared with those with ≥20 individuals, by month. Dashed lines connect one or both points with <10 groups sighted that month. October-April percentages are significantly different from those of May-September ($P < 0.001$, equality of percentage test with arc sine transformation).

occurred most often in the morning (and were not surface feeding), larger groups were most often associated with feeding bouts in the afternoon (Table 2).

The larger the group size, the longer the feeding activity lasted (Table 3). The number of birds also increased with dolphin group size, and with length of feeding (Table 3). Species of birds, in approximate order of decreasing numbers, were the black-headed gull, *Larus dominicanus*; cormorants, *Phalacrocorax brasilianus* and *P. magellanicus*; terns, *Sterna* spp.; different species of Pro-

TABLE 2.—Average speed and time of day related to group size estimates, and percentage of times dusky dolphins of three different group sizes were associated with feeding activity. Groups with <20 individuals were seen feeding less frequently than larger groups ($P < 0.001$, testing quality of percentages, arc sine transformation of t-statistic).

Item	Dolphin group size (estimate)		
	<20	20–50	>50
Number of theodolite readings used for speed data	66	37	30
Average speed (km h)	5 7	7 4	13 8
Standard deviation	2 30	2 60	3 45
Average time of day, Argentine local time (h min)	10 12	13 20	14 06
Standard deviation expressed in hours and minutes	2 40	2 57	2 45
Number of times seen feeding (a)	130	177	190
Number of times seen while not feeding (b)	540	117	77
Percentage of times seen feeding during total sightings (100a / a + b)	19	60	71

TABLE 3.—Estimated number of dusky dolphins and birds (see text) in feeding bouts of different lengths (t'-test of equality of means when variances are assumed to be heteroscedastic).

Dolphin group size	Mean length of feeding by dolphins			Mean number of birds		
	n	Mean[1]	SD	*n*	Mean[1]	SD
<10	19	6 3ns	4 42	19	75*	73 8
≥10- 20	91	11 1**	12 00	91	115**	82 3
≥20- 50	116	16 5**	14 38	116	163**	116 5
≥50	87	25 8	24 23	87	246	117 8

[1]ns = not significant; *P- 0 05, **P 0 01

cellariiformes; the giant petrel, *Macronectes giganteus*; and black-browed albatross, *Diomeda melanophris*. Terns were usually the first birds to begin flying over and diving into feeding dolphin groups. Then gulls and finally larger birds aggregated at the feeding area.

The most striking behavior of dusky dolphins we observed was their aerial displays. To find out why these displays occurred, we noted the frequency of this activity at different times. We saw all aerial displays described by Norris and Dohl (1980) for the Hawaiian spinner dolphin, *Stenella longirostris*. These were leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, spins, and noseouts. The most "acrobatic" of these leaps was the head-over-tail leap. The spin was performed frequently by the Hawaiian spinner dolphin, but it constituted <1% of leaps in the present study. When it was seen, it was also classified as acrobatic, along with the head-over-tail leap, for further analysis.

Two other aerial displays seen in dusky dolphins were the headfirst reentry leap and its apparent variant, "humping." In the headfirst reentry, the dolphin leaped clear of the water and then arched its back strongly while flipping the tail to make a headfirst reentry. While humping, the same motion occurred except that the snout and tail did not leave the water during the body arch.

Leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins usually occurred in groups. That is, one animal started a particular leap, and then continued it from 3 to about 20 times. Because we could often not be certain that the same individual was performing the leaps during a leap sequence, we do not have complete quantification for this phenomenon. However, in 45 of over 1,000 leaps it was certain that the same animal leaped throughout a sequence, because we followed it visually while it swam below the surface between leaps. In all 45 instances, the leap type per sequence did not change, and a mean of 4 (SD = 2.2) leaps per sequence was performed. Although the first five or so leaps were performed with "exuberance," as animals leaped clear of the water and reentered forcefully, successive leaps were not as high, possibly as the animal tired.

The headfirst reentry and humping did not occur in sequence, but were usually performed only once by an animal within about 30 s. Because animals stayed underwater for long times between leaps, we could never be certain that the same animal leaped later on. Instead, the 30-s estimate was derived from counts of total leaps occurring in a particular group size, and must therefore be treated with caution. The headfirst reentry and humping were often performed in concert with one or two others leaping in the same manner at the same time. While all other aerial behaviors left individuals close to the water surface between leaps, the headfirst reentry and humping took them farther below the surface, and we saw them swimming out of sight at about a 75° angle.

As was described by Norris and Dohl (1980), leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins made noise as the animals reentered the water. That is, they created sharp bursts of sound when the animals slapped the water with their flukes or body upon reentry. Hydrophones detected the sounds underwater at approximately 0.5 km distance, but not at 1.0 km distance during four recording sessions under optimal (no wind or waves) conditions. Norris and Dohl also mentioned that sounds made by these leaps attenuate relatively rapidly, but gave no distance estimates.

Headfirst reentry and humping, however, made little or no sound above or below the water (hydrophones did not detect sound 10 m from the activity). Dolphins slid out of and into the water along their longitudinal body axis during these two leap types. Because we believe that the noise made by most leaps may be biologically meaningful, we separated them into "plain noisy" (the leap, backslap, headslap, and tailslap) and "acrobatic noisy" (head-over-tail and spin) leaps, and distinguished them from noiseless or "clean" leaps (headfirst reentries and humping). The noseout did not make noise and was often difficult to see from the boat or from shore. It was therefore not quantified.

We observed dolphins in feeding bouts for 145 h, and observed them during periods when we saw no feeding bouts for 309 h, or over twice as long. Nevertheless, we saw a significantly higher fre-

quency of noisy and clean leaps while dolphins were surface feeding (Table 4). More noisy leaps were made during and after surface feeding than before, and those few noisy leaps which occurred before surface feeding were most often "plain" or nonacrobatic. During surface feeding, plain and acrobatic leaps occurred with about equal frequency, while after surface feeding most leaps were acrobatic. The noiseless or "clean" head-first reentry leap and humping behavior occurred more often before and during surface feeding than after surface feeding.

Our general views of behavior introduced above were as follows: When not surface feeding, dolphins usually moved in small (<20 individuals) groups (Table 2) with sporadic but relatively infrequent aerial behavior (Table 4). They usually moved slowly (about 6 km/h) at this time. Immediately previous to feeding bouts, they moved more rapidly for short periods (mean time = 6.2 min, SD = 4.53), often creating whitewater as they surged through the water at speeds ≈10 km/h (Table 1). We gained the impression that between such surges, they stayed underwater for longer periods than their normal diving times (mean dive time = 21 s, Würsig in press), often disappearing from sight for over 60 s. This pattern of movement lasted from a few minutes to as long as 1 h. When it stopped and dolphins were again found more often near the surface, they moved slowly and stayed in basically the same location. At this time, noiseless (clean) and noisy (plain) leaps began (Table 4). When we were near this activity in a boat, we were able to see a fish school usually 2-3 m in horizontal diameter, and 0.5 m vertical height, near the water surface.

Every time (65 occasions) the fish were observed they were southern anchovy 6-15 cm long. When we spotted the fish school near the surface, we also saw terns beginning to dive for the fish, and gulls coming from the vicinity. Plain noisy and clean leaps continued, and acrobatic leaps began to appear (Table 4). During surface feeding, many of the clean displays were composed of humping behavior. During humping, dolphins rapidly moved singly or in pairs through the fish school after coming almost vertically from deeper water, caught one to five fish in their mouths, and then descended again at a steep angle. Dolphins were also seen near and around the feeding bout nucleus, chasing and feeding on individual fish not part of the tight school.

If the surface feeding dolphins were not joined by a nearby group or groups within several minutes, the feeding bout died down. We lost sight of the fish, either because the school had been reduced by dolphins and birds or because it moved away from the surface. Often, however, other dolphin groups in the vicinity converged on the feeding bout, moving rapidly in a straight line towards the feeding birds and dolphins from as far away as 8 km, measured by theodolite on one occasion. A more usual distance was 2-3 km. As a result of this movement, the feeding bout grew larger—up to an estimated 300 dolphins and thousands of birds—and lasted for a correspondingly longer time (Table 3). Surface feeding appeared to stop when dolphins rapidly moved away from the activity, or when they began deep dives and clean leaps once again. In either case, we no longer saw the fish school. Birds stopped flying and diving in a concentrated area and settled on the water or followed

TABLE 4.—Observed incidences of aerial behavior in dusky dolphins. Numbers represent number of 15-min periods during which a particular type of leap was seen. Frequency of leaping within that period has not been quantified. "Noisy leaps, in general" represent leaps which made noise but were not separated into "plain" or "acrobatic" during data gathering. All significance testing used the equality of percentages, arc sine transformation for the statistic t_s.

	Time of leaping	a Noisy leaps, in general	b Plain noisy leaps	c Acrobatic noisy leaps	d Clean leaps
A	During the 15 min before feeding	24	17	0	35
B	During feeding (average time of 15 min)	109	13	15	32
C	During the 15 min after feeding	84	1	20	12
D	Without feeding	45	22	3	25
	Total	262	53	38	104

Comparisons

Amount of noisy leaps, in general, a, associated with feeding, A-C (83%) versus without feeding, D (17%), significant difference, P 0.001

Amount of noisy leaps, in general, a, before feeding, A (22%) versus after feeding, C (78%), significant difference, P 0.001

Amount of noisy leaps before feeding, A, plain, b (100%) versus acrobatic, C (0%), significant difference, P 0.001

Amount of noisy leaps after feeding, C, plain, b (4.8%) versus acrobatic, D (95.2%), significant difference, P 0.001

Amount of plain noisy leaps, b, before feeding, A (94.4%) versus after feeding, C (5.6%), significant difference, P 0.001

Amount of acrobatic noisy leaps, c, before feeding, A (0%) versus after feeding, C (100%) significant difference, P 0.001

Amount of clean leaps, d, associated with feeding, A-C (76%) versus without feeding, D (24%), significant difference, P 0.001

Amount of clean leaps, d, before feeding, A (74%) versus after feeding, C (26%), significant difference P 0.01

the rapidly moving dolphin group. Dolphins tended to stay together for up to several hours once groups had converged to feed, and feeding activity usually started again in these larger groups. When it did so, it lasted longer than when fewer dolphins were feeding, and therefore larger groups were more often seen in association with feeding bouts (Table 2).

Group Organization and Calving Periodicity

As mentioned previously, the most common nonfeeding group size was about 6-15 animals. In general, these groups were composed of adults, and at times included juveniles and calves. We were not able to determine sex of individuals by observing them from boat or shore, but captures of individuals prior to radio tagging (Würsig in press) demonstrated that males and females usually travelled together in these small groups. We saw small calves (about equal to or less than one-third adult size) from November through February. Furthermore, we saw "juveniles" (about one-half to two-thirds of the size of adults) or young under 1 yr of age during April-May and August-September (Table 5). The sample size was too small, however, to say definitely that young were born only during the summer, and births may have been more spread out over the year. Nevertheless, the data suggest a summer calving peak.

Although we saw small calves and young in small groups, we also saw groups of 8-20 adults and as many calves on six separate occasions. We called these groupings "nursery" groups, on the assumption that the adults may have been females, and the calves their young. During all six sightings of nursery groups, most or all other animals in the vicinity were engaged in feeding activity and aerial behavior 0.5 to several kilometers distant from the nursery group. During 12 other sightings of calves and adults, they were found in small groups in the ratio of approximately 1 calf to 10 adults and were not engaged in large-group feeding activity (although on 3 of the 12 occasions, we saw calves in small groups that were feeding). We suspect from these observations that young normally travel with adults in small groups, but when many groups coalesce to feed and socialize (see below), calves and certain adults split off at some time and form temporary nursery groups.

TABLE 5—Sightings of calves and juvenile dusky dolphins. Incidence of calves during November to February was significantly higher than in the rest of the year ($P < 0.001$, Raleigh test, Greenwood and Durand 1955).

Month	Number of sightings		Month	Number of sightings	
	Calves	Juveniles		Calves	Juveniles
Jan	4	0	July	0	0
Feb	1	0	Aug	0	2
Mar	0	0	Sept	0	2
Apr	0	1	Oct	0	0
May	0	1	Nov	2	0
June	0	0	Dec	3	0
			Total	10	6

If there is a calving peak during the year, then most successful matings are probably also carried out in a relatively restricted time period. Most apparent copulations, consisting of rapid belly-to-belly swimming and frequent pelvic thrusts by one or both animals, appeared to take place in large groups during and after surface feeding. Most of these large groups were found in summer (Figure 11). However, it was difficult to approach small, nonsurface feeding groups, and we have few data on their underwater behavior and possible mating attempts. Although we saw some apparent mating in groups of all sizes and at all times of the year, we were not able to quantify these observations.

When we saw small groups of 6-15 animals, we usually saw many of them, up to about 30 such groups, in an area approximately 10 km in diameter. However, we were able to count these groups only under the best conditions, on a calm sea. When these groups converged to surface feed, the upper limit of group size estimate was 300 animals, and this estimate—made by different observers and at different times of year—did not vary appreciably. It thus appears that small groups made up part of a larger school or herd of animals. We do not know how stable small groups were over time, although evidence has been presented by Würsig (in press) which suggested that at least some groups remained stable over a period of at least several days, and appeared to remain together in "subgroups" of a large group during and after feeding bouts.

Interspecific Interactions

Dolphins associated with the boat at times by rapidly moving towards a moving boat from as far as 2-3 km. They would then ride the bow and stern pressure waves of the boat in characteristic dolphin fashion. This activity took place mainly when the dolphins had been surface feeding for a long

time and were thus in large groups. Table 6 shows a few instances of this behavior, when we were certain whether or not the dolphins had been feeding. The data confirm the impression that dolphins which had been in or near feeding bouts approached the boat, while groups which had not been surface feeding avoided or ignored it. When the dolphins associated with the boat, a high level of acrobatic noisy leaps was also evident. Of course, it is likely that the dolphins were merely associating with the boat, and that the humans on board were irrelevant.

Dolphins also associated with the southern right whale, *Eubalaena glacialis*, and the sea lion, *Otaria flavescens*, by moving around and among them in a manner similar to that described for bottlenose dolphins (Würsig and Würsig 1979). This activity also appeared related to whether dolphins had or had not been surface feeding. Differences in behavior between "fed" and nonfeeding dolphins were striking, and we labeled them different "activity levels," following the definition of this term by Norris and Dohl (1980).

After feeding, dolphins at times balanced kelp (pieces of *Macrocystis* sp.) on their pectoral flippers. In one individual this persisted for at least 1 h. The activity of kelp-balancing, we suspect, may be termed "play."

Dolphins interacted with other odontocete cetaceans as well. Groups of from one to six killer whales, *Orcinus orca*, appeared for brief periods throughout the year (Table 7). On the six occasions when we saw them within about 1 km of dusky dolphins, the dolphins moved rapidly in a tightly bunched group away from the killer whales. On three occasions when dolphins were within 1 km of land, they moved towards the shore, and then proceeded along shore in water less than 1 m deep, the closest to shore we ever saw this species. It was reported to us by reliable observers (Jen and Des Bartlett[5]) that killer whales in our study area once surfaced within a school of dusky dolphins, with one whale dripping blood from its mouth, perhaps indicative of having actually fed on a dolphin. However, we have no conclusive evidence that killer whales habitually feed on dusky dolphins.

Risso's dolphin *Grampus griseus*, associated with dusky dolphins from October through March 1974-75 and 1975-76 (Table 7). From two to six individuals consistently stayed within 1-3 km of feeding dusky dolphins during this time. It is possible that Risso's dolphins were feeding on large fish found in the vicinity of southern anchovy, but we have no data for this assumption. Whether or not the larger cetaceans were of actual help to dusky dolphins in finding food, as has been suggested by Norris and Prescott (1961) for pilot whales followed by bottlenose dolphins, and by northern right whale dolphins, is not known.

The bottlenose dolphin, *Tursiops truncatus*, was found in small groupings of 8-22 animals in the study area (Würsig 1978). They usually stayed in shallower water than did dusky dolphins, and were never observed moving in water >39 m. There was, however, some overlap in area covered by both species. On only eight occasions were both species found within 0.5 km of each other. When they were relatively close, each species continued on its previous course, and no interactions appeared to take place (although they may have been interacting by sound). This apparent lack of interaction was especially striking because both dolphin types associated with right whales and sea lions. Dusky dolphins were more abundant when bottlenose dolphins were not, and vice versa (Figure 12).

TABLE 6.—Number of times that dusky dolphin groups associated with the boat by orienting towards it and "bow riding," and number of times they avoided or ignored the boat; both relative to feeding activity (A significant difference from C, $P<0.01$; B significant difference from D, $P>0.001$; chi-square goodness of fit test).

Category	Moved to boat		Ignored boat	
Group not seen surface feeding	A	10	B	18
Group seen surface feeding previously on same day	C	28	D	1

TABLE 7.—The number of days per month when *Grampus griseus* and *Orcinus orca* were seen in the Golfo San José study area.

Month	*Grampus griseus*	*Orcinus orca*	Month	*Grampus griseus*	*Orcinus orca*
Jan	6	2	July	0	0
Feb	12	2	Aug	0	0
Mar	15	2	Sept	0	3
Apr	0	3	Oct	7	0
May	0	1	Nov	0	2
June	0	1	Dec	5	5

DISCUSSION

Dusky dolphins were present in Golfo San José during most or all of the year, but were located in the southeast portion, in the study area, mainly during spring and early summer. They did not

[5]Jen and Des Bartlett, wildlife photographers, P.O. Box 17323, Tucson, AZ 85731, pers. commun. November 1974.

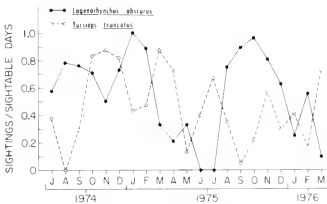


FIGURE 12.—Occurrence data from Figure 2a in conjunction with comparable data on bottlenose dolphins during the same period. The two species occurred in the study area with approximately opposite frequency, i.e., when one species was abundant, the other one was less often seen.

appear to avoid low (≈10° C) temperatures, but may have been avoiding higher (>18° C) temperatures near shore in mid- and late summer. At those times, they were found most often in cooler waters near the mouth of the bay. In Würsig (in press), it was shown that during that time they moved outside of the bay as well. Yet they did not show a well-defined seasonal migration pattern, and marked individuals were resighted in the same location during different seasons. Studies of groups of *Tursiops* sp. have indicated that degree of migration may be different for different populations. For example, bottlenose dolphins off Cape Hatteras, N. C., migrate (Mead 1975), while those of our study site did not (Würsig and Würsig 1979). Shane (1977) and Irvine et al. (see footnote 2) reported localized seasonal movements of bottlenose dolphins in the Gulf of Mexico, with differences between their East Texas and West Florida study sites. Degree of seasonally related movement probably hinges on several environmental and ecological variables, but an important factor for dolphins in temperate waters may be food availability (suggested by Norris 1967, Evans 1971, and others). Thus it seems likely that dusky dolphins moved with the food supply most of the year. The main prey item appears to be southern anchovy and we have some evidence that it is found in deeper offshore waters in spring and summer (Ciechomski 1965) and in large concentrations near the mouth of Golfo San José in late summer (Brandhorst and Castello 1971), at the same time dusky dolphins were feeding there.

Gaskin (1968) stated that dusky dolphins are present around the Hawke Bay area of New Zealand generally only in winter and spring. He related this to the presence of the cold Canterbury Current which comes close to Hawke Bay in winter and spring. Clarke (1957) and Sergeant (1962) described the seasonal migration by pilot whales as being regulated mainly by seasonal abundance of squid and certain schooling fish. Wilke et al. (1953) also found seasonal movement patterns for the Dall porpoise, *Phocoenoides dalli;* the northern right whale dolphin, *Lissodelphis borealis*; and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*. Norris and Prescott (1961) and Evans (1971) reported that the common dolphin, *Delphinus delphis,* moved closer to the shore of California in fall and winter, and moved farther offshore in spring and summer. They suggested that this movement was food related. Brown and Norris (1956) stated that whitesided dolphins off California were most often found near shore in winter and spring, and offshore in summer and fall. They also reported that the movements of the northern anchovy, *Engraulis mordax,* corresponded with the seasonal dolphin movements. Their observations of *L. obliquidens* thus agree with those of *L. obscurus* of the present study.

Frequency of feeding in the highly visible manner described, with birds flocking overhead, was seasonal. It occurred less often in winter than at other times. In winter, anchovy are found in water >100 m (which is deeper than Golfo San José), and farther north, around lat. 36°-37° S (Brandhorst et al. 1971). Thus it is probable that dolphins were not feeding on southern anchovy in winter in the study area. Yet it is not possible that mammals as small and as constantly active as dusky dolphins stopped feeding completely for several months. We can only guess that other feeding was done on prey below and not at the surface, and possibly more individually instead of as a concerted group effort. At any rate, in winter we observed very little aerial behavior and rapid movement usually attendant on surface feeding. Instead, dolphin groups consistently moved slowly and in small groups near shore. Stomach content samples would be helpful in solving this ambiguity.

Dolphins exhibited a daily feeding cycle as well. Morning surface feeding activity lasted for shorter times than in the afternoon, so that dolphins were more often seen feeding in the afternoon. They moved in shallow water (5-10 m) in the morning, but most afternoon surface feeding occurred in 35-45 m. We gained the impression that im-

mediately before feeding, dolphins were diving for longer periods, perhaps going down deep to hunt for food. This impression was not quantified in direct association with feeding because we were unable to identify particular individuals and thus obtain length of dive records. However, we have evidence from radio-tracked dusky dolphins indicating that there is a length of dive-surface feeding time association (Würsig in press). Dive times from six dusky dolphins radio-tracked in summer showed a consistent increase in length during afternoon, with average night and morning dives about 14 s. Noon and afternoon dives rose to as high as 32 s in average duration. One animal radio-tracked in the austral winter (July-August 1974) showed no such length of dive increase in the daytime and actually surfaced more frequently in the afternoon than at other times of the day and night. This is an indication that feeding in the winter was different from feeding in the summertime. Since we believe that long dives in summer are associated with surface feeding in deeper water, it is likely that the extremely shallow and brief dives which occurred at night (Würsig in press) in summer were not associated with feeding, and that perhaps the animals were resting near the surface much of the night. This is the reverse of what was found in the common dolphin off California (Evans 1971, 1974), which dives for long periods at night—and is believed to be feeding at that time—and dives relatively shallowly during the day. Once again, this difference may be food related. While the common dolphin is thought to feed upon the deep scattering layer which rises out of deeper water enough for the dolphin to dive to it at night, no defined deep scattering layer can exist in the relatively shallow nearshore waters of the present study (Hersey and Backus 1962). Instead, dolphins feed on anchovy during the day, and move into deeper water as the day advances. Whether or not anchovy move into deeper water and are followed by the dolphin is not known. Perhaps the daily movement into deeper water was simply a consequence of being in shallow, nearshore water during night and early morning (to be discussed later), and having to go into deeper water in order to feed more efficiently. It is known that individuals of southern anchovy schools disperse during nighttime (Brandhorst and Castello 1971). This dispersal may make nighttime feeding on anchovy more difficult or impossible, and therefore dolphins may rest at night while feeding during the day in summer.

As an apparent consequence of feeding, dolphins were also found more often in deep water in spring, summer, and fall than in winter. Norris and Prescott (1961) suggested a similar movement trend for *Delphinus delphis* in California waters.

Group sizes were more often larger during the surface feeding season. The reason for this was a direct relationship between surface feeding activity and group size. Small groups usually engaged in surface feeding for only brief periods. The longer the feeding bout, the larger the number of dolphins present. Dolphins appeared to begin feeding in the morning and continued feeding through most of the afternoon; thus, there was a general increase in group size as the day advanced. The many small groups in the morning (and presumably night as well) covered a large (up to about 10 km in diameter) area, but nearest neighbors were usually no more than 0.5 km apart. We assume that they were probably within acoustic range of each other. Why did surface feeding activity last longer when dolphin numbers increased as groups joined? Perhaps larger schools of fish attract more dolphins and keep them feeding for a longer time. It is also possible that more dolphins are more efficient at herding and maintaining the fish school as a tightly clustered unit against the water surface. As an alternative explanation, it might be assumed that the small groups stopped feeding after brief periods because individuals were satiated. In a larger group, with perhaps more individuals per fish school size and more competition, this would presumably take longer. Since small schools which fed briefly were, however, seen to feed more and more as the day advanced, it seems unlikely that they had fed to satiation previously. Therefore, either larger fish schools simply attract more dolphins, or it is of direct advantage to animals to feed in larger groups, and a mechanism for telling nearby groups that herding of foodfish is in progress may have evolved. Various investigators have reported seasonal variations in group sizes, but none appear to link such variations to a particular feeding mode as in the present study. Gaskin (1972) stated that dusky dolphins off New Zealand are found in smaller schools in winter and larger ones in summer, basically the same as in our study. New Zealand dusky dolphins feed on small squid and on surface fish, but it is not clear whether their relative dependence on these prey changes seasonally.

How do other groups know about the feeding bout 0.5-1.0 km distant? It is unlikely that at that

distance animals are actively echolocating on the fish school, and thus some behavior of the feeding dolphins is implicated. Perhaps underwater vocalizations serve as cues. The possibility of different sound emissions by dolphins feeding and not feeding has not yet been investigated in the present study, although Tyack (1976) found such a variation in wild bottlenose dolphins. The incidence of noisy—omnidirectional sound source—leaps increases before and during feeding, and these may provide cues to nearby dolphins. Norris and Dohl (1980) discussed the likelihood of leap sounds serving a communication function. We believe that the likelihood of such a function specifically in dusky dolphin feeding is great. If noisy leaps serve to attract or inform nearby schoolmates, and are at least in part designed to do so, this recruitment behavior may be analogous to the "drumming" recruitment of African chimpanzees, described by Reynolds and Reynolds (1965) and others. Saayman and Tayler (1979) suggested that recruitment may occur in *Sousa* sp. off South Africa as well, but they did not link it to the possibility of aerial behavior in their population.

How do groups orient towards feeding locations from a distance of more than several kilometers? Our underwater recordings of sounds created by leaps suggests that they probably do not propagate much over 1 km. Norris and Dohl (1980) also found rapid attenuation for underwater Hawaiian spinner dolphin leap sounds. But, we observed dolphins that were leaping towards a large feeding bout from as far as 8 km. One possible explanation is that at least one dolphin swam to the distant group with information about the feeding bout, a feat not unknown in the animal kingdom (von Frisch 1967, on honey bees). We have no evidence that such messenger service may take place, and suggest a possible alternative. (Although Eberhard and Evans 1962, Evans and Dreher 1962, and Dreher and Evans 1964 reported that individuals of the Pacific bottlenose dolphin, *Tursiops gilli*, have been seen detaching from a group, moving to "investigate" something, and then going back to the group. Their interpretation of scouting behavior, however, is open to speculation.) When we saw dolphins swimming towards a feeding bout from more than a few kilometers, we saw individuals leaping out of the water in high forward leaps, clearing the water by as much as three times their own length, and thus leaping as high as 4-5 m. This leaping became lower and finally subsided altogether as the animals came closer to the activity. It seems possible that dolphins are using in-air vision to orient to the feeding bout, taking the birds flying above the activity and the leaping dolphins of the activity as a cue. We present this as a tentative hypothesis because many investigators do not believe that dolphins have a high degree of long-range in-air visual acuity. Dral (1975), Herman et al. (1975), and Rivamonte (1976), however, believe that *Tursiops* sp. may have good in-air vision at infinity. Perhaps dolphins gain information about the feeding bout in some other manner, and are leaping that high and often simply as part of their rapid movement (although such high leaps are not seen during after-feeding rapid movement). The high leaps may decline when the dolphins get near the activity because they are tiring. If it should prove, however, that dolphins are capable of long-range vision, and use it in this manner, it would mean that the birds associated with dolphin feeding—up to now assumed to represent a parasitic or neutral role as they scavenge on the doiphins' herding efforts—may serve as a signal to other dolphins. Dolphin leaps would assume a similar in-air signaling function. To observers, the number of birds above an activity was a sign of the feeding activity's "success," and if dolphins can see these birds, there is no reason to assume that they could not as well gage such activity level.

Various different types of leaps and aerial displays are associated with different stages of surface feeding. What function could these leaps serve? To answer this question we will attempt to reconstruct a typical feeding bout in detail: Before surface feeding, dolphins move rapidly, and dive for long periods, indicating that they are covering a large distance and are looking for fish deeper than a few meters below the surface. Immediately before and during feeding, forward movement stops and long dives continue, interspersed with clean, noiseless leaps. During these leaps, animals reenter the water headfirst and rapidly swim down. We therefore believe that the clean leaps allow dolphins to breathe rapidly, and then forcefully and efficiently return to the depths. The humping variant of this leaping type appears similar to the headfirst surface dive employed by experienced skin divers.

As long dives decrease, a tightly bunched fish school, usually numbering several thousand fish in an area 3-5 m in diameter, is first seen at the surface. It thus appears that dolphins actively herd fish towards the surface, probably to use the

surface as a wall through which the prey cannot escape. This function has also been suggested by Norris and Dohl (in press), and shown to be carried out by some large predatory fishes by Major (1976; cited by Norris and Dohl in press).

Noisy leaps, which started at some point before the fish school appeared, continue throughout surface feeding. We gained the subjective impression that these leaps occurred on the periphery of feeding bouts. This may be because breaching directly into the fish school would certainly not be of advantage in keeping it tight against the water surface. As well, it may serve to keep fish from escaping, and thus may be an acoustic or vibration "netting" effect. We often saw dolphins tailslapping rapidly (2-3 slaps/s) while moving in a tight circle around feeding bouts, and this action may further serve to keep fish from escaping (it has been described by Norris and Dohl (1980) and labeled "motorboating").

Besides the function of recruiting nearby groups to the feeding bout either purposefully or incidental to keeping fish from escaping, there is a third possibility. The splashes of noisy leaps create an underwater omnidirectional sound which may actually serve to frighten fish and cause them to school more tightly. Although work has been done on schooling relative to pressure waves (Bobbi Low[6]) as far as we know, no studies exist on sounds and fright reactions in schooling fish.

While the feeding bout continues, clean leaps and humpings continue as well, and dolphins still dive steeply. They also come up at a sharp angle, and individuals move rapidly through the bunched fish school, appearing at the other side of the school with several fish in their mouths. They then dive steeply again, and usually resume "attacks" on the fish school from below. The dolphins may stay below the fish much of the time to keep the school from escaping downward, and possibly to herd other fish to the surface to continue or prolong feeding. This is not the first indication of apparent cooperative herding and feeding in dolphins. It appears that many different species cooperate in herding, and it has been described for representatives of the genera *Orcinus, Tursiops, Sousa, Phocoena, Delphinus,* and others (see Norris and Dohl in press). Many terrestrial predators do so as well (Wilson 1975).

Acrobatic noisy leaps are most often seen during and after feeding. These may herd fish and recruit nearby groups, but they appear to require much energy and coordination which seems unnecessary just to make noise. We believe with Norris and Dohl (1980) that they may serve a "social facilitation" function, signaling a high activity level as individuals reaffirm and strengthen social and possibly sexual bonds. Saayman and Tayler (1973, 1979) describe similar high activity levels in *Sousa* sp. when two or more groups meet, and provide a similar assessment. We suggest that individual animals have taken care of the basic requirement of feeding and are now prepared to spend time socializing and "playing."

After feeding, dusky dolphins are more willing to associate with boats, human swimmers, whales, sea lions, and inanimate objects such as kelp. This may be an outgrowth of the high level of social activity at that time. Although we also saw much apparent mating after feeding, we were not able to compare it with amount of mating in small, nonsurface-feeding groups.

When many small groups coalesced to form a large one, did the smaller units remain intact or was movement of dolphins throughout the large group "random"? We saw individuals which had been spaghetti-tagged in a small group traveling together within a feeding bout a few days after tagging (Würsig in press), and thus have some indication that the small group remained intact. This agrees with data by Norris and Dohl (1980) on Hawaiian spinner dolphins. They found that there is fluidity in schools, but that small groups of 4-10 animals may be the only units with longer term continuity. We have no long-term information on group stability. However, studies of other dolphins suggest that the small-unit group composition is constantly changing (Saayman and Tayler in press, humpback dolphins; Shane 1977; Würsig 1978; Wells et al. in press, bottlenose dolphins). This flexibility in small-group composition at least superficially resembles chimpanzee group structure, and Saayman and Tayler (1979) and one of us (Würsig 1978) independently speculated that the similarity comes from feeding on unpredictable and patchy food distribution (see also Nishida 1968). If a similar group structure is found in dusky dolphins, it might be possible that individuals move randomly throughout the large after-feeding group, and that the entire group of up to 300 animals forms the more stable breeding unit or population.

[6]Bobbi Low, professor, University of Michigan, Ann Arbor, MI 48109, pers. commun. 1976.

Captured animals were of both sexes (Würsig in press). As well, there were usually only 1 or 2 calves or small young within a group of about 15 animals, suggesting that mating is not highly polygynous. Given data from captivity (Evans and Bastian 1969 and Caldwell and Caldwell 1972 provided reviews) suggesting that promiscuity is a prominent feature of most odontocete cetaceans at least in unnatural circumstances, it is likely that the dusky dolphin social system is promiscuous as well. However, Bateson (1974) suggested rather stable relationships between some spotted, *Stenella attenuata*, and spinner dolphins for play, mating, and sleep.

We found that young were born mainly in the austral summer. If we assume an 11-12 mo gestation period (Sergeant et al. 1973 for bottlenose dolphins), most effective matings took place outside the winter season. If sexual activity continues throughout the year, then we can assume that there is a physiological change in males or females that allows conception to peak during the spring or summer. Seasonal changes in testis weight have been found for several cetacean species (for example, Ridgway and Green 1967 for *Delphinus delphis* and *Lagenorhynchus obliquidens*). It is possible that a similar physiological change may exist in dusky dolphins. This might relegate some activity appearing to serve a sexual function to the role of greeting or bond-strengthening ceremonies as has been suggested by Caldwell and Caldwell (1967), Bateson (1974), and others. We suspect, but have no definitive proof, that most mating occurs in large groups after surface feeding. Since this feeding occurs mainly in spring and summer, it correlates well with the summer calving peak. Nevertheless, if this is so, it would not invalidate the possibility of a seasonal physiological cycle, nor of "mating" at times serving a purely social function.

Groups which had about 10-20 adults and as many calves occurred at times. We saw these nursery groups mainly at the periphery of large feeding activities. They did not appear to participate in the high-activity level characteristic of large feeding bouts and after-feeding. Perhaps, when small groups feed, females with young feed and then split off as activity increases. This can be of adaptive value. Young may in this way avoid possible aggression and competition within the large feeding aggregation, and they may avoid possible predation by killer whales and sharks attracted to the activity. We saw large (3-5 m) unidentified sharks moving in dolphin feeding activity on four separate occasions, but they did not appear to bother the adult dolphins engaged in feeding.

The relationship of dusky dolphins and bottlenose dolphins was in some ways puzzling. Dusky dolphins moved in generally deeper water than bottlenose dolphins, but the two at times probably came into acoustic range of each other. Yet they did not appear to take notice of each other, although both species independently sought contact with southern right whales, sea lions, and the boat. Dusky dolphins were found in shallow water in the morning, but bottlenose dolphins were in even shallower water in the morning, then moved into intermediately deep water around noon, then into shallow water once again. It has been suggested (Würsig and Würsig 1979) that bottlenose dolphins may have been feeding on southern anchovy, the same food as that of dusky dolphins in these intermediate waters. At any rate, by that time of day, dusky dolphins were more often found in deeper water, and as a result, their food niches did not appear to overlap. As well, the two species were found with approximately opposite frequency within sight of the study area at different times of year. This suggests that one or both species may at times have actively avoided the other, although alternative explanations such as different ecological requirements may be more important.

Bottlenose dolphins moved in small groups close to shore, dusky dolphins moved in small groups while not feeding, but in larger groups around feeding time. Bottlenose dolphins appeared to spend most of their nearshore time feeding individually or perhaps in groups of two and three on large solitary fishes inhabiting nearshore rocks. Large groups are possibly not of advantage in exploiting a presumably scattered food resource. On the other hand, dusky dolphins appeared to hunt in small groups spread out over a large area, thus increasing their food-finding efficiency for a patchily distributed food resource. When food was found, they rapidly coalesced, and appeared to herd prey cooperatively, allowing more efficient feeding.

Dusky dolphins fed near the surface in deeper water in the afternoon, and moved slowly and with little activity in early morning. We suggested that the surface-feeding pattern may be associated with availability of fish at different times of day and in different areas of water. A similar change in area from nonfeeding to feeding was found for

Hawaiian spinner dolphins (Norris and Dohl 1980) and for *Sousa* sp. (Saayman and Tayler 1979). But what about the consistently shallow-water movement in the morning (and all day in winter) when dolphins did not appear to be surface feeding much of the time? Their activity level was low and they did not move rapidly. They ignored or avoided boats as well as other marine mammals. They moved in small, tight groups and we therefore gained the subjective impression that they were schooling in an almost "fishlike" manner. Because level of activity was low, objects in their paths were avoided or ignored, and schooling was tight, we believe that the dolphins were resting at this time.

There is some evidence that killer whales may prey on dusky dolphins. On three occasions when killer whales came close to dolphin groups, the dolphins moved into extremely shallow water. At the same time, they moved rapidly along shore, perhaps to avoid nearshore predation, of which killer whales are known to be capable on more stationary prey, such as elephant seals and sea lions (Norris and Prescott 1961; Tomilin 1967; pers. obs.). As well, their nearshore movement may serve to hide them from possible *Orcinus orca* echolocation, which might be confused and inefficient in very shallow water.

These observations make it likely that nearshore movement while resting is a defense against predation. In shallow water, killer whales (and possibly deepwater sharks) cannot come from below, nor from the flanking shoreline. When danger comes from the open sea, dolphins can retreat to very shallow waters in which larger predators cannot maneuver as efficiently. Norris and Dohl (1980) postulated a similar function for nearshore resting of Hawaiian spinner dolphins, suggesting that these animals possibly avoid large deepwater sharks during morning periods of low activity. Saayman and Tayler (1979) also saw *Sousa* sp. very close to shore when killer whales were near, and suggested that the dolphins might avoid predation in a similar manner. In the present population, it is possible that nearshore movement during low-activity levels may serve other functions as well, but we believe that the predator-avoidance hypothesis may be at least part of the reason.

CONCLUSION

In the preceding discussion, we attempted to link observed behavior patterns to observed or possible ecological variables. We recognize that this endeavor is highly incomplete, and that many more alternative explanations will be made available in the future. One important factor that may have been somewhat obscured in the results and discussion of behavior should be emphasized. Dolphin behavior in captivity as well as in the wild appears highly plastic and variable. For example, dusky dolphins feed on southern anchovy. Yet many species are more catholic feeders (for example, Gunter 1942, Leatherwood 1975, for *Tursiops truncatus;* and Perrin et al. 1973, for *Stenella* spp.), and it is certain that dusky dolphins engage in other feeding than surface feeding described here. We hope that future work will shed light on other feeding modes, whether subsurface feeding is done cooperatively as is surface feeding, or whether it is performed more often by single dolphins on nonaggregated prey. Such an analysis may help us understand the dramatic difference in movement patterns and general activity levels between times when dolphins feed cooperatively on the surface and when they feed in other ways.

ACKNOWLEDGMENTS

Jen and Des Bartlett, Peter Tyack, Marty Hyatt, and Russ Charif helped gather data. Jan I. Wolitzky wrote the computer program for analyzing theodolite track data, and Matt Lamishaw patiently worked at the computer. Roger and Katy Payne provided material and intellectual support. George C. Williams, Kenneth Norris, Randall Wells, J. L. McHugh, Douglas Smith, and an anonymous reviewer for the *Fishery Bulletin* critically read the manuscript. Charles Walcott supported and encouraged all phases of the research. We are especially grateful to him.

This study was supported by the New York Zoological Society, the Committee for Research and Exploration of the National Geographic Society, and the Program for Neurobiology and Behavior of the State University of New York at Stony Brook.

LITERATURE CITED

BATESON, G.
1974 Observations of a cetacean community. *In* J. McIntyre (editor), Mind in the waters, p. 146-165. Charles Scribner's Sons, N.Y.

BRANDHORST, W., AND J. P. CASTELLO.
1971. Evaluacion de los recursos de anchoita (*Engraulis*

anchoita) frente a la Argentina y Uruguay. Inf. Tec. Proyecto Desarollo, Mar del Plata 32, 47 p.

BRANDHORST, W., J. P. CASTELLO, R. PEREZ HABIAGA, AND B. H. ROA.
1971. Evaluacion de los recursos de anchoita (*Engraulis anchoita*) frente a la Argentina y Uruguay. Inf. Tec. Proyecto Desarollo, Mar del Plata 34, 39 p.

BROWN, D. H., AND K. S. NORRIS.
1956. Observations of captive and wild cetaceans. J. Mammal. 37:311-326.

BROWNELL, R. L., JR.
1965. A record of the dusky dolphin, *Lagenorhynchus obscurus*, from New Zealand. Nor. Hvalfangst-Tidende. 54(8):169-171.

CALDWELL, D. K., AND M. C. CALDWELL.
1972. The world of the bottlenosed dolphin. J. B. Lippincott Press, Phila., 157 p.

CALDWELL, M. C., AND D. K. CALDWELL.
1967. Dolphin community life. Los Ang. Cty. Mus. Q. 5(4):12-15.

CALDWELL, M. C., D. K. CALDWELL, AND J. B. SIEBENALER.
1965. Observations on captive and wild Atlantic bottlenosed dolphins, *Tursiops truncatus*, in the northeastern Gulf of Mexico. Contrib. Sci. Los Ang. Cty. Mus. 91, 10 p.

CASTELLO, H. P., AND PINEDO.
1977. Botos na Lago dos Patos Natureza em Revista, Fund. Zoobot. Rio Grande do Sul 2:46-49.

CIECHOMSKI, J. D. DE.
1965. Observaciones sobre la reproduccion, desarrollo embrionario y larval de la anchoita argentina (*Engraulis anchoita*). Bol. Inst. Biol. Mar., Mar del Plata 9, 29 p.

CLARKE, R.
1957. Migrations of marine mammals. [In Engl. and Norw.] Nor. Hvalfangst-Tidende 46:609-630.

DRAL, A. D. J.
1975. Vision in cetacea. J. Zoo. Anim. Med. 6:17-21.

DREHER, J. J., AND W. E. EVANS.
1964. Cetacean communication. *In* W. N. Tavolga (editor), Marine bio-acoustics, p 373-393 Pergamon Press, N.Y.

EBERHARDT, R. L., AND W. E. EVANS.
1962. Sound activity of the California gray whale, *Eschrichtius glaucus*. J. Audio Eng. Soc. 10:324-328.

EVANS, W. E.
1971. Orientation behavior of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188:142-160.
1974. Radio-telemetric studies of two species of small odontocete cetaceans. *In* W. Schevill (editor), The whale problem: a status report, p. 386-394 Harv. Univ. Press, Camb., Mass.
1976. Distribution and differentiation of stocks of *Delphinus delphis* Linnaeus in the northeastern Pacific. Contribution 18 of the Scientific Consultation on Marine Mammals, Bergen, Norway, 72 p.

EVANS, W. E., AND J. BASTION.
1969. Marine mammal communications: social and ecological factors. *In* H. T. Anderson (editor), The biology of marine mammals, p. 425-475. Acad Press, N.Y.

EVANS, W. E., AND J. J. DREHER.
1962. Observations on scouting behavior and associated sound production by the Pacific bottlenose porpoise (*Tursiops gilli* Dall). Bull. South. Calif. Acad. Sci. 61:217-226.

FRISCH, K. VON.
1967. The dance language and orientation of bees. (Translated by L. E. Chadwick). Belknap Press of Harv. Univ. Press, Camb., Mass., 566 p.

GASKIN, D. E.
1968. Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. N.Z. J. Mar. Freshwater Res. 2:527-534.
1972. Whales, Dolphins and Seals. Heinemann Educational Books, Lond., 200 p.

GASKIN, D. E., G. J. D. SMITH, AND A. P. WATSON.
1975. Preliminary study of movements of harbor porpoise (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can. J. Zool. 53:1466-1471.

GREENWOOD, J. A., AND D. DURAND.
1955. The distribution of length and components of the sum of n random unit vectors. Ann. Math. Stat. 26:233-246.

GUNTER, G.
1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J. Mammal. 23:267-276.

HERMAN, L. M., M. F. PEACOCK, M. P. YUNKER, AND C. J. MADSEN.
1975. Bottlenosed dolphins: double-slit pupil yields equivalent aerial and underwater diurnal acuity. Science (Wash., D.C.) 189:650-652.

HERSEY, J. B., AND R. H. BACKUS.
1962. Sound scattering by marine organisms. *In* M. N. Hill (editor), The sea: ideas and observations on progress in the study of the seas, vol. 1, p. 498-539. Wiley, N.Y.

IRVINE, B., AND R. S. WELLS.
1972. Results of attempts to tag Atlantic bottlenosed dolphins (*Tursiops truncatus*) Cetology 13:1-5.

LEATHERWOOD, S.
1975. Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. 37(9):10-16.

LEATHERWOOD, S., AND R. REEVES.
1978. Porpoises and dolphins. *In* D. Haley (editor), Marine mammals of eastern North Pacific and Arctic waters, p. 99-111. Pacific Search Press, Seattle.

MAJOR, P. F.
1976. The behavioral ecology of predator-prey interactions in schooling fish. Ph.D. Thesis, Univ. California, Santa Cruz, 75 p.

MEAD, J. G.
1975. Preliminary report on the former net fisheries for *Tursiops truncatus* in the western north Atlantic. J. Fish. Res. Board Can. 32:1155-1162.

NISHIDA, T.
1968. The social group of wild chimpanzees in the Mahali Mountains. Primates 9:167-224.

NORRIS, K. S.
1967. Some observations on the migration and orientation of marine mammals. *In* R. M. Storm (editor), Animal orientation and navigation, p. 101-125. Oreg. State Univ. Press, Corvallis.

NORRIS, K. S., AND T. P. DOHL.
1980. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish Bull., U.S. 77:821-849.
In press The structure and functions of cetacean schools.

In L. Herman (editor), Cetacean behavior. Wiley Interscience, N.Y.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans in Californian and Mexican waters. Univ. Calif. Publ. Zool. 63: 291-401.

ODELL, D. K.
1975. Status and aspects of the life history of the bottlenose dolphin, *Tursiops truncatus*, in Florida. J. Fish. Res. Board Can. 32:1055-1058.
1976. Distribution and abundance of marine mammals in south Florida: preliminary results. Univ. Miami Sea Grant Spec. Rep. 5:203-212.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

PIZZARO, M. J.
1976. Analisis de los resultados de la primera campaña oceanografica en el Golfo San Jose. Cent. Nac. Patagónico Inf. Tec. 1.10.2:1-18.

REYNOLDS, V., AND F. REYNOLDS.
1965. Chimpanzees of the Budongo Forest. *In* I. DeVore (editor), Primate behavior, p. 368-424. Holt, Rinehart, and Winston, N.Y.

RICE, D. W.
1977. A list of the marine mammals of the world. U. S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-711, 15 p.

RIDGWAY, S. H., AND R. F. GREEN.
1967. Evidence for a sexual rhythm in male porpoises, *Lagenorhynchus obliquidens* and *Delphinus delphis* bairdi. Nor. Hvalfangst-Tidende 56:1-8.

RIVAMONTE, L. A.
1976. Eye model to account for comparable aerial and underwater acuities of the bottlenose dolphin. Neth. J. Sea Res. 10:491-498.

SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER.
1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. Koedoe 15:1-24.

SAAYMAN, G. S., AND C. K. TAYLER.
1973. Social organization of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. J. Mammal. 54:993-996.
1979. The socioecology of humpback dolphins (*Sousa* sp.) *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals, Vol. 3: Cetaceans, p. 165-226. Plenum Press, N.Y.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). Behavior 44:212-233.

SERGEANT, D. E.
1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fish. Res. Board Can., Bull. 132, 84 p.

SERGEANT, D. E., D. K. CALDWELL, AND M. C. CALDWELL.
1973. Age, growth, and maturity of bottlenosed dolphins (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.

SHANE, S. H.
1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. Thesis, Texas A&M Univ., College Station, 239 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. Freeman, San Franc., 776 p.

TAYLER, C. K., AND G. S. SAAYMAN.
1972. The social organisation and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Ann. Cape Prov. Mus. Nat. Hist. 9:11-49.

TOMILIN, A. G.
1957. Mammals of the U.S.S.R. and adjacent countries. Vol. 9, Cetacea. [In Russ.] Izd. Akad. Nauk SSSR, Mosk., 756 p. (Translated by Isr. Program Sci. Transl., Jerusalem, 1967, 717 p.)

TYACK, P.
1976. Patterns of vocalization in wild *Tursiops truncatus*. Senior Thesis, Harvard Univ., Camb., Mass., 44 p.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
In press. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), Cetacean behavior. Wiley Interscience, N.Y.

WILKE, F., T. TONIWAKI, AND N. KURODA.
1953. *Phocoenoides* and *Lagenorhynchus* in Japan, with notes on hunting. J. Mammal. 34:488-497.

WILSON, E. O.
1975. Sociobiology, the new synthesis. Harv. Univ. Press, Camb., Mass., 697 p.

WURSIG, B.
1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. Biol. Bull. (Woods Hole) 154:348-359.
In press. Radio tracking dusky porpoises (*Lagenorhynchus obscurus*) in the south Atlantic. *In* Mammals in the seas. FAO Fish. Ser. 5.

WURSIG, B., AND M. WURSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.
1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fish. Bull., U.S. 77:399-412.

GROWTH AND SURVIVAL IN NEWLY SETTLED SPAT OF THE MANILA CLAM, *TAPES JAPONICA*

JOHN G. WILLIAMS[1]

ABSTRACT

Substrate abundances of adult Manila clam, *Tapes japonica*, were manipulated in July 1976 on a portion of beach dug commercially in the southern region of Puget Sound, Washington. Differences in clam spat growth and survival were measured between samples taken from substrates having varying levels of adult clam abundance.

The clam spat settled at 0.206 mm long. Initial growth of clams settling in the fall was much slower than for clams settling in the summer, 9 months versus 2 months, respectively, to reach approximately 2.5 mm long. Summer settling clams form a visible growth checkmark by October of their first year at approximately 5-8 mm. Fall settling clams form their first visible checkmark during their second October at approximately 14-16 mm. The length of clams was found to be significantly less for clams growing in substrates with natural or high adult clam abundances versus those from substrates with no adult clams.

Only 1.2% of the initial population of clams that settled in September 1976 survived until June 1977. The most likely cause of this mortality was by meiofaunal predators, particularly nematodes. By June, no difference in survival rates was detectable between clams from substrates that contained no adult clams versus those from substrates with natural or high adult clam abundance.

Clam spat movement occurred along the beach and may have contributed to the high spat mortality.

The Japanese little-neck or Manila clam, *Tapes japonica* Deshayes, is a native to Japanese and Korean waters, but was introduced into Puget Sound, Wash., along with the Pacific oyster, *Crassostrea gigas*, in the 1930's (Quayle 1964). It has since become an important part of the commercial Puget Sound hard-shell clam fishery with approximately 1 million lb harvested annually. It has also been so heavily utilized by the sport fishery that the populations on some Puget Sound beaches have been almost eliminated.

The majority of research on the Manila clam has been performed in Japan (see Tamura 1966 for a review of the Japanese literature). Because the water temperatures and climate in Puget Sound are cooler than those in most of the Japanese study areas, the results published by the Japanese with respect to spawning times, growth, and population numbers can be misleading when applied to clam populations in this area. Studies conducted on the west coast of the United States and Canada dealt with gonad development (Holland and Chew 1974), planktonic larval stages (Quayle and Bourne 1972), and growth and/or survival after settling and after some arbitrary body size, usually based on sieve retention, had been reached (Jones 1974; Glock 1978; Lukas[2]). Nosho and Chew (1972) made the only attempt to investigate early settling stages of the Manila clam. However, due to the sieve size they used, they were unable to detect newly settled spat. The lack of early life history information is probably related to the difficulty in sorting out newly settled spat from gravel samples, and in specific indentification. Loosanoff et al. (1966) found it difficult to identify pelagic larvae to species and cited this as a reason for incomplete life histories of many pelecypods. Quayle (1952) found that identification of spat was even more difficult than the identification of planktonic larvae.

I began a study in the summer of 1976 to describe the growth and survival of Manila clams from settling size to formation of the first growth ring. In addition, since the study was located in an area with large numbers of adult Manila clams, I investigated the possibility that the pres-

[1]Washington Cooperative Fishery Research Unit, College of Fisheries, University of Washington, Seattle, WA 98195.

[2]Lucas, G. 1973. Clam-abalone spawning and rearing. Commer. Fish. Res. Dev. Act. July 1, 1970 to June 30, 1973. Fish. Comm. Oreg. Proc. Rep., 19 p.

Manuscript accepted May 1979.
FISHERY BULLETIN: VOL. 77, NO. 4, 1980

ence of adults may influence or be associated with spat growth and survival.

METHODS

In 1976 a study site was chosen in southern Puget Sound on a narrow estuary called Little Skookum Inlet (Figure 1). The site was on intertidal land from which Manila clams were commercially harvested. There was easy access to the beach, but because of its private ownership, the probability of people tampering with the experimental plots was low.

Plot Construction

To study the possible influence of adult clams on the growth and survival of spat, I constructed plots in which I experimentally manipulated the beach material to yield different concentrations of adult clams. Each plot contained four treatments, as follows:

Treatment 1. No adult clams and new substrate. All beach material was removed to a depth of 15 cm to ensure removal of adult clams. Gravel from the high intertidal (+3 m) was then carried down to fill the excavated hole to the existing beach level.

Treatment 2. No adult clams and old substrate. All beach material was removed to a depth of 15 cm and then sifted through a 12 mm mesh screen to remove the adult clams. All screened material and any large rocks retained on the screen were then returned to the excavated hole and enough additional screened material was added from residue of Treatment 1 to bring the treatment level to the same height as the beach.

Treatment 3. Moderate adult clam density (control). A shovel blade was inserted vertically, 15 cm into the substrate on the edge of the treatment. The handle was pulled back and forth 3 or 4 times until the surface above the blade was loosened. The shovel blade was inserted and agitated around the perimeter of the treatment until the entire surface area of the plot had been disturbed. No clams were added to or subtracted from the treatment, and no counts of naturally occurring clams in the treatment were made prior to the settling experiments.

Treatment 4. High adult clam density. This treatment was disturbed in the same manner as

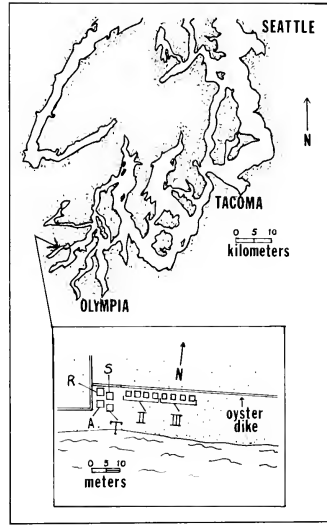


FIGURE 1.—Diagrammatic representation of the study site for the Manila clam on Little Skookum Inlet in southern Puget Sound, Wash., on a minus tide (MLLW). Plots A, II, and III were established in July 1976. Plots R, S, and T were established in July 1977. Plots A, R, S, and T were 2 × 2 m squares divided into 16 sections each and Plots II and III each contained four 1.5 × 1.5 m sections in a row

Treatment 3. In addition, enough adult clams between 2.0 and 5.0 cm in length were placed on the surface of the treatment to create a surface density of approximately 480/m². This density was the number of clams necessary to completely cover the surface area.

In all cases, the day following the construction of Treatment 4, no clams remained on the beach surface, and a large number of new siphon holes were apparent. In no case were any adult clams found in Treatments 1 or 2, and it was thus assumed that the clams added to Treatment 4 buried within the treatment and did not move to adjacent treatments or outside the plot. I as-

sumed that any predation on the clams before they were able to bury within the substrate did not substantially affect the magnitude of the adult clam density, as compared with the other treatments.

I constructed Plots A, II, and III in July 1976, and Plots R, S, and T in July 1977 at a tidal height ranging from +0.25 m to +0.75 m (MLLW datum), as determined by the height of the nearby oyster dikes (Figure 1). For Plots A, R, S, and T, wooden lath stakes were driven into the ground to delineate 2 × 2 m squares, that were then subdivided by stakes into four rows and four columns. The result was sixteen 0.25 m^2 subareas in each plot. Four replicates of Treatments 1-4 were then constructed within each plot to form a 4 × 4 Latin square array of treatments. For Plots II and III, stakes were driven into the ground to delineate a 1.5 m wide by 12.0 m long plot. Treatments 1-4 were randomly assigned to subareas within the plot so that the resulting configuration consisted of four different 1.5 × 1.5 m treatments, separated by 1.5 m spaces between each treatment, within each plot.

A continuously recording thermograph was buried 1 cm below the surface gravel next to Plot A in October 1976. The recording tape was replaced monthly.

The large plots were constructed to minimize possible edge effects caused by the close proximity of treatments to each other. To further minimize possible edge effects, samples were taken only from the inside 0.25 m^2 area of each treatment in both the large and small plots.

Sampling

To check for newly settled clams, each week I took two or three gravel samples beside each plot by twisting a 20.28 cm^2 clear plastic tube 2 cm deep into the beach. A small hand trowel was then shoved down beside and rotated under the tube as it was removed from the gravel, preventing any material from falling out. The contents of the tube were then transferred to a bottle or plastic bag. A 10% formaldehyde solution with a concentration of 0.01% phloxine B dye was then added to the container.

In the laboratory, I washed the gravel samples through a series of Tyler[3] sieves. Sieving down to mesh size of 0.149 mm was necessary to insure retainment of the smallest, newly settled spat in freshly preserved samples. The residue from the finest sieve was placed in a Petri dish under a compound dissecting scope (50×) and examined for clam spat.

In 1976, when a large larval settlement was detected from the weekly gravel samples, I sampled all of the treatment areas in each plot. I constructed a sampling template from a piece of 1.91 cm thick plywood that had the inside 0.125 m^2 removed. Seine twine was stretched over the opening to form a 5 × 5 grid with each square 5.72 cm on a side.

For each individual treatment area in a plot, five squares in the grid were randomly selected as the sample sites from which to take cores. After removing the cores, the holes were filled to beach level with gravel taken from beside the plot, at a depth of 4 cm, in order to avoid introducing newly settled spat to the plots.

To follow the growth and survival from settling size, I took 10 cores per treatment in November and December 1976 and in January, March, and April 1977 from Plots A and II. The location of the cores within each treatment was randomly selected, excluding all core areas previously utilized. In June 1977 the remaining core areas in the different treatments were sampled. For each sampling period, all cores in each treatment were sieved in the laboratory, the clams were counted, and a height and length measurement was taken on the first 30 clams encountered per treatment.

Sample Sizes

Twenty core samples per treatment were taken immediately after newly settled clams were observed. Using methods given by Elliott (1971), I determined that the number of clam spat per core per treatment had a negative binomial distribution. The counts were transformed ($\log_{10} X$) and a mean and variance computed. These numbers were utilized in Elliott's formula for the determination of sample sizes. A standard error equal to 20% of the mean and a 95% confidence were used. The results showed that a sample size of 5 for each treatment would have been sufficient. Based on this and the amount of time necessary to process each core, 10 cores per treatment were chosen as the sample size for subsequent sampling periods.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

Summer Sampling in 1977

To follow the growth of the 1976 fall settlement for 1 yr, three random 0.25 m^2, 3 cm deep gravel samples were taken from near Plot A in early August 1977, and again in the middle of September. No treatment effect determinations were possible due to a lack of sufficient study plots. Material was preserved by freezing, instead of by a formaldehyde solution. In the laboratory the material was thawed and washed through Tyler sieves (1.190 mm minimum mesh size), and then the residue on the screens was placed in a large cake pan. The clams were sorted by eye, and a height and length measurement was taken on all clams.

Core samples taken from Plots R, S, and T, in the summer and fall of 1977 to test for larval settlement were used as the basis for determining the growth of the clam spat that settled in July 1977.

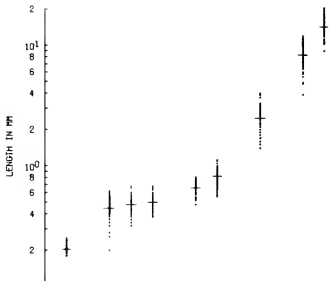


FIGURE 2.—Plot of individual and mean length measurements of Manila clams recovered during sampling periods. Sample sizes from September 1976 to September 1977 were 129, 136, 97, 72, 67, 94, 61, and 110.

RESULTS

Growth

To test for possible changes in the height-length ratio due to growth, a linear regression was run on $\log_{10}$-transformed height versus length measurements for clams from settling size through 1 yr. Correlation was high (r = 0.997) and thus only length measurements were used to express results. A plot of clam lengths determined from samples taken after the initial settlement in September 1976 through the following 12 mo is shown in Figure 2.

The average length of newly settled clams was 0.206 mm (N = 129; SE = 0.01). The clam spat that settled in September 1976 grew about 2.5 times their settling length in 2 mo. Little growth occurred between November and January; growth commenced again by the middle of March. By June the spat had attained a length of 2.17-2.7 mm.

In contrast to the growth of the fall settlement, the clams that settled in July 1977 attained an average length of 2.82 mm (N = 47; SE = 0.12) by the middle of September. This was a growth of 13.5 times their size at settling in 2 mo and was slightly larger than the size reached in 9 mo by clams from the fall settlement.

Growth rings were laid down in October. Clams that settled in July attained an average length of 6.16 mm (N = 42; SE = 0.51) by this time. Clams that settled in the fall also formed rings their first October, but since they were so small, the mark was not discernable by the following summer. By September 1977 the clams from the fall settlement had attained an average length of 14.93 mm (N = 110; SE = 0.26). Approximately 0.5 mm growth occurred before the end of October, at which point their first growth ring was visible. Clams that settled in July were about 23 mm long 1 yr later.

No differential growth was detectable until June 1977 between clams that settled in fall 1976 into the different experimental treatment substrates. A Kruskal-Wallis rank sums test on clams sampled in June detected a significant difference (P<0.001) between those sampled from substrates with no adult clams and those from substrates with adult clams. The treatments were ranked by the average length of clams that each contained (Treatment 2 had the largest clams; Treatment 3 had the smallest). A series of one-tailed Mann-Whitney pairwise comparisons (pairwise P<0.05) were performed to test which treatments differed significantly (Hollander and Wolfe 1973). The following were the results (no significant difference between pairs underlined in common):

2 1 4 3

Clams from substrates with no adults (Treatments 1, 2) averaged 2.70 mm (N = 55; SE = 0.08) long, and clams from substrates with moderate (Treatment 3) and high (Treatment 4) adult clam abundances averaged 2.17 mm (N = 39; SE = 0.08).

Survival

The density of newly settled clams sampled from 105 cores ranged from 19 to 93, with a mean of 54.3. Only 1.2% of the clams (equivalent to 250-450/m²) survived until June 1977, 9 mo after the fall 1976 settlement (Figure 3). The largest loss in clams occurred during the first 2 mo after settling when the density decreased by 57%. During the third, fourth and next 2 (combined) mo after settling, the average density decrease from the previous sampling period was 34%, 56%, and 35%, respectively. A Kruskal-Wallis test on the June data detected no differential (P>0.50) survivorship between clams that had settled into substrates with adult clams versus those that settled into substrates with no adult clams.

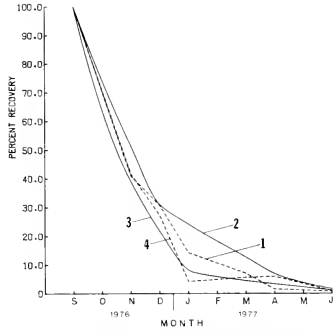


FIGURE 3.—Survival of Manila clams at each sampling period for Treatments 1-4 expressed as a percentage of the initial levels at settlement.

DISCUSSION

Growth

There has been a great disparity in the reported size of 1-yr-old Manila clams. Three areas in Japan have reported three different lengths: in Hokkaido, 8 mm (Yamamoto and Iwata 1956); in the Inland Sea, 18 mm (Ohba 1959); and in Ariake Bay (South Japan), 27 mm (Tanaka 1954). Rodde et al. (1976) grew Manila clams to 34 mm in 1 yr under hatchery conditions with high temperatures and nutrient rich water. Nosho and Chew (1972) estimated that Manila clams in Hood Canal, Wash., were 24 mm at the end of 1 yr. These conflicting reports have created some difficulties for scientists in attempting to determine the age of Manila clams found in Puget Sound beaches. The fact that I found two sizes of clams that resulted from settlements only a few months apart makes this understandable. In some cases, others have based growth data on checks in the shell without studying the early stages of growth. However, without the knowledge about the time of year that a clam cohort settled and the period of growth until the formation of the first visible checkmark, the determination of the age of a clam can be difficult.

The results of my research showed that growth rings were formed by the end of October. For clams that settled in the summer the first visible check was formed at 3-4 mo, but for those settling in the fall (just 2-3 mo later), the first visible mark was formed in 13 mo. The modal lengths, that I found until the first visible checkmark was formed, of 5-8 mm and 14-16 mm for the summer and fall cohorts should give scientists a more concise baseline upon which to judge growth data for the Manila clam.

Although there was a difference in the growth rates between clams that settled in the summer and those that settled in the fall, the length of newly settled clams that I observed was the same for both periods and the same as those found by Loosanoff et al. (1966) at the Milford Laboratory in Connecticut and by Yoshida (1953) in Japan. The clams from the fall settlement more than doubled in size in 2 mo, but then their growth almost ceased for a 3 mo period and slowly increased until March. This slow winter growth was very similar to Japanese findings on larger Manila clams (Yoshida 1935; Yamamoto and Iwata 1956; Ikematsu 1957; Ohba 1959). In southern Puget Sound, Glock (1978) found no growth during this same period for Manila clams with lengths from 12 to 20 mm. Wilbur and Owen (1964) stated that growth is generally negligible for most molluscan species below 5°-10° C, which

corresponded to the temperatures found in Little Skookum Inlet during the winter months (Table 1). The growth for the summer settling clams was much higher, and other studies with Manila clams of the same settling size have reported similar or higher initial growth. Yoshida (1953) found clams settling in early June reached 0.9 mm by the end of July. Clams raised in 22°-29° C water under hatchery conditions, with an optimal food supply, were 5 mm 90 days after settling (Rodde et al. 1976). The small size at settlement for the Manila clam and the slow initial growth of clams that settled in the fall underscores the necessity to use a small mesh size when sampling for spat so as not to possibly mask a large part of their early life.

In addition to a difference in the growth rates between summer and fall settling clams, the lengths of clams that I recovered in June were significantly greater ($P<0.001$) in treatments without adult clams than in treatments with adult clams. A similar decreased growth with increased densities has also been shown for larger Manila clams in other studies. Sagara (1952) found this for clams >30 mm, but indicated that clams <20 mm were not affected by density. Ohba (1956) found decreased growth in 10-12 mm clams and related it to competition for food. In other studies, Hancock (1973) found reduced growth with *Cardium edule* in areas of overpopulation and a marked reduction in size in locally overcrowded areas. Finally, in a hatchery-rearing experiment with 14 mm Manila clams, Langton et al. (1977) found that growth increased with ration size in crowded conditions. A decrease in available food to juveniles was implicated as the controlling factor that caused the decrease in clam growth observed in treatments with adult clams, as compared with those in treatments without adults. There were not sufficient study plots available to determine whether this differential growth continued during the summer. The results of these experiments indicates that the harvest of adult clams from a beach will allow for a better growth of undersized clams. This result coincides with the general view of commercial Manila clam harvesters in Puget Sound (Taylor[4]).

TABLE 1.—The daily average and the extreme substrate temperatures (1 cm below surface) between sampling periods for the Manila clam in Little Skookum Inlet, Wash., at the +0.6 m tide level

Sampling period	N	Temperatures (°C) Average	Extremes
1976			
Oct 24-Nov 20	30	11 6	10 5-12 5
Nov 20-Dec 20	30	9 7	6 5-10 5
Dec 20-Jan 16, 1977	27	7 8	4 0- 9 0
1977			
Jan 16-Feb 2	17	8 6	3 0- 9 0
Mar 11-Apr 8	28	9 5	5 5-20 0
Apr 8-May 6	28	12 2	11 0-18 5
May 6-June 4	29	12 8	12 0-20 0
June 4-July 4	30	15 6	14 5-28 0
July 4-6	3	16 7	16 5-21 5
July 30-Aug 4	6	17 8	16 5-19 0
Aug 25-Sept 21	27	16 7	15 5-23 0
Sept 21-Oct 12	21	15 6	10 0-16 5

Survival

Approximately 1.2% of the clams that settled in September 1976 survived until June 1977. Japanese studies on Manila clams have reported similar low levels of survivorship 4-9 mo after initial settlements. Ikematsu (1957) found that spat densities of 5,000/m² in March were only 1.0% of the 500,000/m² he found the previous November. Ohba (1959) estimated settling densities of 25,000/m² in October, but found only 8.0% of that (2,000/m²) by the following June. In studies on a number of clam species other than Manila clams, Muus (1973) reported that regardless of clam densities at settling, the number of clams recovered per unit area decreased rapidly until a density of several hundred per square meter was approached. The level of survivorship from the fall settlement was similar to these studies but although it was low, the number of spat that it represented (250-450/m²) was more than 2.5 times greater than the density of adults (approximately 100/m²) considered as an adequate level at which a beach can be dug commercially (Taylor see footnote 4).

Not only was the survivorship from the fall settlement low, but the majority of the clam spat mortality occurred during the first 2 mo after settling (57%) and only about 10% of the clams survived to 0.7 mm long (6 mo). One or more of a number of factors are usually identified as causes of high mortality in biological populations. In the case of benthic marine invertebrates, Hancock (1970) stated that survival after settlement will depend upon: a) environmental conditions, notably temperature; b) food supply, which may be affected by intra- and interspecific competition; c) space competition; d) parasites and disease; e) ac-

[4]Justin Taylor, Totten Seafood, Route 1, Box 372A, Olympia, WA 98502, pers. commun. June 1977.

cidental ingestion of newly settled young (of some molluscs by adults of the same or different species; f) physical damage or disturbance; and g) predation. Most of the above factors did not appear to be significant in this study.

a) Yoshida (1953) experimented with 1.0-3.8 mm Manila clams and found a survival of 90% or greater in water temperatures averaging 7° C. The water temperatures at Little Skookum averaged 8.9°-12.7° C during winter and probably were an insignificant cause of mortality, except during the coldest part of January (Table 1). Low water temperature probably attributed to the slight increase in clam spat mortality observed at this time.

b) When Cahn (1951) surveyed the Japanese Manila clam fishery, he cited starvation under overcrowded conditions of newly settled spat as a probable cause of death. The survival rate in this study, however, remained fairly equal between treatments with no adult clams and those with high adult clam densities. Thus, the expected cropping of the food supply to spat that settled among the adults did not appear to affect the spat's survival. In addition, almost nothing is known about the food requirements of newly settled spat, so adequacy of food supply as a controlling factor would be difficult to determine.

c) Lack of sufficient space for growth between two consecutive year classes was proposed by Hancock (1973) as one of the largest factors controlling survival of newly settled spat in *C. edule*. He proposed that space requirements for growth of shells would conflict in two adjacent year classes, with the smaller cockles being forced from the substrate as they grew. In nonadjacent year classes, 0-group cockles could maintain their position between shells of older adult clams. This hypothesis was based on clams first observed when 10 mm long. Space limitation did affect survival of the spat in this study, because their size was quite small compared with the space available for growth.

d) There was no evidence of parasites and/or disease in either the adult stocks or the newly settled spat.

e) Under experimental conditions, Kristensen (1957) found that inhalation by adult cockles of newly settled spat could cause death of the small spat, even when the larvae were discharged soon afterward. Hancock (1973), however, did not feel that the presence of adults adversely affected survival of settled young in his studies at Burry Inlet, but he felt that mortalities were related to oyster catcher, *Haematopus oachmani*, predation. Since he did not look at the spat until 5 mo after they had settled, it would be difficult to determine at which stage in their early life history the largest mortality occurred. In the present study, the largest initial settlement occurred in Treatment 1, but by April this treatment had not only the lowest survival but also the lowest absolute density of the four treatments. If mortality was caused by ingestion by adults, then a higher density would have been expected for Treatment 1, which contained no adults.

f) Shellbourne (1957) studied small oysters and found that shifting surface sands subjected newly settled spat and juveniles to increased mortality due to abrasion. Quayle (1952) felt the largest cause of mortality for the spat of *Venerupis pullastra* was the unsuitability of the substrate. Glock (1978) planted small (2-4 mm) hatchery-reared Manila clams on a southern Puget Sound beach and then covered some of the area with protective mesh covering. He had a much higher survival rate under the areas with plastic mesh, and attributed this in part to stabilization of the sediment. He also found predation rates to be low. In this study, the Treatment 1 areas in Plots A, II, and III were readily observable through the third month after settling, due to a slight difference in color of the gravel brought down from the high intertidal area. This observation indicated that any movement of the surface gravel must have been slight in order not to mask the visible differences of this treatment. In the laboratory, I subjected the spat to considerable mechanical agitation during the process of washing and sieving; however, only a few of the thousands of spat that I observed had damaged shells. I also found some unbroken, empty clam shells that were equal in size to live clams sampled, but never a number of shells equivalent to the mortality observed. I concluded that abrasion did not cause substantial mortalities in this study.

g) Thorson (1966) felt that the biological factor with the greatest effect on survival of newly settled larvae was predation. Muus (1973) came to the conclusion after a very complete study on the early life history of newly settled bivalves in Denmark. Since the largest mortality in this study occurred when the spat were quite small, it seemed most probable that if predation were the cause, then the majority of the loss would be to

meiofaunal predators (defined as organisms that are retained on sieves 0.04-0.1 mm and passed through sieves 0.5-1.0 mm (McIntyre 1969; Coull 1973)), that were nearly the same size. Swedmark (1964) listed turbellarians, coelenterates, and nematodes as interstitial predators. Thorson (1966) cited studies that have shown turbellarians, nematodes, and harpacticoid copepods to be predators on newly settled spat. Although only a few turbellarians and no coelenterates were recovered during the study period, a large number of nematodes and harpacticoids were included in each core sampled. In spite of the citation by Thorson, the harpacticoids in this study were not likely to have eaten even the smallest clam spat, as these particular species are considered almost exclusively detritus feeders (Sibert et al. 1977; Illg[5]). The degree to which nematodes may have accounted for loss in clam spat is unknown. Although larger predators (shore crabs, drilling snails, sea stars, fish, birds) may account for significant predation losses on larger clams, their effect on survival of the newly settled spat was probably low. Large, active predators would not likely have expended the energy to forage for the small spat that would have provided little energy in return.

Of all the above factors listed, I concluded the major cause for the large loss in spat that I observed was due to predation by meiofaunal predators. Since some empty clam shells were found on the beach and vigorous sieving in the laboratory did not damage the shells of the spat, only predation could have accounted for both the high mortalities and the destruction or removal of shells. I assumed that nematodes were the dominant predator.

Movement of Clams on the Beach

Two experiments were performed (November 1976 and May 1977) to test for movement of small clams on the beach. In each case, 2 cm of surface gravel was removed from a plot that was 0.25 m^2, to insure that no small clams remained. One month after the start of each experiment, core samples were taken and small clams were found in the center of each plot that had been previously clam free. It was not known whether this movement was active or passive. Active movement implies that clams physically moved (probably by foot action) across the beach. Passive movement implies physical transport of clams across the substrate, with or without movement of surface gravel. In the present study, byssus threads were detectable on clams as small as 0.45 mm long. This indicated that they had the ability to attach to the substrate which would decrease their susceptibility to movement by currents. To the contrary, Sigurdsson et al. (1976) proposed that some postplanktonic bivalve larvae use their byssus threads as a method for dispersal. The method of transport would be analogous to the gossamer flight by young spiders. Either of these two methods for utilization of byssus threads may have been used by some of the calm spat at the study site.

Baggerman (1953), with *C. edule*, found that transportation of clams over the substrate may have been an important factor in the final distribution of clams. In this study, transportation may have played an important part in the growth and survival of the spat. Growth was shown to be significantly greater in treatments without adult clams than in treatments with adult clams. The adults thus may have directly caused a decrease in growth of juveniles by decreasing the availability of food, and/or indirectly they may have influenced clam spat to actively seek new substrates in which to resettle to avoid competition. Additionally, in the process of resettlement, clam spat may have become susceptible to a larger number of predators.

ACKNOWLEDGMENTS

Thanks to K. K. Chew, J. L. Congleton, P. A. Jumars, and P. L. Illg for their advice and assistance. Daniel B. Qualye helped with the identification of young Manila spat.

Office space and materials for field work were provided by R. R. Whitney, Leader, Washington Cooperative Research Unit at the University of Washington. Michael Shepard, T. Schink, D. Skidmore, and R. Carter provided assistance with the field work. My especial thanks to J. Taylor who allowed me to use his beach for this study. His wisdom gained from years of commercial clam and oyster harvesting provided me with valuable insight into the biology of the Manila clam.

[5]Paul Illg, Department of Zoology, University of Washington, Seattle, WA 98195, pers. commun. February 1977.

LITERATURE CITED

BAGGERMAN, B.
1953. Spatfall and transport of *Cardium edule* L. Arch. Neerl. Zool. 10:315-342.

CAHN, A. R.
1951. Clam culture in Japan. U.S. Fish Wildl. Serv. Leafl. Fl-399, p. 12-24.

COULL, B. C.
1973. Estuarine meiofauna: a review: trophic relationships and microbial interactions. *In* L.H. Stevenson and R. R. Colwell (editors), Estuarine microbial ecology, p. 499-511. Belle W. Baruch Library in Mar. Sci.

ELLIOTT, J. M.
1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25, 148 p.

GLOCK, J. W.
1978. Growth, recovery and movement of Manila clams, *Venerupis japonica*, planted under protective devices and on open beaches at Squaxin Island, Washington. M.S. Thesis, Univ. Washington, Seattle, 67 p.

HANCOCK, D. A.
1970. The role of predators and parasites in the fishery for the mollusc *Cardium edule* L. *In* P. J. den Boer and G. R. Gradwell (editors), Dynamic numbers population, p. 419-439. Proc. Adv. Study Inst. Osterbeck.
1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-V. Reun Cons. Int. Explor. Mer 164:113-131.

HOLLAND, D. A., AND K. K. CHEW.
1974. Reproductive cycle of the Manila clam (*Venerupis japonica*), from Hood Canal, Washington. Proc. Natl. Shellfish. Assoc. 64:53-58.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. John Wiley and Sons, N.Y., 503 p.

IKEMATSU, W.
1957. Ecological studies on the clam, *Tapes japonica* (Reeve) II. On the setting season and the growth in early young stage. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 22:736-741.

JONES, C. R., III.
1974. Initial mortality and growth of hatchery-reared Manila clams, *Venerupis japonica*, planted in Puget Sound, Washington beaches. M.S. Thesis, Univ. Washington, Seattle, 90 p.

KRISTENSEN, I.
1957. Differences in density and growth in cockle population in the Dutch Wadden Sea. Arch. Neerl. Zool. 12:350-453.

LANGTON, R. W., J. E. WINTER, AND O. A. ROELS
1977. The effect of ration size on the growth and growth efficiency of the bivalve mollusc *Tapes japonica*. Aquaculture 12:283-292.

LOOSANOFF, V., H. DAVIS, AND P. CHANLEY.
1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia 4:351-435.

MCINTYRE, A. D.
1969. Ecology of marine meiobenthos. Biol. Rev. (Camb.) 44:245-290.

MUUS, K.
1973. Settling, growth and mortality of young bivalves in the Oresund. Ophelia 12:79-116.

NOSHO, T., AND K. K. CHEW.
1972. The setting and growth of the Manila clam, *Venerupis japonica* (Deshayes), in Hood Canal, Washington. Proc. Natl. Shellfish Assoc. 62:50-58.

OHBA, S.
1956. Effects of population density on mortality and growth in an experimental culture of a bivalve, *Venerupis semidecussata*. Biol. J. Okayama Univ. 2:169-173.
1959. Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. Biol. J. Okayama Univ. 5:13-42.

QUAYLE, D. B.
1952. Structure and biology of the larvae and spat of *Venerupis pullastra* (Montagu). Trans. R. Soc. Edinb. 62(1):255-297.
1964. Distribution of introduced marine mollusca in British Columbia waters. J. Fish. Res. Board Can. 21:1155-1181.

QUAYLE, D. B., AND N. BOURNE.
1972. The clam fisheries of British Columbia. Fish. Res. Board Can., Bull. 179, 71 p.

RODDE, K. M., J. B. SUNDERLIN, AND O. A. ROELS.
1976. Experimental cultivation of *Tapes japonica* (Deshayes)(Bivalvia) in an artificial upwelling culture system. Aquaculture 9:203-215.

SAGARA, J.
1952. On the relationship between population density and growth of the clams, *Venerupis semidecussata* and *Meretrix meretrix lusoria*, with the interactive influence upon their growth. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 18:249-262.

SHELLBOURNE, J. E.
1957. The 1951 oyster stock in the Rivers Crouch and Rouch, Essex, and the influence of water currents and scour on its distribution: with an account of comparative dredging experiments. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 21(2):1-27.

SIBERT, J., T. J. BROWN, M. C. HEALEY, B. A. KASK, AND R. J. NAIMAN.
1977. Detritus-based food webs: exploitation by juvenile chum salmon (*Oncorhynchus keta*). Science (Wash., D.C.) 196:649-650.

SIGURDSSON, J. B., C. W. TITMAN, AND P. A. DAVIES.
1976. The dispersal of young post-larval bivalve molluscs by byssus threads. Nature (Lond.) 262:386-387.

SWEDMARK, B.
1964. The interstitial fauna of marine sand. Biol. Rev. (Camb.) 39:1-42.

TAMURA, T.
1966. Marine aquaculture. Suisan Zoshokugaku. Kigen-sha, Shuppan, Tokyo. (Translated from Jpn., Natl. Sci. Found., Wash., D.C.) (NTIS PB194051T.)

TANAKA, Y.
1954. Spawning season of important bivalves in Ariake Bay—III *Venerupis semidecussata* (Reeve). [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 19:1165-1167.

THORSON, G.
1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.

WILBUR, K. M., AND G. OWEN.
1964. Growth. *In* K. M. Wilbur and C. M. Yonge

(editors), Physiology of mollusca, Vol. I, p. 211-242. Academic Press, N Y

YAMAMOTO, K , AND F. IWATA.
1956. Studies on the bivalve, *Venerupis japonica*, in Akkeshi Lake. II. Growth rate and biological minimum size. [In Jpn., Engl. summ.] Bull. Hokkaido Reg. Fish. Res. Lab. 14:57-62.

YOSHIDA, H.
1935. On the full-grown velagers and early young-shell stages of *Venerupis philippinarum* (Adams and Reeve). [In Jpn., Engl. summ.] Venus, Jpn. J. Malacol. 5:264-273.
1953. Studies on larvae and young shells of industrial bivales in Japan. [In Jpn., Engl. summ.] J. Shimonoseki Univ. Fish. 3:1-105.

DEVELOPMENT AND OCCURRENCE OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES FLAVIDUS* AND *SEBASTES MELANOPS* (SCORPAENIDAE) OFF OREGON[1]

WAYNE A. LAROCHE AND SALLY L. RICHARDSON[2]

ABSTRACT

Developmental series of larvae and juveniles of two important and very similar species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are described and illustrated: *S. flavidus* (10.1-105.0 mm standard length) and *S. melanops* (10.6-111.6 mm standard length). Descriptions include a literature review, identification, distinguishing features, general development, morphology, fin development, spination, scale formation, pigmentation, and color of fresh specimens. The main differences between *S. flavidus* and *S. melanops* within the size range described are pectoral fin ray number (usually 18 versus 19), lateral line pore number (usually >50 versus <50), and caudal peduncle depth/caudal peduncle length ratio (mean values 0.73, 0.64, 0.64, 0.80 versus 0.88, 0.78, 0.74, 0.92 in postflexion larvae, transforming, pelagic juvenile, and benthic juvenile specimens, respectively). Occurrence of these two species in waters off Oregon is discussed. Small benthic juveniles of *S. flavidus* seem to inhabit deeper waters, >20 m depth, than those of *S. melanops*.

Comparisons are made among known larvae and juveniles of *Sebastes* species. Identification problems within the *S. flavidus-S. melanops/S. entomelas-S. mystinus* groups are discussed.

Rockfishes, *Sebastes* spp., represent an important commercial and recreational resource along the west coast of North America. In 1976, landings of rockfishes (all species) were 14,000 t, constituting 24% of the total trawl catch by the United States and Canada, second only to Pacific cod landings (Pacific Marine Fisheries Commission[3]). Since the decline of Pacific ocean perch, *S. alutus*, landings in the late 1960's, more rockfish species have been subjected to increasing fishing pressure (Verhoeven 1976). This situation, together with concern over managing the resource, has emphasized the need to determine the condition of rockfish stocks particularly in order to avoid overexploitation (Gunderson[4]). Knowledge of the early life stages, especially pelagic juveniles, is important since they provide valuable tools for resource assessment, systematics, evolution, and other emerging research areas.

This paper contributes new information on the early life history of two important rockfish species: yellowtail rockfish, *S. flavidus*, and black rockfish, *S. melanops*. They were among the five principal species in the Oregon trawl landings of "other rockfish" from 1963 to 1971, contributing 33 and 12% of the total landings during those 9 yr (Niska 1976). They are also important in the Oregon sport catch but landing data are not available.

Larval and juvenile development of these two species is described for the first time and occurrence of young off Oregon is discussed. Particular attention is given to problems involved with identification due to the extreme similarity of these two species as larvae and juveniles.

METHODS

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. The collections were obtained with 70 cm bongo nets, neuston nets, meter nets, Isaacs-Kidd midwater trawls, beam trawls, otter trawls, beach seines, and dip nets off the Oregon coast and in Oregon tidepools and estuaries since 1961. Samples were taken during all months of the

[1]From a final report for NOAA NMFS Contract No. 03-7-208-35263 submitted 15 September 1978 to NMFS Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, P.O. Box AG, Ocean Springs, MS 39564.

[3]Pacific Marine Fisheries Commission. 1978. Data series. Bottom or trawl fish section. Pac. Mar. Fish. Comm., Portland, Oreg., p. 1-472, 500-509.

[4]Gunderson, D. 1976. Proceedings of the 1st rockfish survey workshop. Processed rep., 14 p. Northwest Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, Wash.

Manuscript accepted June 1979
FISHERY BULLETIN VOL. 77, No. 4, 1980

year and along the entire Oregon coast, but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1' N). All specimens were preserved in 5 or 10% Formalin[5] and transferred to ≈40% isopropyl alcohol.

Our approach to identification, methods of making counts and measurements, and terminology for development and spination follow Richardson and Laroche (1979). Body parts measured include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle.

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Caudal peduncle depth = shortest vertical distance between dorsal and ventral margins of caudal peduncle.

Caudal peduncle length = horizontal distance from base of posteriormost dorsal ray to posterior margin of hypural elements.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip.

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine; posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series).

Length of angle gill raker = distance from tip of gill raker to point of articulation with gill arch.

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise.

When the two posteriormost dorsal and anal fin rays arise from the same pterygiophore, they are counted as one.

A modified descriptive approach is used to minimize repetition which would result due to the extreme similarity in the development of *S. flavidus* and *S. melanops*. Descriptions are combined for both species and differences are noted as they occur. Reference to tabularized development morphology data, including relative body proportions and fin and head spine development, is made wherever practical to condense the description.

SEBASTES FLAVIDUS (AYRES) AND *SEBASTES MELANOPS* GIRARD (Figures 1-6)

Literature.—Pigment patterns of preextrusion larvae of *S. flavidus* were described by Delacy et al. (1964), including a figure, Westrheim (1975), and Moser et al. (1977). Preextrusion larvae (mean total length = 4.5 mm) have a row of usually ≈16 melanophores ($\bar{x}$ = 10, range 8-12 on 20 specimens) along the ventral body midline which stops short of the anus by at least four myomeres. The gut is pigmented and melanophore(s) are usually present on the ventral body surface near the notochord tip.

Larvae and juveniles of *S. melanops* have not been described.

Identification (Tables 1-3; Appendix Table 1).—Fifty-one specimens of *S. flavidus* (10.1-105.0 mm)

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

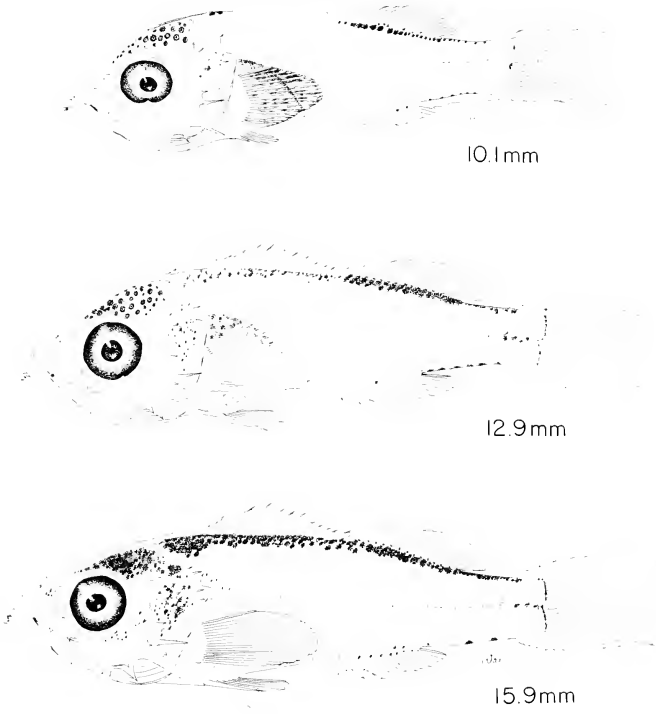


FIGURE 1.—Planktonic larvae (10.1, 12.9, 15.9 mm) of *Sebastes flavidus*

were selected for the developmental series from 556 specimens identified. Juveniles were identified by the following combination of characters recorded from juvenile and adult specimens:

Gill rakers = 33-39
Lateral line pores = 46-57, usually 50-54
Pectoral fin rays = 17-19, usually 18
Anal fin soft rays = 7-9, usually 8
Dorsal fin soft rays = 14-15
Preocular spine = absent
Supraocular spine = absent
Interorbital space = flat to convex
Black blotch at base of spinous dorsal fin = present.

Fifty-eight specimens of *S. melanops* (10.6-111.6 mm) were selected for the developmental

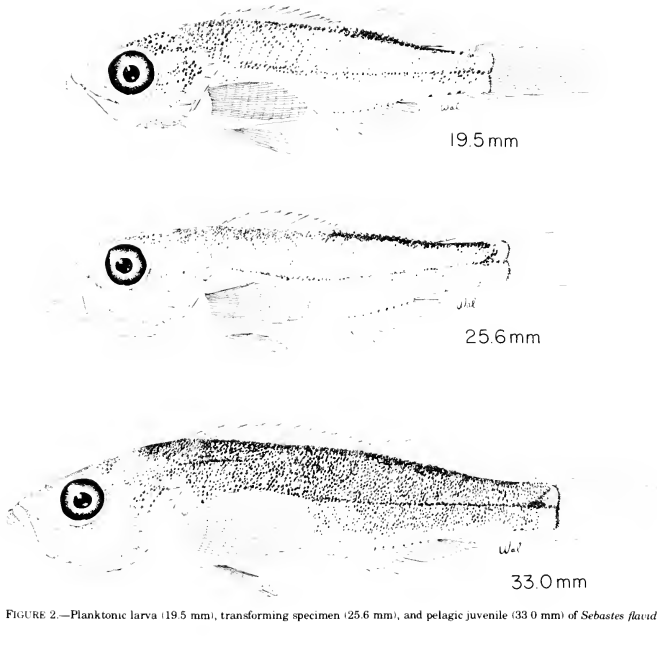


FIGURE 2.—Planktonic larva (19.5 mm), transforming specimen (25.6 mm), and pelagic juvenile (33.0 mm) of *Sebastes flavidus*.

series from 365 specimens in our collections. Juveniles were identified by the following combination of characters recorded from our juvenile and adult specimens:

Gill rakers	= 34-40
Lateral line pores	= 45-54, usually 47-50
Pectoral fin rays	= 18-20, usually 19
Anal fin soft rays	= 7-9, usually 8
Dorsal fin soft rays	= 14-16, usually 14-15
Preocular spine	= absent
Supraocular spine	= absent
Interorbital space	= flat to convex
Black blotch at base of spinous dorsal fin	= present.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. flavidus* and *S. melanops*, respectively, have the best fit to the above characters. *Sebastes melanops* usually has 19 rather than 18 pectoral rays and a lower number (<50 rather than >50) of lateral line pores than *S. flavidus* based on counts made on juveniles and adults collected from Yaquina Bay, Oreg., and the Pacific Ocean nearby (Appendix Table 1). Juvenile specimens were identified by us as *S. flavidus* and *S. melanops* using the above characters together with color pattern (intensity of melanistic pigment on caudal fin) and location of capture (*S. flavidus* from depths >25 m and *S. melanops* from depths < 15 m). Of 52 *S. flavidus*

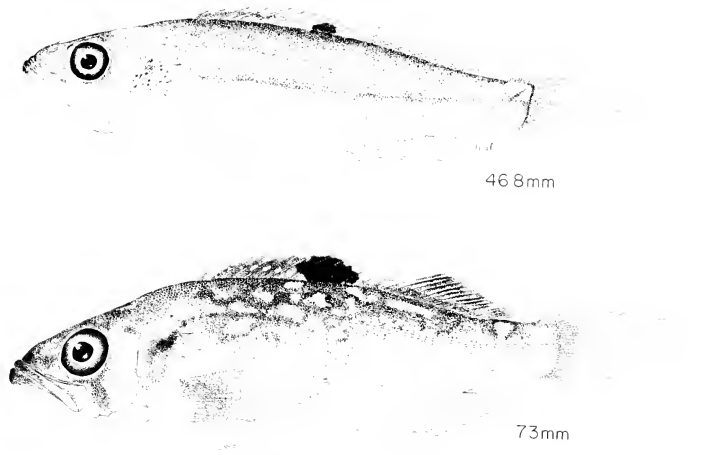


FIGURE 3.—Pelagic juvenile (46.8 mm) and benthic juvenile (73 mm) of *Sebastes flavidus*.

taken off Yaquina Bay (the area offshore of which most larval and pelagic juvenile *S. flavidus* were collected), 96% had a pectoral fin ray count of 18 on one or both sides. Of 66 *S. melanops* taken in Yaquina Bay and adjacent tidepool and shallow subtidal locations (the area offshore of which most larval and pelagic juvenile *S. melanops* were collected), 95% had a pectoral fin ray count of 19 on one or both sides. Mean numbers of lateral line pores were 52.33 ± 0.52 (95% confidence) ($N = 48$) and 49.20 ± 0.42 (95% confidence) ($N = 66$) on the left side of *S. flavidus* and *S. melanops*, respectively. No significant difference was found between counts made on the left and right sides for either species. Two specimens of *S. flavidus* had 19 pectoral fin rays on both sides but lateral line pores numbered >50 on both sides. Three specimens of *S. melanops* had 18 pectoral fin rays on both sides but lateral line pores numbered <51 on both sides. Thus the number of pectoral fin rays and lateral line pores allow positive identification of *S. flavidus* in most cases. Although diagonal scale rows below the lateral line were not used in making the initial identifications, they are useful when they can be counted and can help verify identifications when other characters are not conclusive (see Appendix Table 1).

Specimens of *S. flavidus* and *S. melanops* were selected for the developmental series only if pectoral fin ray counts on both sides were ≤ 18 and ≥ 19, respectively, to minimize possible confusion. The presence of discrete melanophores at the articulation of dorsal and anal fin soft rays and melanophores along the posterior margin of the hypural plate together with counts helped link the developmental series and distinguish the specimens from all other Oregon species. The more slender and longer caudal peduncle of *S. flavidus* and the deeper, shorter caudal peduncle of *S. melanops* (Table 2) helped tie each series together, confirm identifications, and eliminate confusion between the two species.

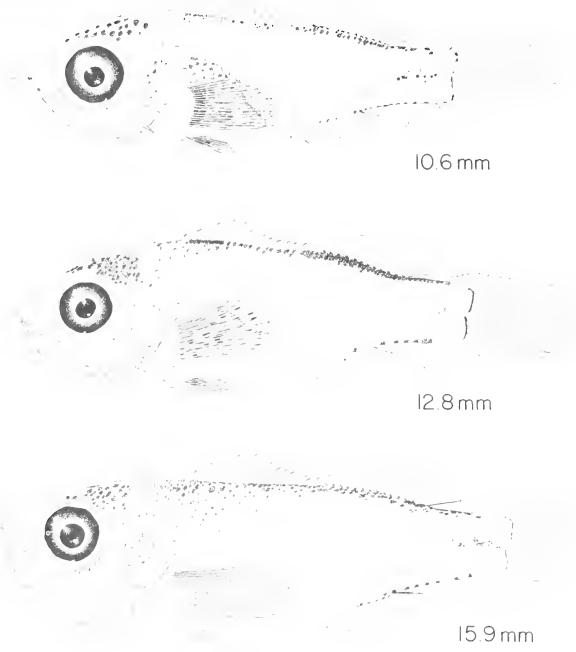


FIGURE 4.—Planktonic larvae (10.6, 12.8, 15.9 mm) of *Sebastes melanops*.

Distinguishing Features.—Characters useful to distinguish the smallest identified larvae (10-11 mm) of *S. flavidus* and *S. melanops* from those of other *Sebastes* species are the moderately pigmented pectoral and pelvic fins, presence of pigment along the dorsal body surface under the dorsal fin, internal and external melanophores above the notochord at and anterior to the point of notochord flexion, melanophores along the dorsal and ventral margins of the caudal peduncle, and melanophores at the articulation of some dorsal and anal rays. The relatively long and narrow caudal peduncle and presence of 18 pectoral rays distinguishes *S. flavidus*, and the relatively deep and short caudal peduncle and presence of 19 pectoral rays distinguish *S. melanops*. Meristics,[6] lack of preocular and supraocular spines, flat to

[6]The term "meristics" is used to refer to all countable characters which are usually arranged in series.

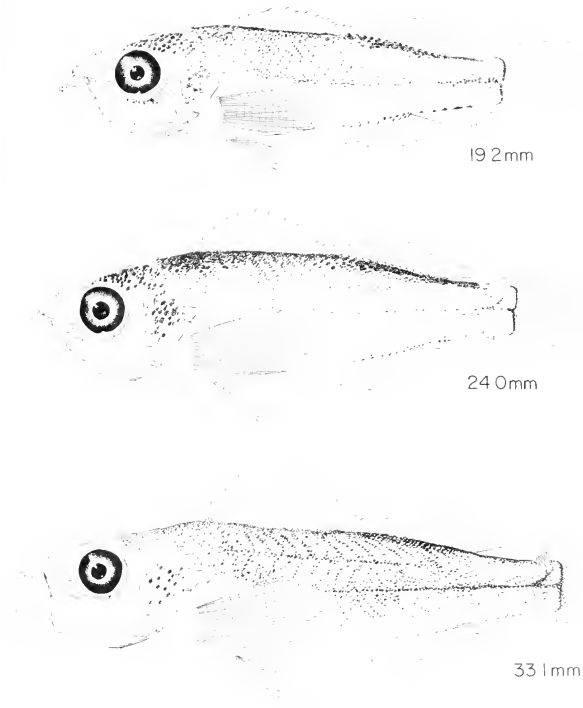


FIGURE 5.—Pelagic larvae (19.2, 24.0, 33.1 mm) of *Sebastes melanops*

convex interorbital space, body and fin pigmentation, and body morphometry together serve to distinguish larger larvae and juveniles from those of other Oregon species.

General Development.—Notochord flexion is complete on the smallest larva of *S. flavidus* (10.1 mm) and *S. melanops* (10.6 mm) identified. Transformation from postflexion larvae to pelagic juveniles occurs between 23 and 27 mm in *S. flavidus* and between ~24 and 33 mm in *S. melanops* as indicated by the structural change of the "prespines" in the dorsal and anal fins to sharp, hard spines. Melanistic pigmentation gradually increases over the body through the larval and transformation periods and shows no marked change during transformation. Transition from pelagic to benthic habitat usually occurs when

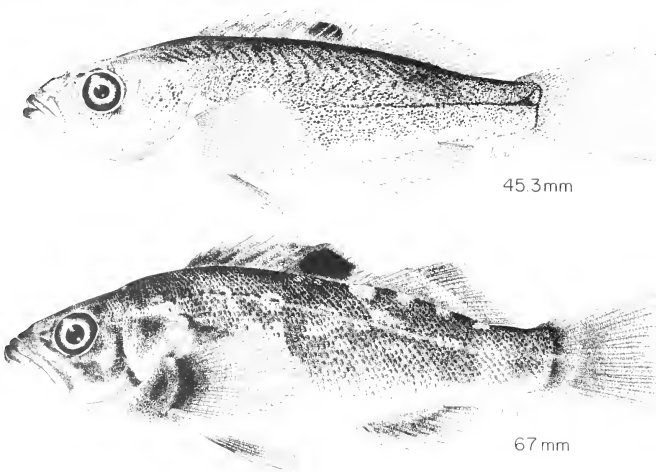


FIGURE 6.—Pelagic juvenile (45.3 mm) and benthic juvenile (67 mm) of *Sebastes melanops*.

fish are between 40 and 50 mm in both species. The largest pelagic juvenile and the smallest benthic juvenile observed were 45 mm and 42 mm for *S. flavidus* and 47 mm and 38 mm for *S. melanops* (see Figures 7-10).

Morphology (Tables 2, 4, 5).—Various body parts were measured on 51 selected specimens of *S. flavidus* (10.1-105.0 mm) and 58 specimens of *S. melanops* (10.6-111.6 mm). Relative growth trends are summarized in Table 2.

The most important morphometric character which will separate most *S. flavidus* from *S. melanops* is the caudal peduncle depth/length ratio. While the depth and length of the caudal peduncle change only slightly during development, their ratio changes notably. In *S. flavidus* it decreases from 73 to 64 or 65% in pelagic stages, increasing again to 80% in benthic juveniles. In *S. melanops* it decreases from 88 to 74-77% in pelagic stages and then increases to 89% in benthic juveniles. This ratio is usually smaller in *S. flavidus* than in *S. melanops* for all specimens of similar size. Caudal peduncle depth is generally less and caudal peduncle length is generally greater in *S. flavidus* than in *S. melanops*.

Fin Development (Tables 1-4).—Pectoral fins are formed and have the adult complement of 17-19 (usually 18 in *S. flavidus* and 19 in *S. melanops*) fin rays in the smallest specimens (10 or 11 mm) in the series. The fins in both species are moderate in length, reaching 24 or 25% SL in juveniles.

The adult pelvic fin complement (I, 5) is present by 10 or 11 mm in both species. The pelvic fins are of moderate length, averaging 13-18% SL during the pelagic period. Pelvic spine length is always less than pelvic fin length.

The adult complement of 8 + 7 principal caudal rays is present on the larvae of both species along with six superior and five inferior secondary caudal rays. Counts of superior and inferior secondary rays made on three stained juvenile *S.*

TABLE 1.—Meristics from larvae and juveniles of *Sebastes flavidus* off Oregon, based on unstained specimens. Counts of left and right pelvic fin rays (I,5;I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7;7) were constant from the smallest to largest specimen listed.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
10.1	(1),15	IIF,8	18	18	—	—	—	—	—	—
10.3	XIIF,14	IIF,8	18	18	—	—	—	—	—	—
10.7	XIIF,14	IIF,8	18	18	—	—	—	—	—	—
11.4	XIIF,15	IIF,8	18	18	—	—	—	—	—	—
11.8	XIIF,14	IIF,8	18	18	—	—	—	—	—	—
11.8	XIIF,15	IIF,8	18	18	—	—	—	—	—	—
11.9	XIIF,15	IIF,8	18	18	—	—	—	—	—	—
12.0	XIIF,15	IIF,8	18	18	—	—	—	—	—	—
12.2	XIIF,15	IIF,8	18	18	—	—	—	—	—	—
12.7	XIIF,15	IIF,8	18	18	23+8=31	23+9=32	—	—	—	—
12.8	XIIF,15	IIF,8	18	18	23+9=32	24+9=33	—	—	—	—
12.9	XIIF,15	IIF,8	18	18	23+9=32	23+9=32	—	—	—	—
13.1	XIIF,15	IIF,7	17	18	22+8=30	23+9=32	—	—	—	—
13.7	XIIF,15	IIF,7	18	18	23+9=32	23+9=32	—	—	—	—
14.4	XIIF,15	IIF,8	18	18	24+9=33	23+9=32	—	—	—	—
14.8	XIIF,14	IIF,8	18	18	24+9=33	23+9=32	—	—	—	—
15.8	XIIF,15	IIF,9	18	18	24+9=33	24+9=33	—	—	—	—
15.9	XIIF,14	IIF,7	17	18	24+10=33	23+9=32	—	—	—	—
16.4	XIIF,15	IIF,8	18	18	24+10=34	24+10=34	—	—	—	—
16.8	XIIF,15	IIF,7	18	18	24+10=34	25+10=35	—	—	—	—
18.9	XIIF,15	IIF,8	18	18	24+10=34	24+10=34	—	—	—	—
19.5	XIIF,15	IIF,8	18	18	25+10=35	24+10=34	—	—	—	—
19.8	XIIF,15	IIF,8	18	18	25+10=35	25+10=35	—	—	—	—
20.5	XIIF,15	IIF,9	18	18	25+10=35	24+11=35	—	—	—	—
21.3	XIIF,15	IIF,8	18	18	25+10=35	25+10=35	—	—	—	—
22.3	XIIF,15	IIF,8	18	18	24+10=34	25+10=35	—	—	—	—
[2]23.6	XIIF,15	IIF,8	18	18	25+11=36	26+10=36	—	—	—	—
[3]23.7	XIIF,15	III,8	18	18	25+11=36	26+11=37	—	—	—	—
[3]24.2	XIIF,15	III,8	18	18	26+11=37	26+11=37	—	—	—	—
[3]24.8	XIIF,15	IIF,8	18	18	25+10=35	25+11=36	—	—	—	—
[3]25.6	XIIF,15	III,8	17	17	25+10=35	25+11=36	—	—	—	—
[3]26.6	XIV,15	IIF,8	18	18	24+10=34	24+10=34	—	—	—	—
[3]26.7	XIIF,15	III,8	18	18	27+10=37	26+11=37	—	—	—	—
[4]28.6	XIII,15	III,8	18	18	25+10=35	26+11=37	—	—	—	—
[4]29.2	XIII,15	III,8	18	18	26+10=36	26+10=36	—	—	—	—
[4]29.6	XIII,15	III,8	18	18	26+10=36	27+11=38	—	—	—	—
[4]30.4	XIII,15	III,8	18	18	25+11=36	26+11=37	—	—	—	—
[4]33.0	XIII,14	III,8	18	18	26+11=37	27+11=38	—	—	—	—
[4]33.1	XIII,15	III,8	18	18	25+10=35	25+10=35	—	—	—	—
[4]35.2	XIII,14	III,8	18	18	26+11=37	26+11=37	—	—	—	—
[4]36.4	XIII,14	III,8	18	18	26+11=37	27+11=38	—	—	—	—
[4]37.6	XIII,15	III,8	18	18	25+11=36	25+10=35	—	—	—	—
[4]41.9	XIII,15	III,8	18	18	28+11=39	28+11=39	—	—	—	—
[4]43.6	XIII,15	III,8	18	18	25+10=35	25+11=36	—	—	—	—
[4]45.2	XIII,15	III,8	18	18	27+11=38	28+11=39	—	—	—	—
[5]67.6	XIII,14	III,8	18	18	26+11=37	26+11=37	54	54	56	56
[5]71.5	XIII,15	III,8	18	18	27+11=38	26+11=37	46	53	—	55
[5]72.5	XIII,14	III,8	18	18	26+11=37	27+10=37	52	53	54	54
[5]77.5	XIII,14	III,8	18	18	26+11=37	25+10=35	50	53	55	56
[5]81.0	XIII,14	III,7	18	18	26+11=37	26+11=37	52	53	—	—
[5]105.0	XIII,14	III,8	18	18	27+11=38	26+11=37	55	56	57	—

[1]Forming
[2]Posteriormost dorsal and anal spine appears as a soft ray
[3]Transforming
[4]Pelagic juvenile
[5]Benthic juvenile

flavidus (49, 50, and 52 mm long) were 12/13, 12/13, and 12/12, respectively. Counts on four stained juvenile *S. melanops* (42, 43, 47, and 48 mm long) were 12/13, 12/12, 12/12, and 12/13, respectively. Adult complements of the dorsal and anal fin spines and rays can be counted by ≈11 or 12 mm. The transition of the 13th dorsal and 3d anal fin "prespines" to spines is complete by ≈27 mm in *S. flavidus* and ≈33 mm in *S. melanops*.

Spination (Tables 2, 4-7).—Spines present on the left side of the head of the smallest (10.1 mm) larval *S. flavidus* include the parietal; first, second, third, and fourth posterior preopercular; first and third anterior preopercular; postocular; pterotic; superior opercular; first inferior infraorbital; first superior infraorbital; inferior posttemporal; and the developing interopercular (indicated by a small blunt projection). The smallest

TABLE 2.—Body proportions of larvae and juveniles of *Sebastes flavidus* and *S. melanops*. Values given are percent of standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from measurements listed by developmental stage (as indicated by footnotes) in Tables 4 and 5.

Item	*Sebastes flavidus*	*Sebastes melanops*
Body depth at pectoral fin base/SL		
Postflexion	28·2 ± 1·72 (25·3-30·8)	29·6 ± 1·77 (26·3-32·8)
Transforming	24·5 ± 0·62 (23·6-25·6)	26·1 ± 0·79 (25·2-27·5)
Pelagic juvenile	24·8 ± 1·08 (23·3-26·9)	25·9 ± 0·72 (24·7-26·7)
Benthic juvenile	30·0 ± 1·00 (28·4-31·0)	30·9 ± 1·94 (27·0-33·0)
Body depth at anus/SL		
Postflexion	22·3 ± 1·01 (20·6-24·2)	24·3 ± 1·24 (21·8-26·1)
Transforming	20·0 ± 0·51 (19·2-20·7)	21·9 ± 0·89 (20·9-23·3)
Pelagic juvenile	21·3 ± 0·99 (19·9-23·4)	22·2 ± 0·71 (20·9-23·6)
Benthic juvenile	25·6 ± 1·11 (23·5-26·3)	26·4 ± 0·75 (25·3-27·4)
Snout to anus length/SL		
Postflexion	57·3 ± 1·77 (53·5-61·2)	58·0 ± 2·15 (54·0-62·2)
Transforming	60·0 ± 1·23 (57·5-60·5)	58·9 ± 3·02 (55·8-62·6)
Pelagic juvenile	60·3 ± 1·02 (58·8-62·3)	61·3 ± 1·65 (59·4-65·3)
Benthic juvenile	63·2 ± 1·22 (62·2-65·6)	63·0 ± 3·43 (59·4-70·7)
Snout to pelvic fin origin/SL		
Postflexion	37·9 ± 1·86 (34·4-42·7)	38·8 ± 1·86 (35·8-42·9)
Transforming	35·9 ± 0·49 (35·3-36·7)	37·3 ± 1·94 (34·8-39·3)
Pelagic juvenile	36·2 ± 0·73 (35·3-37·7)	36·8 ± 1·63 (35·2-40·1)
Benthic juvenile	39·7 ± 2·37 (37·2-43·0)	38·2 ± 2·38 (35·4-41·8)
Head length/SL		
Postflexion	38·6 ± 1·78 (35·4-42·7)	38·5 ± 1·95 (34·8-42·9)
Transforming	35·0 ± 0·91 (33·7-36·0)	35·0 ± 2·19 (31·9-37·8)
Pelagic juvenile	33·4 ± 1·34 (31·9-36·0)	33·3 ± 1·45 (31·1-35·3)
Benthic juvenile	35·2 ± 2·52 (33·4-40·0)	34·8 ± 1·83 (32·3-37·3)
Eye diameter/HL		
Postflexion	32·0 ± 2·06 (27·1-35·4)	30·8 ± 1·61 (26·9-34·1)
Transforming	28·9 ± 0·72 (27·8-29·8)	28·6 ± 1·90 (26·0-30·6)
Pelagic juvenile	27·2 ± 1·29 (25·7-29·1)	26·3 ± 1·49 (24·0-28·9)
Benthic juvenile	26·8 ± 1·78 (24·1-29·5)	25·6 ± 1·70 (23·4-28·7)
Upper jaw length/HL		
Postflexion	42·6 ± 1·84 (39·0-45·9)	42·1 ± 2·21 (37·3-45·7)
Transforming	40·5 ± 2·35 (37·5-44·0)	41·2 ± 2·02 (37·6-42·7)
Pelagic juvenile	42·1 ± 1·33 (39·2-44·4)	41·4 ± 1·71 (39·3-44·2)
Benthic juvenile	42·5 ± 2·89 (39·3-46·5)	44·2 ± 4·16 (35·3-48·4)
Snout length/HL		
Postflexion	27·4 ± 1·74 (23·9-30·6)	27·6 ± 1·65 (25·0-31·4)
Transforming	26·3 ± 0·38 (25·6-26·7)	26·7 ± 1·13 (25·8-28·0)
Pelagic juvenile	25·6 ± 1·75 (23·1-29·1)	27·0 ± 2·12 (23·9-30·0)
Benthic juvenile	28·8 ± 3·56 (22·9-32·7)	23·1 ± 1·98 (19·9-26·5)
Interorbital distance/HL		
Postflexion	28·8 ± 1·78 (25·0-31·9)	29·0 ± 2·11 (24·0-32·7)
Transforming	24·8 ± 0·71 (24·1-26·2)	25·9 ± 1·01 (24·7-27·0)
Pelagic juvenile	24·7 ± 1·67 (21·6-28·0)	24·2 ± 1·25 (22·2-26·2)
Benthic juvenile	22·2 ± 0·98 (21·4-24·1)	23·6 ± 1·97 (21·1-26·2)
Angle of gill raker length/HL		
Postflexion	12·1 ± 1·46 (9·0-14·5)	10·9 ± 1·36 (7·3-13·5)
Transforming	14·7 ± 0·84 (13·9-16·1)	12·2 ± 1·92 (10·6-15·0)
Pelagic juvenile	14·4 ± 1·13 (11·7-16·2)	14·1 ± 1·04 (13·1-16·1)
Benthic juvenile	15·0 ± 0·66 (14·4-16·1)	14·9 ± 0·71 (14·1-15·8)
Longest dorsal spine length[1]/HL		
Postflexion	19·4 ± 6·84 (5·0-32·4)	24·0 ± 5·11 (15·2-31·9)
Transforming	32·8 ± 1·53 (31·0-34·5)	—
Pelagic juvenile	35·3 ± 1·68 (33·7-39·3)	36·9 ± 2·46 (33·3-39·5)
Benthic juvenile	34·6 ± 1·81 (31·7-36·7)	35·4 ± 1·35 (33·9-37·8)
Longest dorsal ray length[2]/HL		
Postflexion	30·5 ± 4·39 (19·0-38·1)	32·6 ± 3·70 (25·0-38·3)
Transforming	36·7 ± 1·59 (35·2-39·3)	36·9 ± 3·07 (34·9-40·4)
Pelagic juvenile	40·5 ± 3·00 (37·1-45·8)	40·1 ± 1·62 (38·5-43·0)
Benthic juvenile	43·4 ± 2·34 (40·3-46·1)	46·1 ± 2·34 (45·2-48·5)

Item	*Sebastes flavidus*	*Sebastes melanops*
Longest anal spine length[3]/HL		
Postflexion	16·5 ± 4·96 (10·8-26·3)	19·2 ± 3·99 (11·3-25·6)
Transforming	26·2 ± 2·25 (22·2-28·7)	30·4 ± 2·95 (27·1-32·7)
Pelagic juvenile	30·6 ± 2·41 (26·2-33·6)	32·3 ± 2·44 (28·7-37·7)
Benthic juvenile	33·8 ± 1·36 (31·9-35·4)	34·7 ± 1·97 (31·2-37·1)
Pectoral fin length/SL		
Postflexion	20·1 ± 1·91 (15·8-22·7)	21·7 ± 1·41 (18·5-24·5)
Transforming	22·5 ± 1·01 (21·4-24·3)	24·0 ± 1·08 (22·8-25·5)
Pelagic juvenile	24·6 ± 0·35 (24·1-25·1)	24·2 ± 0·90 (22·4-25·2)
Benthic juvenile	24·1 ± 1·30 (21·8-25·7)	24·7 ± 1·57 (22·9-27·2)
Pectoral fin base depth/SL		
Postflexion	8·5 ± 0·90 (7·2-10·9)	8·8 ± 0·69 (7·7-10·1)
Transforming	7·0 ± 0·22 (6·7-7·3)	7·7 ± 0·18 (7·5-7·9)
Pelagic juvenile	7·0 ± 0·45 (6·1-7·6)	7·8 ± 0·12 (7·6-8·0)
Benthic juvenile	8·4 ± 0·34 (7·8-8·7)	9·4 ± 0·39 (8·5-9·8)
Pelvic fin length/SL		
Postflexion	13·4 ± 1·83 (8·9-16·7)	15·4 ± 1·17 (12·6-17·4)
Transforming	15·5 ± 0·59 (14·6-16·1)	16·4 ± 0·30 (16·1-16·7)
Pelagic juvenile	16·3 ± 0·89 (14·8-17·8)	17·5 ± 0·64 (16·8-18·8)
Benthic juvenile	19·5 ± 0·51 (19·0-20·4)	20·7 ± 1·44 (18·2-23·0)
Pelvic spine length/SL		
Postflexion	10·4 ± 2·46 (6·3-15·7)	12·6 ± 1·57 (9·2-14·9)
Transforming	13·7 ± 0·92 (12·7-15·3)	11·4 ± 0·92 (10·8-12·1)
Pelagic juvenile	13·6 ± 0·88 (12·6-15·4)	14·0 ± 0·56 (12·8-14·5)
Benthic juvenile	12·1 ± 0·72 (11·3-13·2)	13·3 ± 2·04 (10·7-13·9)
Parietal spine length/HL		
Postflexion	8·8 ± 2·17 (4·2-11·8)	7·9 ± 2·00 (4·2-11·4)
Transforming	4·0 ± 0·67 (3·4-4·7)	5·6 ± 0·35 (5·3-5·8)
Pelagic juvenile	1·0 ± 0·45 (0·7-1·7)	1·2 ± 0·64 (0·7-1·6)
Benthic juvenile	—	—
Nuchal spine length/HL		
Postflexion	2·1 ± 1·15 (0·1-3·9)	1·6 ± 0·87 (0·4-3·2)
Transforming	2·1 ± 0·31 (1·8-2·6)	2·6 ± 0·35 (2·4-2·9)
Pelagic juvenile	1·9 ± 0·72 (1·1-2·4)	1·4 ± 0·24 (1·2-1·7)
Benthic juvenile	—	—
Preopercular spine length/HL		
Postflexion	20·1 ± 3·30 (12·8-27·0)	19·5 ± 3·31 (14·5-26·9)
Transforming	12·8 ± 2·16 (10·0-16·0)	13·3 ± 1·11 (11·8-14·4)
Pelagic juvenile	10·2 ± 1·60 (7·8-13·0)	9·6 ± 0·81 (8·4-10·9)
Benthic juvenile	3·2 ± 0·86 (2·4-4·8)	2·3 ± 1·15 (0·4-4·5)
Caudal peduncle depth/SL		
Postflexion	11·3 ± 0·71 (10·0-12·6)	12·8 ± 0·89 (11·4-14·3)
Transforming	9·7 ± 0·43 (9·0-10·2)	11·1 ± 0·54 (10·5-11·7)
Pelagic juvenile	9·7 ± 0·29 (9·3-10·4)	10·3 ± 0·27 (9·7-10·5)
Benthic juvenile	10·5 ± 0·38 (9·9-11·0)	11·3 ± 0·23 (11·0-11·6)
Caudal peduncle length/SL		
Postflexion	15·5 ± 0·89 (13·4-16·8)	14·6 ± 0·70 (13·0-16·2)
Transforming	15·1 ± 0·54 (14·3-15·7)	14·3 ± 0·17 (14·2-14·6)
Pelagic juvenile	15·1 ± 1·06 (14·1-17·8)	13·9 ± 0·66 (12·8-14·9)
Benthic juvenile	13·2 ± 0·88 (12·0-14·5)	12·6 ± 0·69 (11·6-13·4)
Caudal peduncle depth/caudal peduncle length		
Postflexion	73·1 ± 0·960 (0·65-0·83)	88·1 ± 0·069 (0·74-1·06)
Transforming	64·1 ± 0·029 (0·60-0·69)	78·1 ± 0·042 (0·73-0·84)
Pelagic juvenile	64·1 ± 0·046 (0·56-0·74)	74·1 ± 0·034 (0·70-0·81)
Benthic juvenile	80·1 ± 0·072 (0·70-0·90)	92·1 ± 0·021 (0·91-0·94)

[1]Usually fourth or fifth in larvae, fifth or sixth in juveniles
[2]Usually in anterior one-fourth of fin
[3]The second spine in larvae and transforming larvae, the third spine in juveniles

S. melanops (10.6 mm) has a nuchal and supracleithral (as blunt bumps) and a fourth superior infraorbital in addition to the spines listed above.

In both species the parietal spine and ridge are finely serrated on all specimens <34 mm long. Parietal spine length decreases with development becoming overgrown in benthic juveniles. The nuchal spine, always shorter than the parietal, is usually present in larvae and pelagic juveniles and is overgrown by scales and tissue in benthic juveniles. (Table 2 lists the mean nuchal spine/HL value for pelagic juveniles as greater than the

TABLE 3.—Meristics from larvae and juveniles of *Sebastes melanops* off Oregon, based on unstained specimens. Counts of left and right pelvic fin rays (I,5;I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7;7) were constant from the smallest to the largest specimen listed.

Standard Length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
10.6	XIII[1],15	III[1],8	19	19	—	—	—	—	—	—
11.7	XIII[1],15	III[1],8	19	19	—	—	—	—	—	—
11.9	XIII[1],15	III[1],8	19	19	—	23+ 8=31	—	—	—	—
11.9	XIII[1],15	III[1],8	19	19	21+ 8=29	21+ 8=29	—	—	—	—
12.4	XIII[1],15	III[1],8	19	19	22+ 9=31	24+ 8=32	—	—	—	—
12.8	XIII[1],14	III[1],8	19	19	23+ 9=32	22+ 8=30	—	—	—	—
12.8	XIII[1],15	III[1],8	19	19	23+ 8=31	23+ 8=31	—	—	—	—
12.8	XIII[1],14	III[1],8	19	19	21+ 8=29	22+ 9=31	—	—	—	—
13.5	XIII[1],15	III[1],8	19	19	23+ 9=32	23+ 9=32	—	—	—	—
13.6	XIII[1],14	III[1],8	19	19	22+ 8=30	23+ 9=32	—	—	—	—
13.9	XIII[1],15	III[1],8	19	19	22+10=32	22+ 9=31	—	—	—	—
14.0	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
14.9	XIII[1],14	III[1],8	19	19	23+ 9=32	22+ 8=30	—	—	—	—
15.4	XIII[1],13	III[1],8	19	19	21+ 9=30	23+ 9=32	—	—	—	—
15.4	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
15.7	XIII[1],15	III[1],8	19	19	24+ 9=33	24+ 9=33	—	—	—	—
15.9	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
16.4	XIII[1],14	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
16.5	XIII[1],15	III[1],8	19	19	23+10=33	23+ 9=32	—	—	—	—
17.2	XIII[1],14	III[1],8	19	19	24+ 9=33	23+10=33	—	—	—	—
17.4	XIII[1],15	III[1],8	19	19	25+10=35	25+10=35	—	—	—	—
17.4	XIII[1],14	III[1],8	19	19	23+10=33	23+ 9=32	—	—	—	—
17.7	XIII[1],15	III[1],8	19	19	24+ 9=33	24+10=34	—	—	—	—
17.7	XIII[1],15	III[1],8	19	19	24+10=34	24+11=35	—	—	—	—
18.5	XIII[1],14	III[1],8	19	19	23+10=33	24+ 9=33	—	—	—	—
19.0	XIII[1],15	III[1],8	19	19	24+10=34	23+10=33	—	—	—	—
19.2	XIII[1],14	III[1],8	19	19	24+10=34	25+10=35	—	—	—	—
19.2	XIII[1],14	III[1],8	19	19	23+10=33	23+10=33	—	—	—	—
20.7	XIII[1],14	III[1],8	19	19	25+10=35	25+10=35	—	—	—	—
20.7	XIII[1],14	III[1],8	19	19	23+10=33	23+10=33	—	—	—	—
21.0	XIII[1],14	III[1],7	19	19	24+10=34	24+10=34	—	—	—	—
22.9	XIII[1],14	III[1],8	19	19	25+10=35	24+10=34	—	—	—	—
[2]23.2	XIII[1],15	III[1],8	19	19	24+10=34	23+10=33	—	—	—	—
[2]24.0	XIII[1],14	III[1],8	19	19	26+11=37	26+11=37	—	—	—	—
[2]24.0	XIII[1],15	III[1],8	19	19	26+10=36	25+10=35	—	—	—	—
[2]24.6	XIII[1],15	III[1],8	19	19	26+10=36	26+10=36	—	—	—	—
[2]27.9	XIII[1],15	III[1],8	19	19	26+11=37	27+11=38	—	—	—	—
[2]30.6	XIII[1],14	III[1],7	19	19	25+10=35	25+10=35	—	—	—	—
[3]33.1	XIII[1],15	III[1],8	19	19	28+11=39	27+11=38	—	—	—	—
[3]33.9	XIII[1],16	III[1],8	19	19	26+12=38	26+11=37	—	—	—	—
[3]35.2	XIII[1],15	III[1],8	19	19	25+10=35	26+11=37	—	—	—	—
[3]35.8	XIII[1],15	III[1],8	19	19	25+11=36	25+11=36	—	—	—	—
[3]38.2	XIII[1],15	III[1],8	19	19	25+11=36	25+11=36	—	—	—	—
[3]39.2	XIII[1],15	III[1],8	19	19	26+11=37	26+10=36	—	—	—	—
[3]40.0	XIII[1],14	III[1],8	19	19	27+12=39	26+11=37	—	—	—	—
[3]41.0	XIII[1],14	III[1],8	19	19	25+10=35	25+10=35	—	—	—	—
[3]43.8	XIII[1],15	III[1],8	19	19	26+12=38	27+12=39	—	—	—	—
[3]45.3	XIII[1],15	III[1],8	19	19	26+11=37	26+11=37	—	—	—	—
[3]48.4	XIII[1],14	III[1],7	19	19	25+10=35	24+11=35	—	—	—	—
[4]52.5	XIII[1],14	III[1],8	19	19	26+11=37	26+11=37	50	51	54	53
[4]62.5	XIII[1],15	III[1],8	19	19	27+11=38	28+11=39	48	49	54	57
[4]67.0	XIII[1],15	III[1],8	19	19	26+11=37	26+11=37	49	46	55	58
[4]76.1	XIII[1],14	III[1],7	19	19	25+11=36	24+11=35	46	49	49	55
[4]89.4	XIII[1],15	III[1],8	19	19	26+11=37	26+11=37	51	51	56	56
[4]97.7	XIII[1],14	III[1],7	19	19	25+11=36	25+10=35	49	51	57	52
[4]100.9	XIII[1],15	III[1],8	19	19	26+11=37	26+11=37	50	50	53	52
[4]111.6	XIII[1],14	III[1],8	19	19	24+10=34	24+10=34	49	53	58	55

[1]Posteriormost dorsal or anal spine appears as a soft ray
[2]Transforming
[3]Pelagic juvenile
[4]Benthic juvenile

mean parietal spine/HL value. This results from many broken parietal spines on pelagic juveniles as indicated in Tables 4, 5.)

The five spines of the posterior preopercular series are present on specimens of both species by ≈11 or 12 mm. The first spine becomes reduced to a small blunt projection by ≈70 mm. The third spine is always longest but decreases in length from 20 to 2 or 3% HL during development. The second, third, and fourth posterior preopercular spines and the anterior edge of the first spine of the anterior preopercular series are weakly serrated on specimens of *S. flavidus* <17 mm and *S. melanops* <16 mm. Serrations persist on the third posterior preopercular spine of both species to ≈32 mm. The second spine of the anterior series is present occasionally (rarely in *S. melanops*) on one side of the head, particularly on specimens <13 mm. The first and third anterior preopercular spines are visible on specimens <27 and 25 mm (*S. flavidus* and *S. melanops*, respectively), become reduced to small bumps, and are no longer visible on specimens >31 and 29 mm.

The inferior opercular spine forms by ≈11 or 12 mm and is sharp tipped by ≈15 or 16 mm. (Two inferior opercular spines were observed on one

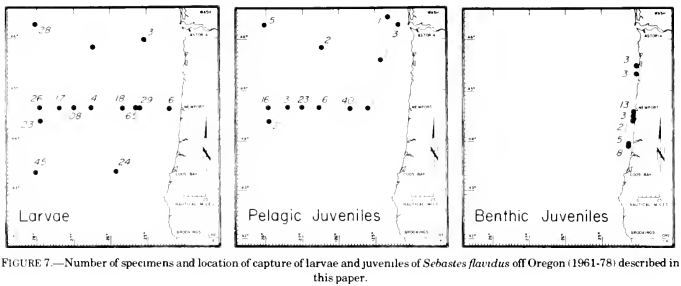


FIGURE 7.—Number of specimens and location of capture of larvae and juveniles of *Sebastes flavidus* off Oregon (1961-78) described in this paper.

side of two specimens of *S. melanops*, 36 and 39 mm long.) The interopercular spine is present on specimens >10 mm and persists as a sharp spine to ≈71 mm on *S. flavidus* and ≈52 mm on *S. melanops*. This spine becomes skin covered and appears as a bump on large specimens.

The ridge anterior to the postocular spine is usually finely serrated on specimens <16 mm in *S. flavidus* and <22 mm in *S. melanops*. Preocular and supraocular spines never develop on either species. The second inferior infraorbital spine is visible as a bump at 10.3 and 11.7 mm on *S. flavidus* and *S. melanops*, respectively, and as a sharp spine by ≈12 mm on both species. A third inferior infraorbital spine appears on both species between 13.5 and 14.5 mm. The second and third inferior spines are reduced to a pair of rounded bony lobes on *S. flavidus* ≈36-67 mm and *S. melanops* 33-50 mm long. *Sebastes flavidus* >67 mm and *S. melanops* >50 mm have a single fleshy lobe which encases the bony lobes. The first superior infraorbital spine is present through the larval periods of both species and becomes reduced and then absent on *S. flavidus* >45 mm and *S. melanops* >38 mm long. The fourth superior infraorbital spine develops by ≈10 mm, is present to ≈45-48 mm, and then is absent in both species. The third superior infraorbital spine appears on *S. flavidus* 15-35 mm and on *S. melanops* 19-33 mm long. A second superior infraorbital spine never develops. The nasal spine appears as a bump between 11 and 12 mm and becomes a sharp spine, between 12 and 13 mm, which persists on all larger specimens of both species.

The tympanic spine never becomes well developed, appearing as a small bump on ≈24-63 mm *S. flavidus* and 30 to ≈40 mm *S. melanops* and as a small spine on larger specimens. The pterotic spine is present on all larvae <24 mm; is usually a bump on specimens 24-41 mm; and is absent on larger specimens. The inferior posttemporal spine is reduced to a bump and then absent on *S. flavidus* >67 mm and *S. melanops* >45 mm. The supracleithral spine and superior posttemporal spine first appear at ≈11 or 12 and ≈19 or 20 mm, respectively, and persist in benthic juveniles. These spines are scale covered on benthic juvenile *S. melanops* <67 mm. The cleithral spine usually appears as a bump at ≈24 mm in *S. flavidus* and at ≈30 mm in *S. melanops*. Specimens >33 mm have a sharp spine which is scale covered in larger juvenile and adult *S. flavidus* and *S. melanops* >67 mm long.

Scale Formation.—Lateral line organs are visible on transforming specimens <14.8 mm in *S. flavidus* and >17.2 mm in *S. melanops*, indicated by a row of light colored spots on the flesh. Developing scales are first visible on unstained specimens ≈23 or 24 mm long in the region above the pectoral fin, near the posttemporal and supracleithral spines, and over the upper two-thirds of the body in the postanal region. The body is scale covered by ≈28 mm.

Pigmentation.—The smallest larvae (10.1 and 10.6 mm) of both *S. flavidus* and *S. melanops* have melanistic pigment on the head over the brain. Melanophores are usually present on the

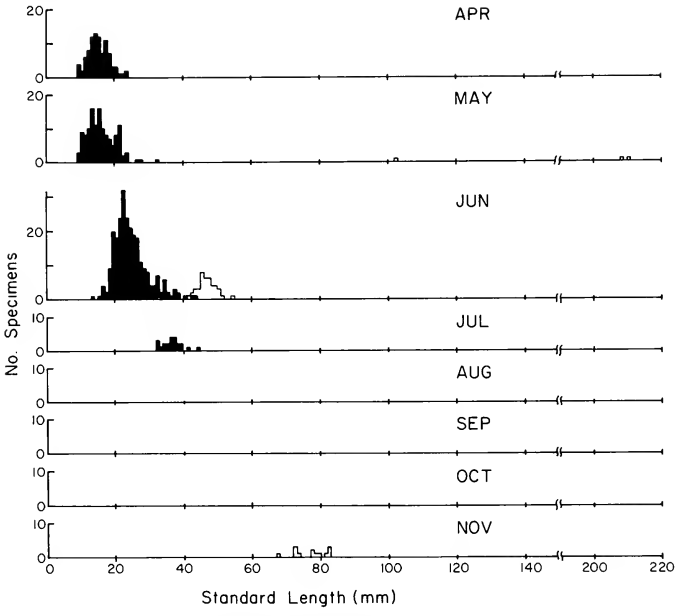


FIGURE 8.—Seasonal occurrence of larvae and juveniles of *Sebastes flavidus* off Oregon. Data from 1961 to 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

inside tip of the lower jaw, along the anterior margin of the maxillary, around the pterotic spines, and on the operculum. The 10.6 mm larva of *S. melanops* also has pigment on the snout, along the posteroventral margin of the orbit, on the cheek, and around the posttemporal spine. An internal melanistic shield covers the gut in both species appearing darkest on the dorsal surface. In *S. flavidus* melanophores are present dorsally on the nape, beneath the second dorsal fin, and on the caudal peduncle. In addition to these, *S. melanops* has melanophores beneath the first dorsal fin, possibly due to a more advanced state of development for this specimen. Several melanophores also occur along the posterior portion of the anal fin base and the ventral margin of the caudal peduncle in both species. Internal and external melanophores are present near the midline of the caudal peduncle and several melanophores are at the margin of the hypural elements. The pectoral and pelvic fin blades are moderately pigmented with expanded, elongated melanophores. The inner side of the pectoral base is also pigmented. A discrete melanophore is pres-

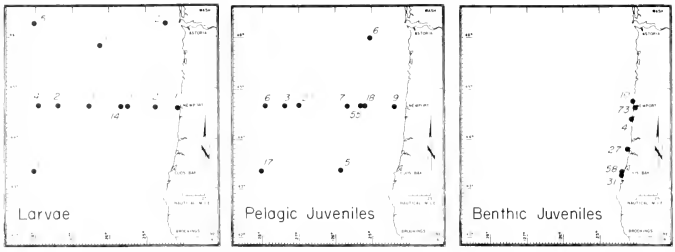


FIGURE 9.—Number of specimens and location of capture of larvae and juveniles of *Sebastes melanops* off Oregon (1961-78) described in this paper.

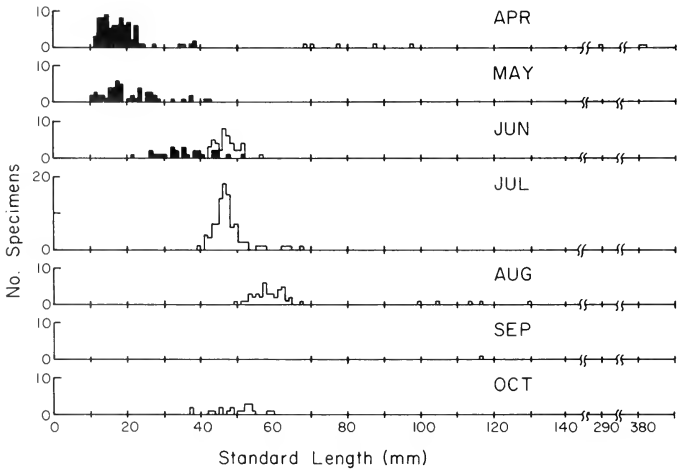


FIGURE 10.—Seasonal occurrence of larvae and juveniles of *Sebastes melanops* off Oregon. Data from 1961 to 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

ent at the articulation of each of several dorsal and anal fin rays (more in the 10.6 mm *S. melanops* than in the 10.1 mm *S. flavidus*).

As larvae develop, pigment increases over the brain. Melanophores are added on the snout, interorbital region, tips of the upper and lower lips,

TABLE 4.—Measurements (millimeters) of larvae and juveniles of *Sebastes flavidus* from waters off Oregon.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal to hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
10.1	12.5	5.5	4.0	1.2	1.7	—	1.1	3.0	2.2	1.1	1.7	1.6	1.1	0.64	0.90	3.9	0.44	—	1.08	—	0.20	0.76	(4)
10.3	13.3	6.3	4.4	1.3	1.9	1.5	1.3	3.1	2.3	1.3	1.6	2.1	1.0	0.83	1.2	4.4	0.50	0.02	—	—	0.57	1.2	0.52
10.7	13.7	5.9	4.3	1.2	1.9	1.4	1.3	3.2	2.4	1.2	1.8	2.0	1.0	0.78	1.1	4.2	0.34	0.04	0.96	—	0.56	1.3	0.48
11.4	14.6	6.6	4.6	1.2	2.0	1.6	1.4	3.4	2.7	1.4	1.8	2.4	1.1	1.1	1.4	4.6	0.44	0.04	0.96	—	0.68	1.2	0.64
11.8	15.0	6.8	4.7	1.2	2.0	1.6	1.4	3.5	2.6	1.4	1.7	1.9	1.1	1.1	1.5	4.7	0.49	—	1.00	—	0.70	1.2	1.00
11.8	15.2	7.1	4.8	1.4	2.1	1.7	1.4	3.5	2.8	1.4	1.7	2.3	1.1	1.3	1.8	4.8	0.53	0.06	—	—	—	—	—
11.9	15.1	6.6	4.7	1.3	1.9	1.5	1.5	3.5	2.5	1.4	1.8	2.2	1.1	0.98	1.4	4.3	0.54	0.04	—	—	0.64	1.3	0.52
12.0	15.0	6.7	4.9	1.3	2.0	1.5	1.5	3.7	2.9	1.5	2.0	2.4	1.0	1.2	1.6	4.6	0.43	0.14	0.98	—	0.76	1.4	0.66
12.2	15.8	6.9	4.8	1.3	2.0	1.7	1.5	3.6	2.8	1.5	1.8	2.4	1.1	1.2	1.6	4.6	0.49	0.05	0.92	—	0.90	1.4	0.92
12.7	—	6.8	5.1	1.4	—	1.7	1.5	3.4	2.8	1.4	1.7	2.4	1.1	1.3	1.6	5.1	0.43	0.07	—	0.54	0.86	1.4	—
12.8	16.3	7.2	5.0	1.3	2.1	1.7	1.5	3.7	2.8	1.5	1.9	2.4	1.1	1.2	1.6	4.8	0.43	0.06	1.04	0.64	0.84	1.3	1.04
12.9	16.6	7.3	4.9	1.5	2.2	1.6	1.5	3.8	3.0	1.5	2.1	2.7	1.1	1.2	1.7	4.9	0.58	0.06	1.17	0.53	0.88	1.5	1.17
13.1	16.7	7.6	4.9	1.4	2.1	1.6	1.5	3.8	3.0	1.5	2.0	2.5	1.1	1.3	1.7	5.0	—	(5)	1.00	0.44	0.83	1.5	1.00
13.7	17.5	7.8	5.3	1.6	2.1	1.6	1.6	4.0	3.2	1.6	2.1	2.8	1.2	1.4	1.9	5.0	0.46	0.17	1.10	0.68	0.96	1.6	1.10
14.4	18.1	8.4	5.3	1.5	—	1.7	1.5	4.0	3.2	1.5	2.0	2.6	1.2	1.4	1.6	5.6	0.53	0.16	1.15	0.58	0.96	1.6	1.15
14.8	—	8.8	5.9	1.5	2.3	1.8	1.7	4.0	3.2	1.6	2.3	3.2	1.2	—	2.1	5.6	—	0.18	—	0.68	1.2	1.8	—
15.8	20.0	8.8	5.9	1.7	2.4	1.6	1.6	4.0	3.3	1.7	2.6	3.0	1.2	1.2	1.9	5.8	—	—	—	0.70	0.96	1.8	0.64
15.9	20.0	9.2	6.1	1.7	2.6	1.8	1.7	4.6	3.8	1.9	2.6	3.4	1.3	1.9	2.5	6.0	0.60	0.20	1.22	0.66	1.4	2.0	1.2
16.4	20.7	9.6	6.1	1.7	2.8	2.0	1.7	4.2	3.6	1.8	2.7	3.4	1.3	2.2	2.4	5.9	0.50	0.18	—	0.78	1.6	1.8	1.3
16.8	21.7	9.8	6.3	1.7	2.7	2.0	1.7	4.8	3.9	1.9	2.6	3.8	1.4	—	2.5	6.3	0.54	—	—	0.80	1.8	2.4	—
18.9	24.0	10.7	6.7	1.8	2.8	2.0	1.9	4.8	3.9	2.1	2.9	3.7	1.4	—	2.6	6.5	0.49	0.18	—	0.80	—	2.2	—
19.5	25.1	11.5	7.2	1.8	3.1	2.3	2.0	5.1	4.2	2.0	3.0	4.4	1.4	2.8	3.1	7.3	0.38	—	1.16	1.00	2.1	2.7	1.6
19.8	25.6	11.5	7.1	1.7	3.2	2.3	1.9	5.4	4.2	2.1	3.2	4.5	1.6	3.1	3.3	7.6	0.40	0.28	1.26	1.00	2.3	2.6	1.8
20.5	26.1	11.5	7.6	1.9	3.4	2.3	2.0	5.4	4.4	2.2	3.2	4.6	1.5	3.0	3.2	7.3	0.32	0.22	1.23	0.90	2.3	2.7	2.0
21.3	26.3	12.5	8.0	2.1	3.2	2.4	2.0	5.6	4.5	2.2	3.3	4.8	1.6	2.7	3.1	7.8	—	0.16	—	1.16	—	2.7	—
22.3	28.3	12.9	8.1	2.2	3.6	2.4	2.1	5.8	4.9	2.3	3.4	5.0	1.6	—	3.1	7.9	0.44	0.26	1.04	1.10	2.3	3.0	2.0
[6]23.6	—	14.1	8.4	2.2	3.5	2.5	2.2	5.7	4.8	2.4	3.7	5.4	1.6	3.4	3.8	8.5	—	0.22	1.34	1.17	2.7	3.3	2.3
[6]23.7	—	13.7	8.4	2.2	3.7	2.5	2.1	5.6	4.9	2.3	3.6	5.1	1.7	3.2	3.7	8.5	—	—	1.18	1.18	2.6	3.0	2.2
[6]24.2	30.7	14.0	8.7	2.3	3.5	2.5	2.1	6.2	4.9	2.4	3.7	5.6	1.7	3.7	3.8	8.6	0.30	0.16	1.20	1.24	3.0	3.3	2.5
[6]24.8	31.4	15.0	8.8	2.3	3.3	2.5	2.2	6.1	5.0	2.5	3.6	5.5	1.8	3.4	4.0	9.0	—	0.20	1.02	1.42	3.0	3.1	2.4
[6]25.6	31.5	15.4	9.0	2.3	3.6	2.6	2.2	6.3	5.1	2.4	4.0	5.7	1.8	3.4	3.8	9.4	0.42	—	1.04	1.3	3.1	—	2.3
[6]26.6	31.7	15.3	9.0	2.4	3.8	2.5	2.2	6.4	5.1	2.4	3.8	5.7	1.8	3.4	4.1	9.4	0.34	0.18	0.90	1.4	2.8	3.3	2.0
[6]26.7	32.9	15.8	9.0	2.4	3.4	2.6	2.2	6.6	5.2	2.5	4.1	6.5	1.8	3.4	3.9	9.5	—	0.18	—	1.3	2.9	3.2	—
[7]28.5	36.2	17.4	10.3	3.0	4.3	2.9	2.6	6.9	6.0	2.8	4.2	—	2.0	4.4	4.9	10.6	0.18	—	1.34	1.2	3.5	4.0	2.7
[7]29.2	36.0	17.4	10.2	2.8	4.0	2.7	2.6	7.1	5.9	2.8	4.2	—	1.9	3.8	—	10.4	—	0.24	—	1.4	—	—	2.8
[7]29.6	37.0	17.5	9.8	2.6	4.2	2.8	2.5	6.9	5.9	2.9	4.4	—	1.8	—	4.8	10.5	—	—	—	1.4	3.3	3.9	3.1
[7]30.4	—	18.4	10.5	2.6	4.4	2.7	2.6	7.6	6.5	3.0	5.4	7.6	2.3	—	5.4	11.0	—	0.24	—	1.7	3.8	—	3.2
[7]33.0	41.3	19.8	10.6	2.7	4.4	2.9	2.8	7.8	6.6	3.1	5.0	8.1	2.3	4.7	5.1	12.1	—	0.12	1.24	1.6	3.8	4.7	3.3
[7]33.1	—	19.7	10.7	2.6	4.5	3.1	3.0	7.9	7.3	3.2	5.0	—	2.3	4.6	5.5	12.0	—	—	1.18	1.6	4.2	—	3.6
[7]35.2	44.3	21.4	11.7	2.7	5.1	3.4	3.0	9.0	7.5	3.3	5.2	8.6	2.6	4.9	5.3	12.5	—	—	1.24	1.6	4.2	4.7	—
[7]36.4	45.5	21.4	12.4	3.0	5.1	3.2	2.9	9.1	7.6	3.5	6.0	8.9	2.5	4.9	6.2	13.2	0.10	(5)	1.08	1.8	4.3	4.6	3.9
[7]37.6	45.9	22.4	12.0	3.1	5.1	3.2	2.8	10.1	8.8	3.9	5.3	9.3	2.8	—	6.1	13.4	(5)	—	1.16	1.7	4.2	4.6	—
[7]41.9	51.8	26.1	14.4	3.9	6.0	3.7	3.4	10.9	8.9	3.9	6.0	10.5	2.7	5.7	6.2	15.8	0.10	—	1.12	2.2	4.9	5.7	4.6
[7]43.6	—	26.6	14.2	3.7	6.3	3.7	3.5	11.2	9.5	4.2	6.3	10.5	3.2	5.5	7.1	15.4	0.10	—	1.30	2.0	—	—	4.7
[7]45.2	55.6	27.7	14.4	3.4	6.2	3.9	3.5	11.0	9.9	4.4	6.7	11.0	3.2	5.7	7.6	16.4	(5)	—	1.40	2.2	4.9	6.6	4.1
[8]67.6	79.3	42.4	22.7	7.2	9.7	6.7	5.0	19.2	15.9	6.9	9.8	16.0	5.9	—	13.4	27.8	0.14	—	1.08	3.5	8.2	9.3	7.9
[8]71.5	85.7	44.5	24.9	5.7	10.2	6.5	5.4	22.1	18.5	7.5	9.0	18.4	6.0	8.4	13.7	26.9	(5)	—	0.72	4.0	8.8	10.8	8.5
[8]72.5	88.9	45.4	25.4	8.3	11.5	6.7	5.5	22.0	18.2	8.0	9.5	17.5	6.3	8.2	14.0	27.0	(5)	—	0.60	3.7	8.7	11.7	9.1
[8]77.5	94.5	48.8	25.9	7.0	10.4	7.0	5.8	22.7	20.4	8.1	10.7	18.2	6.4	9.5	15.0	29.5	(5)	—	0.96	3.9	9.5	11.5	8.4
[8]81.0	98.9	53.1	29.0	8.7	11.4	7.0	6.2	25.1	21.4	8.7	9.7	19.9	6.3	10.7	16.5	33.3	(5)	—	1.00	4.2	9.2	11.7	9.9
[8]105.0	125.8	66.1	35.3	10.0	16.4	9.7	8.5	31.8	27.4	10.4	13.7	22.9	9.0	12.7	20.0	45.1	—	—	0.92	5.1	11.9	16.0	12.5

[1]Usually fourth or fifth in larvae, fifth or sixth in juveniles
[2]Usually in anterior one-fourth of fin
[3]The second spine in larvae, the third spine in juveniles
[4]Forming
[5]Bump
[6]Transforming
[7]Pelagic juvenile
[8]Benthic juvenile

along the maxillary, and on the cheek and operculum. Pigment increases around the orbit (eventually lining it), and around the posttemporal spine, extending anteriorly over the head. Melanophores line the anterior margin of the cleithrum beneath the operculum.

Pigment on the gut becomes less intense as body musculature increases. The dorsal body surface is pigmented from nape to caudal peduncle in both species by 11 mm. Large stellate melanophores beneath the soft dorsal fin increase in number and are aligned along the muscles surrounding the dorsal pterygiophores, sometimes appearing as lines of pigment. This is the densest pigmentation on larvae. Internal and external melanophores are added along the body midline anteriorly from the caudal peduncle forming a line along the notochord which extends to the head by ≈14 or 15 mm. Melanophores extend ventrolaterally from the nape to the lateral midline by ≈14-16 mm and are added posteriorly along the dorsolateral body surface with development. Initially these melanophores appear along the myosepta, but this pattern becomes obscured as

TABLE 5.—Measurements (millimeters) of larvae and juveniles of *Sebastes melanops* from waters off Oregon.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal to hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
[illegible]	[illegible]	[illegible]	4.4	1.2	1.9	1.5	1.2	3.2	2.5	1.4	1.7	2.0	1.0	1.0	1.5	4.2	0.50	(4)	—	—	0.69	1.10	0.58
[illegible]	[illegible]	6.6	4.8	1.2	—	1.5	1.4	3.6	3.0	1.6	1.9	2.3	1.1	1.2	1.5	4.7	0.50	(4)	1.02	0.35	0.74	1.34	0.70
[illegible]	15.4	7.4	5.1	1.3	2.1	1.6	1.5	3.8	3.1	1.7	1.8	2.4	1.2	1.3	1.6	4.9	—	(4)	—	0.48	0.86	1.28	0.64
[illegible]	15.2	6.9	4.6	1.3	2.1	1.5	1.4	3.7	2.9	1.6	1.8	2.2	1.2	1.1	1.5	4.7	0.44	(4)	—	0.42	0.70	1.30	0.52
[illegible]	16.4	7.3	4.9	1.3	2.1	1.5	1.6	4.0	3.2	1.7	1.9	2.8	1.2	1.5	1.8	4.6	—	0.04	—	0.48	0.96	1.56	0.78
[illegible]	16.9	7.7	5.2	1.3	2.3	1.7	1.5	4.0	3.3	1.8	1.7	2.9	1.2	1.5	1.9	4.9	0.58	0.04	1.40	0.50	1.20	1.68	0.90
[illegible]	16.7	7.6	5.1	1.4	2.1	1.6	1.5	4.2	3.3	1.8	1.8	2.7	1.2	1.4	1.9	4.9	0.46	0.03	1.20	0.46	0.94	1.60	0.84
[illegible]	16.8	7.6	5.1	1.6	2.2	1.6	1.6	4.1	3.2	1.8	1.8	2.8	1.2	1.4	1.8	4.9	0.52	0.04	1.24	0.49	0.90	1.80	0.78
[illegible]	—	7.8	5.4	1.4	2.4	1.6	1.7	4.4	3.5	1.9	1.9	2.9	1.3	1.5	2.1	4.9	0.40	0.04	1.14	0.56	—	1.40	0.98
[illegible]	17.4	8.4	5.4	1.4	2.3	1.7	1.7	4.2	3.4	1.8	2.2	3.0	1.3	1.8	2.3	4.9	—	0.02	1.26	0.58	1.22	1.60	1.00
[illegible]	17.7	8.2	5.6	1.7	2.4	1.8	1.7	4.2	3.5	1.8	2.1	2.8	1.2	1.7	2.0	5.3	0.54	0.06	1.30	0.58	1.08	1.66	0.84
[illegible]	18.6	8.4	5.6	1.7	2.5	1.8	1.7	4.3	3.6	2.0	2.1	3.1	1.3	1.8	2.1	6.0	0.52	0.06	1.24	0.57	1.24	2.02	1.00
14.9	19.9	8.8	6.1	1.7	2.6	1.8	1.8	4.5	3.8	1.8	2.2	3.1	1.4	2.0	2.4	5.9	0.52	0.08	1.36	0.70	1.46	2.10	1.06
15.4	19.5	9.5	6.0	1.7	2.5	1.8	1.7	4.6	3.7	2.0	2.2	3.0	1.4	1.9	2.4	6.3	0.44	0.08	1.20	0.68	1.24	2.16	1.08
15.4	—	9.2	6.0	1.7	2.4	1.8	1.7	4.6	3.6	2.0	2.4	3.3	1.4	2.0	2.3	6.3	0.34	0.10	1.18	0.67	—	1.92	—
15.7	20.6	9.4	5.8	1.7	2.5	1.9	1.8	4.5	3.7	1.9	2.3	3.3	1.3	2.0	2.4	6.1	—	(4)	1.20	0.56	1.14	1.80	1.12
15.9	20.5	9.6	6.0	1.7	2.4	1.8	1.9	4.7	3.8	2.0	2.2	3.4	1.4	—	2.4	6.4	—	(4)	1.16	0.64	1.52	—	—
16.4	21.1	9.5	6.5	1.7	2.7	2.0	1.7	4.6	3.8	2.0	2.3	—	1.4	2.3	2.6	6.1	0.48	0.20	1.03	0.78	1.76	—	1.28
16.5	21.6	9.2	6.0	1.7	2.9	2.0	1.8	4.9	4.2	2.1	2.5	3.6	1.4	2.3	2.5	6.1	0.38	0.08	1.34	0.74	1.70	2.30	1.48
17.2	22.1	9.6	6.6	1.9	2.7	2.0	1.8	4.9	4.0	2.2	2.5	3.7	1.4	2.3	2.5	6.9	0.46	(4)	1.17	0.76	1.68	2.20	1.38
17.4	22.4	9.4	6.3	1.7	2.4	2.0	1.9	5.2	4.3	2.2	2.5	4.0	1.6	2.6	2.8	7.0	—	(4)	1.20	0.80	1.86	2.20	1.46
17.4	22.0	10.0	6.6	1.8	2.8	1.9	2.0	4.9	4.1	2.1	2.6	4.1	1.5	2.5	2.8	6.5	—	0.08	1.20	0.89	—	2.32	1.40
17.7	23.1	9.9	6.3	1.7	2.5	2.1	2.0	5.2	4.6	2.3	2.6	4.2	1.6	2.1	2.8	6.6	0.46	0.10	—	0.78	1.60	2.30	1.30
17.7	22.0	10.2	6.6	1.9	2.8	2.1	1.9	5.1	4.0	2.1	2.4	3.9	1.5	2.5	2.8	6.6	0.56	(4)	1.10	0.70	1.76	2.16	1.46
18.5	23.4	10.6	7.0	1.9	3.0	2.1	2.0	5.1	4.2	2.3	2.4	4.2	1.6	2.4	3.0	7.0	—	—	1.30	0.94	1.98	2.50	1.64
[illegible]	—	10.6	6.9	2.0	2.6	2.1	2.0	5.5	4.5	2.2	2.7	4.5	1.5	2.5	3.2	6.8		0.22	1.12	0.72	1.90	—	1.56
[illegible]	24.7	10.9	7.2	1.9	3.0	2.2	2.0	5.2	4.5	2.3	2.7	4.7	1.6	2.8	3.3	7.6	0.53	0.20	1.27	0.86	2.10	2.40	—
[illegible]	24.4	10.8	7.5	1.9	3.0	2.2	1.8	5.1	4.5	2.2	2.4	4.3	1.5	2.6	3.0	7.0	0.44	0.22	1.10	0.76	1.84	2.38	1.66
[illegible]	25.8	11.4	7.6	2.1	3.2	2.2	2.0	5.8	5.0	2.5	3.0	4.7	1.6	3.0	3.4	8.4	0.32	0.16	1.10	0.90	2.26	2.68	—
[illegible]	25.9	12.0	7.2	2.1	3.1	2.2	2.0	5.8	4.7	2.5	2.8	4.7	1.7	2.8	3.6	8.3	0.36	0.18	1.26	0.80	2.30	—	—
[illegible]	25.9	12.3	7.8	2.3	3.1	2.1	2.0	6.1	4.9	2.5	2.9	4.4	1.7	3.1	3.4	8.8	—	—	1.22	0.90	2.40	—	2.0
[illegible]	27.8	12.3	8.3	2.3	3.1	2.3	2.1	6.1	5.0	2.6	3.5	4.6	1.8	2.9	3.8	8.9	—	—	1.21	1.02	2.60	3.00	2.1
[illegible]	—	12.9	8.3	2.1	3.4	2.5	2.2	6.1	5.2	2.7	3.2	5.2	1.8	2.4	3.8	8.3	0.50	0.17	—	0.90	2.28	3.10	2.0
[illegible]	—	13.4	8.6	2.4	3.6	2.4	2.3	6.1	5.2	2.8	3.4	5.9	1.8	2.9	4.0	8.6	0.46	—	1.24	0.96	—	3.00	—
[illegible]	[illegible]	13.4	8.5	2.2	3.6	2.6	2.2	6.6	5.6	2.8	3.5	5.6	1.9	2.6	4.0	9.0	—	0.20	1.06	0.90	—	3.00	2.3
[illegible]		15.4	9.3	2.6	3.5	2.6	2.3	6.6	5.4	2.7	3.5	5.6	1.9	—	—	10.2	—	(4)	1.10	1.01			—
[illegible]		16.7	8.9	[illegible]	3.7	2.7	2.4	7.2	6.1	3.0	4.0	6.6	2.1	—	4.5	9.7	0.52	—	1.26	1.20	—	—	2.8
30.6	[illegible]	18.5	10.4	2.7	4.4	2.7	2.6	7.7	6.4	3.2	4.4	7.8	2.4	—	5.0	11.9	—	0.30	1.40	1.56	—	4.2	3.4
33.1		20.2	11.7	3.1	4.6	2.9	2.7	8.6	[illegible]	3.4	4.8	8.3	2.6	4.8	5.6	12.1	—	—	1.28	1.64	4.1	4.5	3.5
[illegible]	[illegible]	[illegible]	11.3	[illegible]	4.9	3.1	[illegible]	[illegible]	[illegible]	3.5	4.8	8.3	2.6	5.0	5.8	13.4	(4)	—	—	1.56	4.2	—	3.8
[illegible]	[illegible]	20.9	11.7	2.8	4.9	3.2	2.9	8.7	7.5	3.6	4.8	8.4	2.7	4.9	5.9	12.4	(4)	—		1.64	4.6	4.6	4.0
[illegible]	[illegible]	[illegible]	11.4	2.8	[illegible]	[illegible]	2.9	9.3	7.9	3.6	4.7	8.9	2.8	5.1	6.3	12.6	0.08	—	1.24	1.68	4.5	4.9	3.7
[illegible]	48.2	[illegible]	12.8	[illegible]	5.1	[illegible]	3.1	10.1	[illegible]	4.0	5.2	9.4	2.9	5.3	6.6	14.0	0.20	—	1.24	1.72	4.6	4.9	4.2
[illegible]	49.0	[illegible]	12.2	3.2	4.9	3.3	3.2	9.8	8.2	3.8	5.3	9.3	3.0	5.6	7.1	14.0	(4)	—	—	1.96	4.8	5.0	4.1
[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	9.0	4.2	5.8	9.5	3.2	5.8	7.3	14.3	0.16	—	1.30	1.76	—		3.9
[illegible]		[illegible]	[illegible]	3.4	[illegible]	[illegible]	[illegible]	[illegible]	9.2	4.3	6.1	9.2	3.2	5.7	7.3	14.9	(4)	—	—	2.06	—	—	4.9
[illegible]	[illegible]	[illegible]	[illegible]	4.5	[illegible]	[illegible]	[illegible]	[illegible]	10.0	4.6	6.3	10.1	3.4	5.6	7.4	16.0	0.20	—	1.26	2.00	5.0		4.3
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	10.7	4.7	5.8	11.4	3.6	6.1	8.4	17.0	0.18	—	1.48	2.12	5.5	6.2	4.8
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	6.6	[illegible]	[illegible]	12.2	10.9	4.8	6.9	12.1	3.8	6.5	8.5	19.4	0.28	—	1.48	2.18	—	6.7	5.5
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	15.4	13.3	6.1	7.0	13.2	4.9	6.5	10.5	20.0	—	—	0.78	2.72	6.5	8.3	6.1
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	8.9	[illegible]	[illegible]	[illegible]	16.0	7.0	8.4	14.5	5.9	6.7	12.0	23.0	—	—	0.32	3.20	7.4	8.3	6.5
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	10.4	5.4	5.4	21.2	18.2	7.8	8.9	15.7	6.5	7.8	12.5	23.7	—	—	0.10	3.28	7.6	10.3	7.0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	20.0	8.4	9.5	20.7	7.2	9.5	15.9	31.8	—		0.52	3.92	9.8	12.9	9.9
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	28.1	24.0	9.9	10.4	22.9	8.4	12.0	19.7	37.1	—	—	0.83	4.81	11.0	14.0	11.0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	30.4	25.5	10.9	12.4	22.4	8.3	12.5	19.9	37.2	—		0.88	5.15	12.4	16.7	12.9
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	11.4	12.5	26.4	9.5	14.0	23.2	38.0	—	—	0.80	5.31	13.0	17.5	13.4
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	17.0	[illegible]	[illegible]	[illegible]	[illegible]	12.4	13.2	26.7	10.9	15.5	24.0	39.9	—		1.00	5.73	13.5	18.7	14.0

[1] [illegible]
[2] [illegible]
[3] [illegible]
[4] [illegible]

[illegible] are added between myosepta, particularly along the dorsal one-fourth of the body. Some melanophores remain visible along the ventral margin of the caudal peduncle although they eventually become internal and obscured by tissues. Melanophores are added along the base of the anal fin. Discrete melanophores are added at the articulation of dorsal and anal fin rays and

spines until most of them have a melanophore. Melanophores are added along the caudal fin base, often appearing as a line, and onto the fin membrane. Pigment decreases on the pectoral and pelvic fins and is usually absent on larvae by ≈16-20 mm.

During the transformation period, ≈23-27 mm in *S. flavidus* and ≈23-31 mm in *S. melanops*, pigment gradually increases over the head and body. Melanophores are added on the lips, lower jaw, snout, and dorsolateral areas of the head. Pigment becomes continuous around the orbit. Melanophores are added ventrolaterally beneath the midline band and increase along the ventral body surface above the anal fin.

Pelagic juveniles, ≈28-56 mm in *S. flavidus* and ≈33-52 mm in *S. melanops*, undergo a general increase in pigment with development. The upper head, snout, lips, lower jaw, maxillary, cheek, and gular region become increasingly pigmented with small melanophores. Opercular pigmentation appears less distinct due to scale covering at ≈33 mm. On the side of the body, melanophores are added ventrolaterally until all but the ventral one-eighth is pigmented. Small melanophores increase in number along the ventral surface of the caudal peduncle. Melanophores are added anteriorly and proximally on the first dorsal fin and are eventually scattered over it. A dark blotch develops in the posterior portion of the spinous dorsal fin by ≈35 mm and persists on all larger pelagic juveniles. Melanophores are added to the proximal half of the soft dorsal fin. A few scattered melanophores are added to the pectoral fin and proximal half of the caudal fin. Pigment distinctly lines the caudal fin base.

Benthic juveniles, ≈60 mm, have essentially the same melanistic pigment pattern as the largest pelagic juveniles. Pigmentation at the anterior tips of the lips and along the ventral edge of the maxillary intensifies and a dark bar extends from the posteroventral margin of the eye across the cheek. In *S. melanops* a second dark bar forms dorsal to the first and extends from the eye across the opercle becoming distinct by 76 mm. Melanophores appear on patches of scales covering the dorsal half of the body in both species. These patches overlie the pigment described for pelagic juveniles creating darker patches with lighter areas interspersed where pigmentless scales overlie pigmented areas. The dorsal half of the body has a mottled appearance as a result of this. Melanophores first appear on the pectoral fin base of *S. flavidus* in a patch which extends onto the fin membrane and on the underside of the fin base. Later, additional small melanophores lightly cover the pectoral, anal, and caudal fins while only a few small melanophores appear on the pelvic fin. Benthic juvenile *S. melanops* have melanophores covering all fins, however, the distal margins of those in smaller specimens are usually pigmentless. Although already covered by melanophores, the pectoral fin in small benthic (<63 mm) *S. melanops* has a patch of large melanophores which spread over the dorsal half of the pectoral ray bases and adjacent fin base in the same area which first appears pigmented on the pectoral fin of *S. flavidus*. The spinous dorsal fin, anterior to the black blotch, appears mottled in *S. melanops*. On the soft dorsal fin a more lightly pigmented bar runs through the proximal third of the fin. This bar becomes faint or indistinguishable on specimens ≈67 mm long. Previously described pelagic juvenile body pigment along the anal fin base, at the articulation of the anal fin rays, and on the caudal peduncle becomes completely obscured by scales and tissues on both species, and small melanophores on the scales are alone visible. In general benthic juvenile *S. flavidus* are more lightly pigmented than *S. melanops* taken over similar substrate, however, the pigment patterns are very similar.

Color of Fresh Specimens.—Yellow chromatophores are visible interspersed with melanophores over all body surfaces on pelagic and benthic juveniles of both *S. flavidus* and *S. melanops*. In *S. melanops* they are not numerous enough to give the fish a distinctly yellow cast. The concentration of yellow chromatophores is generally greatest in the areas where melanistic pigment is densest, e.g., the base of the caudal fin, the pigment bar radiating from the posteroventral margin of the eye, darker areas on fins. Yellow pigment is not concentrated around the dorsal fin black blotch. Juveniles generally appear darkly mottled with faintly yellow fins, yellowish areas on the head and body, and cream colored ventrally. However, considerable variation in the intensity of the melanistic pigment of benthic juveniles may occur seemingly dependent upon bottom substrate. When melanistic pigment is less intense, yellow pigment is more outstanding. The yellow tail,

TABLE 6.—Development of spines in the head region of *Sebastes flavidus* larvae and juveniles. + denotes spine present and – denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
10.1	–	+	–	–	+	–	–	–	+	–	+		(1)				+
10.3	–	+	–	–	+	–	–	–	+	+	–		–				+
10.7	–	+	–	–	+	+	–	–	+	+	–		–				+
11.4	–	–	+	+	+	+	+	+	+	(1)	+		+				+
11.8	–	–	–	–	+	+	+	+	+	–	+		+				+
11.8	–	–	–	–	+	+	+	+	+	(1)	–		–		–		+
11.9	–	–	+	+	+	+	+	+	+	+	–	(1)	+				+
12.0	–	–	+	+	+	+	+	+	+	+	–	(1)	+				+
12.2	–	–	+	–	+	+	–	–	–	–	–	(1)	+				+
12.7	–	–	+	–	+	+	–	–	–	+	–		+				+
12.8	–	–	+	–	+	+	–	–	–	+	–	(1)	+				+
12.9	–	–	+	–	+	+	–	–	–	+	+		+				+
13.1	–	(1)	–	–	+	+	–	–	–	–	–	(1)	+				+
13.7	–	–	–	–	+	+	–	–	–	–	+		+				+
14.4	–	–	–	–	+	+	–	–	–	+	–		+				+
14.8	–	–	–	–	+	+	–	–	–	–	–	(1)	+				+
15.8	–	–	–	–	+	+	–	–	–	–	–	(1)	+				+
15.9	–	–	–	–	+	+	–	–	–	–	–	(1)	+				+
16.4	–	–	–	–	+	+	–	–	–	–	+		+				+
16.8	–	–	–	–	+	+	–	–	–	–	–	(1)	+				+
18.9	–	–	–	–	+	+	–	–	–	–	+		+				+
19.5	–	–	–	–	+	+	–	–	–	–	+		+				+
19.8	–	–	–	+	+	+	–	–	–	–	+		+				+
20.5	–	–	–		+	+	–	–	–	–	+		+				+
21.3	–	–	–		+	+	–	–	–	–	+		+				+
22.3	–	–	–		+	+	–	–	–	–	+		+				+
[2]23.6	–	–	–		+	+	–	–	–	–	+		+				+
[2]23.7	–	–	–		+	+	–	–	–	–	+		+				+
[2]24.2	–	–	–		+	+	–	–	–	–	+		+				+
[2]24.8	–	–	–		+	+	–	–	–	–	+		+				+
[2]25.6	–	–	–		+	+	–	–	–	–	+		+				+
[2]26.6	–	–	–	(1)	+	+	–	–	–	–	+		+				+
[2]26.7	–	–	(1)	(1)	+	+	–	–	–	–	+		+				+
[2]28.6	–	–	(1)		+	+	–	–	–	–	+		+				+
[2]29.2	–	–	(1)		+	+	–	–	–	–	+		+				+
[2]29.6	–	–	(1)	(1)	+	+	–	–	–	–	+		+				+
[3]30.4	–	–	(1)		+	+	–	–	–	–	+		+				+
[3]33.0	–	–	–		+	+	–	–	–	–	+		+				+
[3]33.1	–	–	–		+	+	–	–	–	–	+		+				+
[3]35.2	–	(1)			+	+	–	–	–	–	+		+				+
[3]36.4	–	(1)			+	+	–	–	–	–	+		+				+
[3]37.6	(1, 5)	(1, 5)			+	+	–	–	–	–	+		+				+
[4]41.9	[4]	(1, 5)			+	+	–	–	–	–	+		+				+
[4]43.6	[4]	(1, 5)			+	+	–	–	–	–	+		+				+
[4]45.2	[4]	(1, 5)			+	+	–	–	–	–	+		+				+
[5]67.6	(1, 5)	(1, 5)			+	+	–	–	–	–	+		+				+
[5]71.5	(1, 5)	(1, 5)			(1)	+	–	–	–	–	+		+				+
[5]72.5	(1, 5)	(1, 5)			+	+	–	–	–	–	+		+				+
[5]77.5	(1, 5)	(1, 5)			(1)	+	–	–	–	–	+		+				+
[6]81.0	(1, 5)	(1, 5)			(1)	+	–	–	–	–	+		(6)				+
[6]105.0	(1, 5)	(1, 5)			(1)	+	–	–	–	–	+		(6)				+

[1]Bump, indicates beginning of spine formation or bony overgrowth of spine
[2]Transforming
[3]Pelagic juvenile
[4]Parietal and nuchal spines fused
[5]Benthic juvenile
[6]Spine covered by fleshy lobe
[7]Adjacent spines fused
[8]Spine has become scale-covered

characteristic of adults of *S. flavidus*, usually becomes distinct on juveniles ~100 mm long.

Occurrence (Figures 7-10).—Adults of *S. flavidus* occur from San Diego, Calif., to Kodiak Island, Alaska (Miller and Lea 1972). Off Oregon they are most common on the continental shelf between 100 and 200 m (Snytko and Fadeev[7]). Data from Niska (1976) showed that 92% of the total Oregon trawl catch of *S. flavidus* from 1963 to 1971, was taken from depths of 54 to 218 m. Concentrations of adult *S. flavidus* have been found along Astoria Canyon, between lat. 46°10′ N and 46°20′ N, and also between lat. 44°30′ N and 45°

[7]Snytko, V. A., and N. S. Fadeev. 1974. Data on distribution of some species of sea perches along the Pacific coast of North America during the summer-autumn seasons. Document submitted to the Canada-USSR Meeting on Fisheries in Moscow-Batumi, USSR, November 1974, 14 p. (Transl. 3436, Can. Transl. Ser.)

TABLE 6.—Continued.

Standard length (mm)	Infraorbital															
	Inferior			Superior				Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	1st	2d	3d	1st	2d	3d	4th					Superior	Inferior		
10.1	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
10.3	+	(1)	–	+	–	–	+	–	–	–	+	–	+	(1)	–
10.7	+	(1)	–	+	–	–	+	–	–	–	+	–	+	–	–
11.4	+	+	–	+	–	–	+	(1)	–	–	+	–	+	–	–
11.8	+	+	–	+	–	–	–	–	–	–	+	–	+	+	–
11.8	+	+	–	+	–	–	–	–	–	–	+	–	+	(1)	–
11.9	+	+	–	+	–	–	+	–	–	–	+	–	+	–	–
12.0	+	+	–	+	–	–	+	–	–	–	+	–	+	–	–
12.2	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.7	+	+	–	+	–	–	+	(1)	–	–	+	–	+	(1)	–
12.8	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.9	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
13.1	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.7	+	+	–	+	–	(1)	+	+	–	–	+	–	+	+	–
14.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
14.8	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
15.8	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
15.9	+	+	(1)	+	–	+	+	+	–	–	+	–	+	+	–
16.4	+	+	+	+	–	(1)	+	+	–	–	+	–	+	+	–
16.8	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
18.9	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
19.5	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
19.8	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
20.5	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	–
21.3	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
22.3	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[2]23.6	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	–
[2]23.7	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	(1)
[2]24.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]24.8	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	(1)
[2]25.6	+	+	+	+	–	+	+	+	–	–	(1)	–	+	+	+
[2]26.6	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	–
[2]26.7	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	–
[2]23.6	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]29.2	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	(1)
[2]29.6	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]30.4	+	+	+	+	–	(1)	+	+	–	(1)	(1)	+	+	+	+
[2]33.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	(1)
[2]33.1	+	+	+	+	–	+	+	+	–	(1)	+	+	+	+	(1)
[2]35.2	+	+	+	+	–	–	+	+	–	(1)	(1)	+	+	+	+
[2]36.4	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	+
[2]37.6	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	+
[2]41.9	+	(1)	(1)	(1)	–	–	+	+	–	+	–	+	+	+	+
[2]43.6	+	(1)	(1)	(1)	–	–	+	+	–	+	–	+	+	+	+
[2]45.2	+	(1)	(1)	–	–	–	–	+	–	(1)	(1)	+	+	+	+
[2]67.6	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[2]71.5	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[2]72.5	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	(1)	+	+[8]
[2]77.5	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[2]81.0	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[2]105.0	(6)	(6?)	(6?)	–	–	–	–	+	–	+	–	+	–	+	+[8]

N (see footnote 7). Larvae, including transforming specimens, of *S. flavidus* in our collections were captured at stations ranging from 24 to 266 km offshore. Larvae apparently range widely and the limit observed are probably most indicative of sampling effort. Within the size range of identified larvae, there was no apparent distribution pattern relative to specimen size. Pelagic juveniles were similarly distributed. Benthic juveniles were taken close to the coast at depths of 20-37 m.

Adult *S. melanops* reportedly occur from Paradise Cove, Baja California, to Amchitka Island, Alaska (Miller and Lea 1972), although Quast and Hall (1972) noted that records from the Aleutian Islands may have resulted from misidentified *S. ciliatus*. *Sebastes melanops* is most common on the continental shelf at depths <200 m (Dunn and Hitz 1969; Niska 1976). Data tabulated by Niska (1976) for Oregon trawl catches show that 82% of the total *S. melanops* landings, from 1963 to 1971, were taken in depths <54 m while 93% were taken at depths <109 m. Larvae, including transforming specimens, of *S. melanops* in our collections were captured at stations ranging from 5 to 266 km offshore. Pelagic juveniles have a similar distribution. Larvae seem to range widely. However, sampling effort was not uniform over the area and relatively little sampling occurred nearshore, <40 km from

TABLE 7.—Development of spines in the head region of *Sebastes melanops* larvae and juveniles. + denotes spine present and – denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Opercular Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
10.6	-	(1)	+		+	+	+	+	+	–	(1)	–	(1)		-		+
11.7	-	(1)	+		–	+	+	+	+	(1)	(1)	–	(1)				+
11.9	-	(1)	+	+	–	+	–	+	+	(1)	(1)	–	(1)				+
11.9	-	(1)	+	+	–	+	+	–	(1)	(1)	(1)	–	(1)				+
12.4	-	+	+		–	+	–	+	+	+	(1)	–	(1)	–			+
12.8	-	-	+	–	–	+	+	+	+	-	(1)	–	(1)				+
12.8	-	-	+		+	+	+	+	+	-	(1)	–	+				+
12.8	-	-	+	–	+	+	+	+	+	-	+	(1)	+				+
13.5	-	-	+		+	+	+	+	+	-	+	–	+				+
13.6	-	+	+		+	+	+	+	+	-	+	–	+				+
13.9	-	+	+		+	+	+	+	+	-	+	(1)	+				+
14.0	-	-	+		+	+	+	+	+	-	+	(1)	+				+
14.9	-	-	+	–	+	+	+	+	+	-	+	–	+				+
15.4	-	-	+		+	+	+	+	+	-	+	–	+				+
15.4	-	-	+		+	+	+	+	+	-	+	–	+				+
15.7	-	-	+		+	+	+	+	+	-	+	–	+				+
15.9	-	-	+		+	+	+	+	+	-	+	–	+				+
16.4	-	-	+		+	+	+	+	+	-	+	–	+				+
16.5	-	-	+		+	+	+	+	+	-	+	–	+				+
17.2	-	-	+		+	+	+	+	+	-	+	–	+				+
17.4	-	-	+	–	+	+	+	+	+	-	+	–	+				+
17.4	-	-	+		+	+	+	+	+	-	+	–	+				+
17.7	-	-	+		+	+	+	+	+	-	+	–	+				+
17.7	-	-	+		+	+	+	+	+	-	+	–	+				+
18.5	-	-	+		+	+	+	+	+	-	+	–	+				+
19.0	-	-	+		+	+	+	+	+	-	+	–	+				+
19.2	-	-	+		+	+	+	+	+	-	+	–	+				+
19.2	-	-	+		+	+	+	+	+	-	+	–	+				+
20.7	-	-	+		+	+	+	+	+	-	+	–	+				+
20.7	-	-	+		+	+	+	+	+	-	+	–	+				+
21.0	-	-	+		+	+	+	+	+	-	+	–	+				+
22.9	-	-	+		+	+	+	+	+	-	+	–	+				+
[2]23.2	-	-	+		+	+	+	+	+	-	+	–	+				+
[2]24.0	-	-	+		+	+	+	+	+	-	+	–	+				+
[2]24.0	-	-	+		+	+	+	+	+	-	+	–	+				+
[2]24.6	-	(1)	+		(1)	+	+	+	+	-	+	–	+				+
[2]27.9	-	(1)	(1)		-	+	+	+	+	-	+	–	+				+
[2]30.6	-	(1)				+	+	+	+	-	+	–	+				+
[4]33.1	-	(1)				+	+	+	+	-	+	–	+				+
[4]33.9	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]35.2	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]35.8	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]38.2	-	(1)				+	+	+	+	-	+	–	+				+
[4]39.2	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]40.0	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]41.0	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]43.6	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]45.3	(1)	(1)				+	+	+	+	-	+	–	+				+
[4]48.4	(1)	(1)				+	+	+	+	-	+	–	+	(1)			+
[5]52.5	(1)	(1)				+	+	+	+	-	+	–	+	(1)			+
[6]62.5	(1)	(1)				(1)	+	+	+	-	+	–	+	(1)			+
[7]67.0	(1)	(1)				(1)	+	+	+	-	+	–	+	(1)			+
[7]76.1	(1)	(1)					(1)	+	+	-	+	–	+	(1)			+
[8]89.4	—	—					(1)	+	+	-	+	–	+	(1)			+
[9]97.7	(1)	(1)					(1)	+	+	-	+	–	+	(1)			+
[10]100.9							(1)	+	+	-	+	–	+	(1)			+
[11]111.6							(1)	+	+	-	+	–	+	(1)			+

[1]Bump indicates beginning of spine formation or bony overgrowth of spine
[2]Transforming
[3]Parietal and nuchal spines fused
[4]Pelagic juvenile
[5]Spine is bifid
[6]Spine covered by fleshy lobe
[7]Benthic juvenile
[8]Spine has become scale-covered
[9]Adjacent spines fused

the coast. Benthic juveniles have been taken in estuaries, tidepools, and near the coast at depths 20 m.

Parturition times reported for *S. flavidus* are December to February off California (Phillips 1958) and March off Oregon (Westrheim 1975). Larvae 10-20 mm long were taken April through June, although most were taken in April and May. Larvae and pelagic juveniles 20-40 mm long were taken April through July, indicating some

TABLE 7.—Continued.

Standard length (mm)	Infraorbital															
	Inferior			Superior									Posttemporal		Supra-cleithral	Cleithral
	1st	2d	3d	1st	2d	3d	4th	Nasal	Coronal	Tympanic	Pterotic	Superior	Inferior		
10.6	+	–	–	+	–	–	+	–	–	–	+	–	+	(1)	–
11.7	+	(1)	–	+	–	–	+	(1)	–	–	+	–	+	+	+	–
11.9	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	+	–
11.9	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	+	–
12.4	–	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
13.5	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
13.6	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
13.9	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
14.0	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	+	–
14.9	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
15.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	+	–
15.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
15.7	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	+	–
15.9	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
16.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
16.5	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
17.2	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
17.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
17.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
17.7	+	+	+	+	–	–	+	+	–	–	+	–	+	–	–	–
17.7	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
18.5	+	+	+	+	–	–	+	+	–	–	+	–	+	+	+	–
19.0	+	+	+	+	–	–	+	+	–	–	+	+	+	+	+	–
19.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	–
19.2	+	+	+	+	–	–	+	+	–	–	+	+	+	+	+	–
20.7	+	+	+	+	–	(1)	+	+	–	–	+	+	+	+	+	–
20.7	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	–
21.0	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	–
22.9	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	–
223.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	–
224.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	+	–
224.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	+	–
224.6	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	+	–
227.9	+	+	+	+	–	–	+	+	–	(1)	(1)	+	+	+	+	–
230.6	+	+	+	+	–	–	+	+	–	(1)	+	–	–	–	–	(1)
233.1	+	+	+	+	–	(1)	+	+	–	+	(1)	+	+	+	+	+
233.9	+	(1)	(1)	+	–	–	+	+	–	(1)	(1)	+	+	+	+	+
235.2	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	–	+	+	+	+	+
235.8	+	(1)	(1)	(1)	–	–	+	+	–	–	–	+	+	+	+	+
238.2	+	(1)	(1)	–	–	–	(1)	+	–	(1)	(1)	+	(1)	+	+	+
239.2	+	(1)	(1)	–	–	–	(1)	+	–	(1)	–	+	+	+	+	+
240.0	+	(1)	(1)	–	–	–	(1)	+	–	(1)	–	+	+	+	+	+
241.0	+	(1)	(1)	–	–	–	(1)	+	–	(1)	(1)	+	+	+	+	+
243.8	+	(1)	(1)	–	–	–	(1)	+	–	–	–	+	(1)	+	+	+
245.3	+	(1)	(1)	–	–	–	–	+	–	–	–	+	–	+	+	+
248.4	+	(1)	(1)	–	–	–	(1)	+	–	–	–	+	–	+	+	+
252.5	(6)	(1)	(1)	–	–	–	–	+	–	–	–	+	–	+	+	+ [8]
262.5	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+	–	+	–	+ [8]
267.0	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	(1)	–	+ [8]	–	+ [8]	+ [8]	+ [8]
276.1	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+ [8]	–	+ [8]	–	+ [8]
289.4	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+ [8]	–	+ [8]	–	+ [8]
297.0	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+ [8]	–	+ [8]	+ [8]	+ [8]
300.9	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+ [8]	–	+ [8]	+ [8]	+ [8]
311.6	(6)	(6 ?)	(6 ?)	–	–	–	–	+	–	–	–	+ [8]	–	+ [8]	–	+ [8]

variability and protraction of parturition time. Benthic juveniles were taken only in June and October due to limited samples.

Parturition times reported for *S. melanops* are February to April (Hart 1973) and January off Oregon (Westrheim 1975). Larvae 10-20 mm long were taken April through May. Larvae and pelagic juveniles 20-40 mm long were taken April through June, indicating some variability in spawning time and duration. Benthic juveniles first appeared in June samples.

Comparisons.—Prior to this paper, developmental series of 10 of the 69 northeast Pacific (including Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S. crameri*, *S.* Gulf Type A, *S. helvomaculatus*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978; Richardson and Laroche 1979). While exhibiting some similarities to larval and juvenile *S. flavidus* and *S. melanops*, the previously described develop-

mental series differ in many characters. Most apparent is the early lack of pigment and the later development of distinct pigment saddles under the dorsal fins of postflexion and pelagic juvenile *S. crameri*, *S. helvomaculatus*, *S. levis*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger*. The only species described to date which has pigment along the dorsal surface under the dorsal fins in postflexion larvae and pelagic juveniles, similar to that of *S. flavidus* and *S. melanops*, is *S. jordani*. However, *S. jordani* has a very short snout to anus distance/SL ratio, 36 to 53% SL, compared with 57 to 60.3% SL and 58.0 to 61.3% SL for postflexion larvae and pelagic juveniles of *S. flavidus* and *S. melanops*, respectively. *Sebastes cortezi*, *S.* Gulf Type A, and *S. macdonaldi* are all deeper bodied than *S. flavidus* and *S. melanops*, and both *S.* Gulf Type A and *S. macdonaldi* have much longer parietal spines.

Other Oregon species which are easily confused with *S. flavidus* and *S. melanops* during larval and juvenile development are the widow rockfish, *S. entomelas*, and the blue rockfish, *S. mystinus*. However, pelagic and benthic juveniles of these species are separable based on the presence of preocular and supraocular spines, usually >15 dorsal soft rays, and usually >8 anal soft rays (see Appendix Table 1).

Sebastes mystinus is separable from the other three species at all sizes after fin formation has occurred, ≈9.0 mm, since it is the only species which usually has 16 dorsal soft rays and 9 anal soft rays. *Sebastes entomelas* and *S. mystinus* both usually have 18 pectoral rays which distinguish them from *S. melanops*, which usually has 19 rays. *Sebastes flavidus* and *S. entomelas* are the only pair of species which are not readily separated by fin counts. However, both *S. entomelas* and *S. mystinus* develop supraocular spines, which appear on specimens larger than ≈17 mm, while *S. flavidus* and *S. melanops* rarely develop supraocular spines. In addition to these characters, larvae and pelagic juveniles of *S. entomelas* and *S. mystinus* either lack or have a reduced number of melanophores at the articulations of the anal fin rays and on the ventral surface of the caudal peduncle. We have a description of the development of *S. entomelas* in preparation.

Sebastes ciliatus (from British Columbia and Alaska) and *S. serranoides* (from California) are other similar species which should be carefully considered when identifying specimens from areas where they also occur. We have not had the opportunity to observe specimens of *S. ciliatus* and cannot assess its potential for causing confusion. We have examined 20 benthic juvenile *S. serranoides*. Although the head spine pattern in *S. serranoides* is the same as in *S. flavidus* and *S. melanops*, *S. serranoides* usually has <18 pectoral rays and >8 anal soft rays which will usually separate them from *S. flavidus* and *S. melanops* (see Appendix Table 1). All of the species discussed, excluding *S. ciliatus* for which we have no information, have to some extent a concentration of melanistic pigmentation on the posterior portion of the spinous dorsal fin occurring on juveniles. *Sebastes flavidus* and *S. melanops* have the most intensely pigmented "black blotch." *Sebastes mystinus* has a more darkly pigmented spinous dorsal fin which presents little contrast from the pigment in the area of the black blotch. *Sebastes entomelas* and *S. serranoides* usually have a less distinct "blotch" with most of the pigment concentrated in a fringe along the posterior distal edge of the spinous dorsal fin membrane.

The most important characters useful in separating larval and juvenile *S. flavidus* and *S. melanops* from each other are pectoral ray number (usually 18 versus 19), lateral line pore number (usually >50 versus <50), and caudal peduncle depth/length ratio (mean values 0.73, 0.64, 0.64, 0.80 versus 0.88, 0.78, 0.74, 0.92 in postflexion larvae, transforming, pelagic juvenile, and benthic juvenile specimens, respectively). *Sebastes flavidus* taken at the same location as *S. melanops* appear to have less dense melanistic pigment. Benthic juveniles of *S. flavidus* seem to inhabit deeper waters, >20 m, while *S. melanops* inhabits estuaries, tidepools, and offshore waters <20 m. Landing data tabulated by Niska (1976) indicates a corresponding difference in "preferred" depth for adults with *S. flavidus* taken chiefly between 54 and 218 m and *S. melanops* taken mainly in water <54 m.

ACKNOWLEDGMENTS

Special thanks are extended to William G. Pearcy for allowing us to use his extensive midwater trawl collections from waters off Oregon. Additional specimens were provided by Carol Anderson, Range Bayer, Carl Bond, William Eschmeyer, Wendy Gabriel, Gary Hepman, Gary Hewitt, Michael Hosie, Earl Krygier, Robert Lea,

and Kate Myers. H. Geoffrey Moser and Sigurd J. Westrheim reviewed the manuscript and offered helpful suggestions.

LITERATURE CITED

DELACY, A. C., C. R. HITZ, AND R. L. DRYFOOS.
1964. Maturation, gestation and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Wash. Dep. Fish., Fish. Res. Pap. 2:51-57.

DUNN, J. R., AND C. R. HITZ.
1969. Oceanic occurrence of black rockfish (*Sebastodes melanops*) in the central north Pacific. J. Fish. Res. Board Can 26:3094-3097.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MOSER, H. G.
1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.
1972. Development and geographic distribution of the rockfish, *Sebastes macdonaldi* (Eigenmann and Beeson, 1893), family Scorpaenidae, off southern California and Baja California. Fish. Bull., U.S. 70:941-958.

MOSER, H. G., AND E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.

NISKA, E. L.
1976. Species composition of rockfish in catches by Oregon trawlers 1963-71. Oreg. Dep. Fish. Wildl., Inf. Rep. 76-7, 80 p.

PHILLIPS, J. B.
1958. "Rockfish review." *In* The marine fish catch of California for the years 1955 and 1956, p. 7-25. Calif. Dep. Fish Game, Fish Bull. 105.

QUAST, J. C., AND E. L. HALL.
1972. List of fishes of Alaska and adjacent waters with a guide to some of their literature. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-658, 47 p.

RICHARDSON, S. L., AND W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-46.

VERHOEVEN, L. A. (editor).
1976. 28th annual report of the Pacific Marine Fisheries Commission for the year 1975. Pac. Mar. Fish. Comm., Portland, Oreg., 48 p.

WESTRHEIM, S. J.
1975. Reproduction, maturation and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

APPENDIX TABLE 1 —Frequency distributions of soft fin rays, lateral line pores, diagonal scale rows below the lateral line, and gill rakers for juvenile and adult *Sebastes entomelas*, *S. flavidus*, *S. melanops*, *S. mystinus*, and *S. serranoides*

		Pectoral fin rays				Dorsal fin soft rays					Anal fin soft rays				Lateral line pores											
Species	Side	17	18	19	20	13	14	15	16	17	7	8	9	10	45	46	47	48	49	50	51	52	53	54	55	56	59
Sebastes entomelas[1]	Left	1	37	2	—	—	4	31	5	—	3	35	2	—	—	—	—	—	—	—	—	4	6	16	13	1	—
	Right	1	37	2	—																	4	4	19	12	1	—
Sebastes flavidus[2]	Left	2	47	3	—	—	30	22	—	—	5	47	—	—	—	1	—	—	1	4	6	15	10	5	5	1	—
	Right	1	48	3	—										—	—	—	—	—	3	11	12	15	3	3	2	1
Sebastes melanops[3]	Left	—	11	55	—	2	26	37	1	—	13	53	—	—	2	2	4	13	16	15	11	1	1	1	—	—	—
	Right	—	3	61	1										1	3	5	9	17	13	13	2	3	—	—	—	—
Sebastes mystinus[4]	Left	3	55	3	—	—	—	5	49	8	—	6	52	4	—	—	—	1	6	16	18	12	9	—	—	—	—
	Right	3	55	4	—										—	—	—	—	4	10	15	22	8	2	—	—	—
Sebastes serranoides[5]	Left	16	4	—	—	—	1	11	8	—	—	3	16	1	—	—	—	—	—	1	—	5	9	3	1	—	—
	Right	15	5	—	—										—	—	—	—	—	—	1	3	12	2	2	—	—

		Diagonal scale rows below lateral line																				Gill rakers on lower bar of 1st gill arch						
Species	Side	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	23	24	25	26	27	28	29
S. entomelas	Left	—	—	—	—	—	—	—	—	—	—	1	2	4	6	12	7	5	2	1	—	—	11	21	7	1	—
	Right	—	—	—	—	—	—	—	—	—	—	1	1	6	5	13	4	7	2	1	—	—	13	22	5	—	—
S. flavidus	Left	—	—	—	—	—	—	—	—	3	12	8	10	6	1	3	—	1	—	—	—	5	14	30	3	—	—
	Right	—	—	—	—	—	—	1	—	1	6	16	9	4	2	4	—	1	—	—	—	1	15	31	4	—	—
S. melanops	Left	1	3	2	6	8	11	19	13	2	1	—	—	—	—	—	—	—	—	—	—	7	13	27	17	2	—
	Right	—	1	1	8	9	12	17	13	4	1	—	—	—	—	—	—	—	—	—	1	6	10	27	18	4	—
S. mystinus	Left	—	—	—	1	9	11	5	14	7	3	3	—	1	—	—	—	—	—	—	2	7	28	19	6	—	—
	Right	—	—	1	—	4	8	7	11	13	4	3	2	1	—	—	—	—	—	—	2	9	21	21	7	1	1
S. serranoides	Left	—	—	—	—	—	—	—	—	—	2	2	3	2	1	—	—	—	—	—	1	8	11	—	—	—	—
	Right	—	—	—	—	—	—	—	—	—	1	2	3	2	2	—	—	—	—	—	1	6	10	3	—	—	—

		Gill rakers on upper bar of 1st gill arch					Total gill rakers on 1st gill arch								
Species	Side	8	9	10	11	12	32	33	34	35	36	37	38	39	40
S. entomelas	Left	—	4	36	—	—	—	—	2	10	21	6	1	—	—
	Right	—	5	33	2	—	—	—	2	14	17	7	—	—	—
S. flavidus	Left	—	—	21	30	1	—	—	4	6	21	18	3	—	—
	Right	1	—	20	30	1	—	1	—	10	17	21	3	—	—
S. melanops	Left	—	1	13	46	6	—	—	4	10	9	21	17	5	—
	Right	—	—	20	41	5	—	—	5	10	8	21	16	5	1
S. mystinus	Left	—	3	43	15	1	1	1	7	25	15	9	3	1	—
	Right	—	2	47	11	2	1	1	8	20	17	9	4	2	—
S. serranoides	Left	—	4	16	—	—	1	3	5	11	—	—	—	—	—
	Right	—	7	13	—	—	—	4	5	10	1	—	—	—	—

[1]All *S. entomelas* were collected at lat 44°39' N, long 124°44' W off Oregon.

[2]All *S. flavidus* were collected at two locations (lat 44°05' N, long 124°55' W and lat 45°33' N, long 124°07' W) off Oregon.

[3]All *S. melanops* were collected from Yaquina Bay, Oreg. (lat 44°37' N, long 124°03' W), or open coast tide pools nearby.

[4]*Sebastes mystinus* from a number of locations between Soberanes Point, Calif. (lat 36°26.54' N, long 121°55.41' W), and the mouth of the Columbia River, Oreg. (lat 46°15' N, long 124°07' W) were examined.

[5]All *S. serranoides* were collected in California between Newport Beach (lat 33°35' N) and San Francisco (lat 37°50' N).

EFFECTS OF TRAP VENTING ON GEAR SELECTIVITY IN THE INSHORE RHODE ISLAND AMERICAN LOBSTER, *HOMARUS AMERICANUS*, FISHERY

MICHAEL J. FOGARTY AND DAVID V. D. BORDEN[1]

ABSTRACT

The incorporation of escapement devices in lobster traps has proven effective in allowing the release of sublegal-sized American lobster, *Homarus americanus*, and reducing the potential for trap related injury and mortality. The present study was undertaken to assess the effects of trap venting on size selectivity and catch per unit effort in the inshore Rhode Island lobster fishery. The use of rectangular vents (42 × 152 mm) resulted in a 79% decrease in the sublegal (<78 mm carapace length) catch. Vented traps tended to consistently catch greater numbers of legal-sized (≥78 mm carapace length) lobster, possibly due to a density dependent effect. The mean size of lobster caught in vented gear was significantly greater than in control traps. An analysis of the effect of trap immersion time indicated that the catch is asymptotic with increasing soak time up to 7 set over days.

Comparisons of the effectiveness of 42 × 152 mm and 44.5 × 152 mm vents indicated that no substantial loss of legal lobster would occur and that escapement rates of sublegal lobster would be dramatically improved with the use of the larger vent size. Vented traps tended to be more efficient in releasing sublegal lobster than traps with equivalent lath spacing, supporting the use of synthetic vents. Vent orientation (horizontal versus vertical) did not affect the escapement of sublegal-sized lobster.

Attempts to adjust the size selectivity of traps to minimize the retention of sublegal-sized lobster have received increasing attention in recent years (Krouse and Thomas 1975; Krouse 1978; Pecci et al. 1978; Nulk 1978; Fair and Estrella[2]). The inverse relationship between lath spacing and the sublegal catch has long been recognized (Templeman 1939; Wilder 1945), while current efforts have been directed toward the development of more precise escapement devices, specifically escape vents of various designs.

A clear reduction in lobster mortality and injury with the use of vented traps has been demonstrated (Pecci et al. 1978); sources of trap related mortality and injury include aggressive interactions within the trap and the effects of handling by fishermen. In addition, predation on surface released sublegal lobster may contribute significantly to mortality (Krouse and Thomas 1975).

Less information is available on the effects of trap venting on the incidental catch of commercially valuable species, particularly the rock crab, *Cancer irroratus*, and the jonah crab, *C. borealis*. Krouse (1978) demonstrated the effectiveness of vents with circular openings in retaining marketable northern crabs *Cancer* spp., while permitting the egress of sublegal-sized lobster. Stasko (1975) earlier promoted the use of circular escape openings in traps modified to retain crabs and release lobster.

A research program designed to substantiate data available on trap venting and apprise local fishermen of new concepts in gear modification was initiated by the Rhode Island Division of Fish and Wildlife in April 1976. This report presents the results of field and laboratory investigations on the effects of trap venting on catch per unit effort (CPUE) and size composition of the lobster catch.

METHODS

Conventional lobster traps were purchased from commercial suppliers and distributed to eight cooperating fishermen. The fishermen participated on a voluntary basis and were chosen to represent a range of geographical areas within

[1]Rhode Island Department of Environmental Management, Division of Fish and Wildlife, 150 Fowler Street, Wickford, RI 02852.

[2]Fair, J. J., and B. Estrella. 1976. A study on the effects of sublegal escape vents on the catch in lobster traps in five coastal areas of Massachusetts. Unpubl. manuscr., 9 p. Massachusetts Division of Marine Fisheries, P.O. Box 707, Sandwich, MA 02563.

Manuscript accepted April 1979
FISHERY BULLETIN: VOL 77, NO 4, 1980

Narragansett Bay and Rhode Island Sound. Five trap styles, representing the most commonly used trap types in this area, were selected for use in the study. Each fisherman was given traps of one type only.

Seven of the fishermen were provided with equal numbers of vented and nonvented traps to be arranged in trawls (strings) of alternating vented and control traps. The escape panels were constructed of 0.061 gage aluminum with a 42 mm × 152 mm opening placed in the parlor section of the trap. Single parlor traps were equipped with one vent placed vertically in the end section of the parlor. Double parlor traps were equipped with two vents positioned horizontally in the sides of each parlor section.

To determine the efficiency of vented traps when compared with traps having equivalent lath spacing and to evaluate the effects of vent orientation (horizontal vs. vertical) on escapement, one of the fishermen was given traps with the following characteristics:

1) control traps (mean lath spacing 31 mm, SD = 6 mm),
2) traps with horizontal vents (42 mm × 152 mm),
3) traps with vertical vents (42 mm × 152 mm),
4) traps with one vertical lath space opened to 42 mm,
5) traps with horizontal vents (44.5 mm × 152 mm),
6) traps with vertical vents (44.5 mm × 152 mm), and
7) traps with one vertical lath space opened to 44.5 mm.

Each trap type was represented once in each trawl and trap order was randomized both within and between trawls.

The fishermen provided with experimental gear recorded the number of legal and sublegal lobster per trap haul. Additional information on fishing location, depth, bottom type, and soak time (set over days) was also recorded. Periodic sampling trips were made by personnel of the Rhode Island Division of Fish and Wildlife, Marine Fisheries Section. While on board commercial lobster boats, we recorded the number of legal and sublegal lobster per trap haul; physical condition including molt status, appendage loss, and the presence of an external egg mass on females; and carapace length (measured from the posterodorsal edge of the eye socket to the posterior margin of the carapace).

RESULTS AND DISCUSSION

Catch Per Unit Effort

Catch per trap haul (CTH) and CTH weighted by immersion time (CTHSOD) were examined for the seven fishermen provided with unmodified control traps and traps equipped with rectangular (42 × 152 mm) escape vents. A total of 18,984 lobster were obtained in 7,002 trap hauls of the experimental gear. The overall catch of sublegal-sized lobster was reduced by 79% in vented traps. Dramatic reductions in the sublegal catch were evident for each individual fisherman with one exception (Table 1). The ratio of sublegal to legal lobster was 1.375:1 in vented gear and 2.746:1 in control traps, again indicating the efficiency of vented traps in releasing sublegal lobster (Table 1). The overall mean CTH for sublegal lobster was 1.299 and 2.330 in vented and control traps, respectively (Table 2). These results support the findings of Krouse and Thomas (1975), Krouse (1978), Pecci et al. (1978), and Fair and Estrella (see footnote 2) in establishing the effectiveness of employing vented gear.

TABLE 1.—Number of legal (≥78 mm CL), sublegal and percentage of legal American lobster; ratio of sublegal to legal lobster (S/L); and the number of trap hauls (TH) in vented and nonvented gear for individual fisherman. Numbers in parentheses are totals adjusted to retain equal sample sizes. Chi-square contingency table analyses (χ_1^2) tested the hypothesis that the catch of legal and sublegal lobster is independent of trap type.

	Vented					Control					
Fisherman	Legal	Sublegal	% legal	S/L	TH	Legal	Sublegal	% legal	S/L	TH	χ_1^2
A	404	1,069	27 42	2 646	528	377	1,526	19 81	4 047	528	26 66**
B	404(401)	743(740)	35 22	1 839	768	401	1,783	18 36	4 446	765	114 44**
C	366	397	47 96	1 084	368	343	789	30 30	2 300	368	60 01**
D	392	273	58 94	0 696	335	249	431	36 61	1 730	335	66 31**
E	253(251)	505(486)	33 36	1 996	209	247	494	33 33	2 000	204	0 05 ns
F	320	729	30 50	2 278	349	243	1,947	11 09	8 012	349	184 71**
G	1,174	838	58 34	0 713	948	1,107	1,180	48 40	1 065	948	42 11**
Total	3,313 (3,308)	4,554 (4,532)	42 11	1 375	3,505	2,967	8,150	26 68	2 746	3,497	498 433**

** = $P < 0.005$, ns = not significant

TABLE 2.—Catch per unit effort of American lobster in vented and nonvented traps for individual fishermen. CTH indicates catch per trap haul; CTHSOD indicates catch per trap haul/set over day; the subscripts L and S indicate the catch of legal (≥78 mm CL) and sublegal lobster, respectively. Data are expressed in numbers of lobster.

	Vented				Control			
Fisherman	C_LTH	C_LTHSOD	C_STH	C_STHSOD	C_LTH	C_LTHSOD	C_STH	C_STHSOD
A	0.765	0.155	2.024	0.410	0.714	0.144	2.890	0.585
B	526	160	967	.294	524	159	2.330	709
C	994	141	1.078	153	932	132	2.144	305
D	1.170	300	814	.209	.743	191	1.286	330
E	1.210	244	2.416	487	1.211	244	2.421	488
F	916	175	2.088	399	696	133	5.787	1.107
G	1.238	251	883	179	1.167	236	1.244	236
Total	0.945	230	1.299	317	0.848	207	2.330	569

Interestingly, vented traps tended to consistently catch more legal-sized lobster than control traps (Tables 1,2). The overall mean CTH for legal lobster was 0.945 in vented traps and 0.848 in nonvented gear (Table 2). We attributed the trend in lower legal catch in control traps to a saturation effect where the probability of a lobster entering a trap declines with increasing density within the trap. In nonvented traps, sublegal lobster occupy space which might otherwise be taken by legal-sized lobster. Direct evidence of catch density dependence of this type in a trap fishery has been demonstrated for two species of *Cancer* (Miller 1979).

The well-established aggressive behavior of lobster when held in confinement supports the concept of a saturation effect for this species. Lobster are characteristically solitary under natural conditions (Cobb 1971; O'Neill and Cobb 1979) and it is reasonable to assume that the presence of lobster within a trap deters further entries. Although relatively little is known of the trap-related behavior of this species, there is an apparent conflict between food (and/or shelter) seeking behavior and avoidance of conspecifics.

Krouse (1978) reported an increase in legal catch in vented traps, supporting conclusions derived in an earlier study conducted in Maine (Krouse and Thomas 1975). Templeman (1939) and Wilder (1945) had earlier demonstrated increased legal catch rates in traps with increased lath spacing.

In the present study, the impact of crowding on the legal catch was most pronounced in small mesh (2.5 cm × 2.5 cm) wire traps (Fisherman F). These traps retained extremely high numbers of sublegals. Vented traps not only retained fewer sublegal lobster, but caught substantially more legal-sized lobster (Tables 1, 2).

To further assess the effectiveness of the vented gear, we tested the hypothesis that the catch of legal and sublegal lobster was independent of trap type (vented vs. control). In two instances where loss of trap resulted in an unequal number of observations, catch totals were adjusted by deleting data from an adjacent trap to retain a balanced design. Lost traps were replaced as quickly as possible. These analyses confirmed that significant differences exist in the catch characteristics of vented and control traps for combined data ($\chi_1^2 = 498.433$; $P<0.005$) and for individual fishermen (Table 1) with a single exception.

Effect of Immersion Time

The importance of incorporating soak time in measures of CPUE has been emphasized in several trap fisheries including that for the American lobster (Thomas 1973; Skud[3]), the European lobster, *H. gammarus* (Bennett 1974), the spiny lobster, *Panulirus argus* (Austin 1977), and the western rock lobster, *P. longipes cygnus* (Morgan[4]).

The immersion (soak) time utilized by individual fishermen is most often a function of the total number of traps deployed and the daily hauling capacity of the boat, although weather conditions frequently interrupt hauling schedules. Each fisherman typically has three or more sets of gear which are hauled in rotation.

Catch data were pooled and examined for the effect of immersion time up to a maximum of 7 set over days. Soak times of >7 days were omitted due to excessive variability. The catch of legal lobster

[3]Skud, B. E. 1976. Soak time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). Int. Cons. Explor. Mer, Special meeting on population assessments of shellfish stocks, No. 8, 25 p.

[4]Morgan, G. R. 1976. Trap response and the measurement of effort in the fishery for the western rock lobster. Int. Cons. Explor. Mer, Special meeting on population assessments of shellfish stocks, Contrib. 16, 18 p.

per trap haul (C_LTH) tended to increase slightly with increasing soak time in both vented and control traps up to 6 days when a slight decline became evident (Figure 1).

A different pattern emerged for the catch of sublegal lobster per trap haul (C_STH) where we noted an initial increase in C_STH in nonvented traps followed by a general decline with increasing soak time. In vented traps, C_STH declined initially followed by a slight increase with time (Figure 1). The decline in C_STH in control traps with immersion times in excess of 2 days may be the result of escapement through the trap heads and mortality within the trap (Bennett 1974; Austin 1977). We attributed the immediate decline in C_STH in vented traps to escapement, indicating the effectiveness of the vents. It is unclear whether the increase in C_STH for the sixth set over day was due to sampling bias or some other factor. Bennett ascribed catch increases with long soak times to decay of the bait with an associated renewed release of chemical attractants.

The catch of legal and sublegal lobster was not proportional to immersion time. This may be due to the combined effects of declining local availability, trap saturation, escapement, and mortality (Bennett 1974; Austin 1977; Skud see footnote 3; Bennett and Brown[5]). Catch per trap haul/set over day (CTHSOD) declined with time in both vented and control traps (Figure 2). Similar observations of declining CTHSOD with increasing soak time have been noted in the Maine lobster fishery (Thomas 1973), the spiny lobster fishery (Austin 1977) and the European lobster fishery (Bennett 1974).

Our data indicated that CTH approached an asymptote with increasing soak time for both legal and sublegal lobster. Following the approach of Sinoda and Kobayasi (1969) and Munro (1974) this relationship may be modelled as:

$$C_n = C_\infty(1 - \exp(-Rs))$$

[5]Bennett, D.B., and C.G. Brown. 1976. The problems of pot immersion time in recording and analysing catch-effort data from a trap fishery. Int. Cons. Explor. Mer, Special meeting on population assessment of shellfish stocks, No. 6, 8 p.

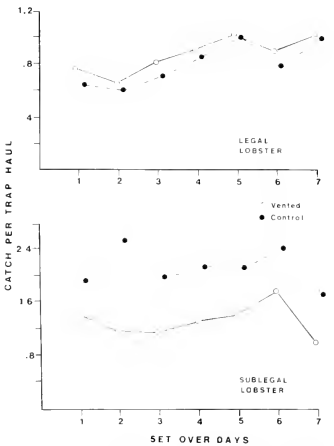


FIGURE 1.—Relationship between catch per trap haul of American lobster and trap immersion time in vented and control traps. Legal lobster are ≥78 mm CL.

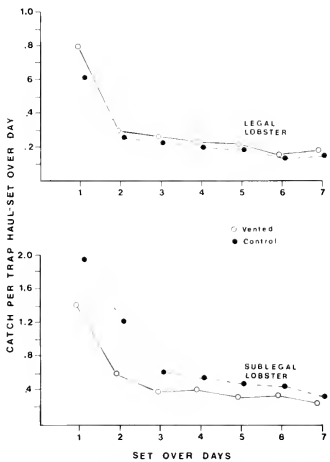


FIGURE 2.—The relationship between catch per trap haul/set over day of American lobster and trap immersion time in vented and control traps.

where C_s is the cumulative catch on day s, C_∞ is the asymptotic catch, and R is the net retention rate assuming constant availability. The term C_∞ is dependent on not only the physical holding capacity of the trap but on any behavioral interactions which serve to limit the catch. The asymptotic catch will be reached when ingress is balanced by escapement.

Parameters of the model were estimated by nonlinear least squares (Hartley 1961). The trend in greater legal catch in vented gear was reflected in the slightly higher estimate of C_∞ in vented traps (Table 3). The substantially lower asymptotic catch level for sublegal-sized lobster in vented gear clearly demonstrated the effectiveness of these traps. Munro (1974) stressed the importance of escapement in determining saturation levels in fish traps.

This model may also be used to standardize effort to a common soak time. Adapting the approach of Sinoda and Kobayasi (1969) and Caddy,[6] weighting coefficients are given by

$$\omega = \frac{1-\exp(-Rs)}{1-\exp(-Rs^*)}$$

where s^* is the standard soak time. The total effective effort (f_{tot}) is then the product of nominal effort (trap hauls) and the weighting coefficient (Caddy see footnote 6)

$$f_{tot} = \sum^{s^*} f_s \omega$$

and the standardized CPUE is given by the catch divided by f_{tot}. Adjustment for variable soak times should greatly improve the precision of catch effort data used in surplus yield modelling.

Size Selectivity

Carapace length (CL) measurements were obtained for a sample catch of 2,943 lobster retained in the experimental traps. The reduction in the sublegal catch retained in vented gear was most pronounced for lobster <75 mm CL (Figure 3). Size selection for lobster >75 mm CL was virtually identical in vented and control traps. The mean size of lobster caught in nonvented traps (75.20 mm) and vented gear (78.99 mm) were significantly different ($t = 12.856$; $P<0.01$).

Retention curves (Krouse and Thomas 1975) constructed for vented and control traps clearly reflect the differences in the retention characteristics for each trap type (Figure 4). The cumulative retention points for each curve at the Rhode Island minimum legal size at the time of this study (78 mm CL) were 56.0% and 69.5% for vented and control traps, respectively.

TABLE 3.—Coefficients and associated standard errors for the model $C_s = C_\infty[1-\exp(-Rs)]$ relating catch per trap haul and soak time in vented and control traps for legal-(≥78 mm CL) and sublegal-sized lobster.

Item	C_∞	R
Vented		
Legal	0 9745 ± 0 0715	0 9879 ± 0 3610
Sublegal	1 3847 ± 0 1596	0 8796 ± 0 6289
Control		
Legal	0 9222 ± 0 0811	0 7428 ± 0 2664
Sublegal	2 1642 ± 0 1127	2 5369 ± 1 7001

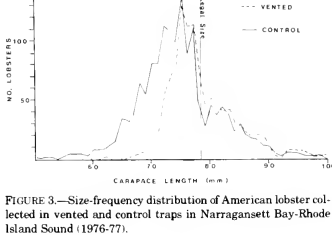


FIGURE 3.—Size-frequency distribution of American lobster collected in vented and control traps in Narragansett Bay-Rhode Island Sound (1976-77).

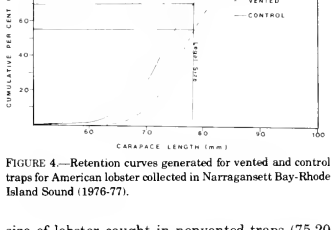


FIGURE 4.—Retention curves generated for vented and control traps for American lobster collected in Narragansett Bay-Rhode Island Sound (1976-77).

[6]Caddy, J. D. 1977. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. Int. Cons. Explor. Mer, Shellfish and Benthos Committee, C.M. 1977/K:18, 21 p.

We observed a general relationship between the mean size of lobster caught and fishing location. Comparisons of the mean size of lobster in sample catches (pooled by trap type) for six fishermen, for which adequate data were available, revealed a segregation by fishing location (Table 4). In general, lobster taken in Narragansett Bay and nearshore Rhode Island Sound samples were significantly smaller ($\alpha = 0.05$) than those taken in offshore Rhode Island Sound when compared using Duncan's multiple range procedure (Steel and Torrie 1960), although one offshore sample did not conform to this pattern. We attributed the smaller mean size in Narragansett Bay and nearshore Rhode Island Sound samples to intense fishing pressure in these easily accessible areas. Krouse (1973) noted a similar correspondence between fishing intensity and size composition of the catch. Areas within Narragansett and Rhode Island Sound with the smallest mean size of lobster also had the lowest CPUE (Table 4).

Characteristics of the habitat may also influence the size composition of the catch. Several authors have observed a correlation between the size of lobster and the size of available shelter sites (Scarratt 1968; Cobb 1971; Stewart 1972). Larger lobsters were found in areas with greater shelter size (Scarratt 1968; Cobb 1971) or in mud areas with a high clay fraction capable of supporting larger burrows (Stewart 1972). Inshore rocky habitats are characterized by ledge and mixed rocky debris which offer smaller shelter sites than offshore mud and rock substrates.

TABLE 4.—Results of Duncan's multiple range procedure comparing mean carapace length (rank ordered) of American lobster from offshore Rhode Island Sound (R.I.S.), nearshore Rhode Island Sound (R.I.S.N.) and Narragansett Bay (N.B.). Means with the same letter code are not significantly different ($\alpha = 0.05$).

Fisherman	N	Mean (SD)	Grouping	Location
C	149	78 382 (8 06)	A	R I S
G	801	78 052 (7 14)	A	R I S
E	107	75 738 (5 76)	B	R I S
F	958	75 603 (6 44)	B	N B
A	71	74 845 (5 41)	B C	R I S N
B	431	73 635 (5 31)	C	N B

Sex Ratios

Comparisons of sex ratios in vented and control traps revealed interesting differences. We noted a female:male ratio of 1.68:1 in nonvented traps and 2.15:1 in vented gear. Contingency table analyses indicated that the sex composition of the catch differed significantly in vented and control traps ($\chi_1^2 = 7.70$; $P < 0.01$). These data suggest differential escapement by males and females. To further assess this possibility, we investigated the relationship between carapace length and carapace width for 437 male and 603 female lobster. Analyses of covariance (Steel and Torrie 1960) indicated that the regression coefficients were significantly different ($F_{1,1036} = 6.74$; $\alpha = 0.01$). The least squares regression equations were

$$CW_m = -0.8901 + 0.6186\ CL_m\ (r = 0.869) \text{ for males and}$$

$$CW_f = -4.3932 + 0.6755\ CL_f\ (r = 0.886) \text{ for females.}$$

In passing through a rectangular vent, the critical body dimension is the carapace width (the minimum body measure). The relatively broader carapace width for females of a given carapace length may result in the retention of proportionately more females, accounting for the observed discrepancy in sex ratios in the experimental gear. It should be noted that Krouse and Thomas (1975) found no significant differences in the carapace width-length relationship for 114 female and 103 male lobster.

Vent Size, Orientation, and Lath Spacing

We examined the effect of vent orientation (horizontal vs. vertical) and lath spacing on escapement. The effectiveness of larger vents (44.5 mm × 152 mm) in retaining legal lobster was also tested. Vent orientation may affect either the probability of a lobster locating the vent or the time required to find the vent, a factor of importance with short immersion times. There may also be differences in size selectivity associated with vent orientation. Analysis of preliminary size composition data indicated that 42 mm vents may in fact be too small for a minimum legal size of 78 mm. Accordingly, we tested 44.5 mm × 152 mm vents in an attempt to determine if legal-sized lobster could escape with the use of this larger vent size. We also evaluated the effectiveness of opening lath spacing to 42 mm and 44.5 mm in comparisons with vents of equivalent size.

A total of 4,487 lobster were obtained in 2,222 trap hauls of the experimental gear. As might be expected, traps with 44.5 mm openings (vented and lath spaced traps) retained markedly fewer sublegal lobster than either traps with 42 mm

openings or control traps (Table 5). The sublegal catch was substantially reduced in comparisons of traps with 42 mm escapement openings and control traps (Table 5). Contingency table analyses indicated that the catch characteristics of each vented trap type were significantly different from control traps (Table 5). Traps with horizontal vents (both size classes) tended to catch fewer legal-sized lobster than control traps (Table 5). We were unable to offer a direct explanation for this observation since, based on morphometric studies and laboratory observations, escapement of lobster ≥78 mm CL through 42 mm vents would be impossible and escapement of legal-sized lobster through 44.5 mm vents would be minimal. The effect of vent orientation on the sublegal catch was negligible. Krouse (1978) found no significant differences in the catch characteristics of traps equipped with horizontal and vertical vents.

Traps with increased lath spacing tended to retain more sublegals than traps equipped with equivalent-sized vents (Table 5) suggesting that synthetic vents were more efficient escapement devices. In this experiment the opened lath spacing was oriented vertically in the end panel of the parlor section of the trap. Although the vent width determines the selection characteristics of the trap, the length and orientation of the vent (or lath spacing) may directly affect the probability of locating the opening. Vertically positioned escape openings offer a target equal to the width of the opening, a relatively small area while horizontally positioned vents proffer a much larger target. Laboratory observations indicated that escapement openings were located by an apparently random search process, suggesting that larger target areas will be located more quickly and efficiently.

The catch of legal-sized lobster tended to increase slightly or remain constant with increasing soak time for each trap type with the exception of control traps, which demonstrated a decline as immersion time increased (Figures 5, 6). The catch of sublegal lobster remained consistently low with increasing soak time in traps with 44.5 mm escapement openings while that for traps with 42 mm openings exhibited considerable variability (Figures 5, 6).

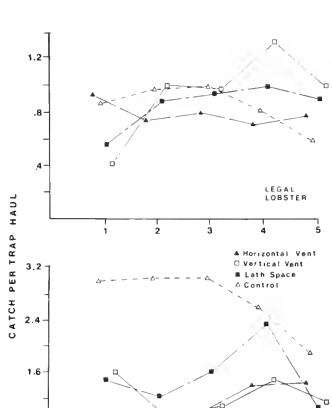


FIGURE 5.—Relationship between catch per trap haul of American lobster and trap immersion time in 42 mm vertical vented, 42 mm horizontal vented, 42 mm lath spaced, and control traps.

TABLE 5.—Number of legal (≥78 mm CL), sublegal, and percentage of legal American lobster; and ratio of sublegal to legal lobsters (S/L) and catch per unit effort in experimental traps. CTH and CTHSOD denote catch per trap haul and catch per trap haul/set over day, respectively. The subscripts L and S indicate the catch of legal and sublegal lobster. The abbreviations V, H, and L refer to vertical and horizontal vent orientation and lath spacing. Numbers in parentheses are totals adjusted to retain equal sample sizes. Chi-square contingency table analyses compared the catch characteristics of control traps with each individual trap type.

Vent type	Legal	Sublegal	% Legal	S/L	TH	C_LTH	C_LTHSOD	C_STH	C_STHSOD	χ_1^2
Control	296(292)	913(904)	24 48	3 084	316	0 936	0 436	2 889	1 068	
V 42 mm	318(315)	369(360)	46 28	1 160	318	1 000	0.369	1 160	429	96 44**
H 42 mm	245(243)	357(352)	40 69	1 457	319	768	0 284	1 119	414	50 39**
L 42 mm	282(278)	454(442)	38 31	1 609	318	886	0 328	1 427	528	42 66**
V 44 5 mm	288(284)	136(132)	67 92	472	318	905	0 335	427	158	256 58**
H 44 5 mm	265(265)	112(111)	70 29	422	318	833	0 307	352	130	263 31**
L 44 5 mm	299	153	66 15	511	313	955	0 353	488	180	246 60**

**P< 0 005

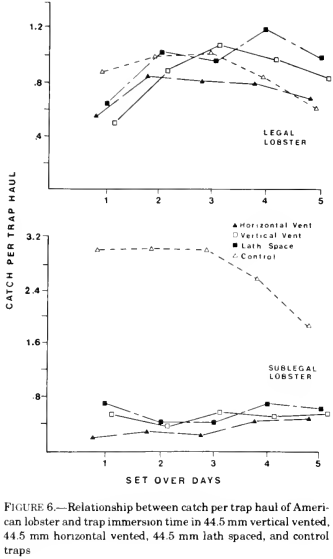


FIGURE 6.—Relationship between catch per trap haul of American lobster and trap immersion time in 44.5 mm vertical vented, 44.5 mm horizontal vented, 44.5 mm lath spaced, and control traps

CONCLUSIONS

The beneficial effects of incorporating escape vents in standard lobster traps are well established (Krouse and Thomas 1975; Krouse 1978; Pecci et al. 1978). A reduction in lobster injury and mortality and a reduction in onboard sorting time are among the benefits accrued through the use of escapement devices (Krouse and Thomas 1975; Pecci et al. 1978). Lobster damage is related to the effects of fishing activity both directly as a result of handling (Scarratt 1973; Krouse 1976) and indirectly as a result of aggressive encounters in the trap (Pecci et al. 1978). Although interspecific aggression levels are relatively low under natural conditions (Cooper and Uzmann 1977), the artificially close confines of a trap may increase the probability of aggressive behavior.

The results of the present study confirm the utility of employing escapement devices in lobster traps. We noted substantial reductions in the catch of sublegal-sized lobster, reducing the probability of injury and mortality. Vented traps tended to consistently capture more legal-sized lobster than control traps. We attributed this increase to an inverse relationship betweeen density in the trap and the probability of new entries.

This apparent increase in relative gear efficiency may have a significant impact on catch rates if widely applied and should be closely monitored. Given the critically high levels of fishing mortality for lobster in virtually all sectors, this increase in trap fishing power is presently inadvisable. The use of 100% retention of legal-sized lobster as the primary criterion for the establishment of escape vent dimensions should therefore be modified to allow for some minimal escapement of legal lobster and to maximize escapement of sublegal lobster.

ACKNOWLEDGMENTS

This research was made possible by a grant through the Southern New England Fisheries Development Program, NOAA, under grant 03-6-043-35132. We express our appreciation to the fishermen who contributed to the successful completion of this study. We also wish to thank Barbara Simon for computer programming and data management and Linda Gray for typing the manuscript. J. Stanley Cobb, John Cronan, and John Stolgitis reviewed the manuscript and offered helpful suggestions.

LITERATURE CITED

AUSTIN, C. B.
1977. Incorporating soak time into measurement of fishing effort in trap fisheries. Fish. Bull., U.S. 75:213-218.

BENNETT, D. B.
1974. The effects of pot immersion time on catches of crabs, *Cancer pagurus* L. and lobsters, *Homarus gammarus* (L.). J. Cons. 35:332-336.

COBB, J. S.
1971. The shelter-related behavior of the lobster, *Homarus americanus*. Ecology 52:108-115.

COOPER, R. A., AND J. R. UZMANN.
1977. Ecology of juvenile and adult clawed lobsters, *Homarus americanus*, *Homarus gammarus*, and *Nephrops norvegicus*. *In* B. F. Phillips and J. S. Cobb (editors), Workshop on lobster and rock lobster ecology and physiology, p. 187-208. Aust. Div. Fish. Oceanogr., Circ. 7.

HARTLEY, H. O.
1961. The modified Gauss-Newton method for the fitting of non-linear regression functions by least squares. Technometrics 3:269-280.

KROUSE, J. S.
1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. Fish. Bull., U.S. 71:165-173.
1976. Incidence of cull lobsters, *Hamarus americanus*, in commercial and research catches off the Maine coast. Fish. Bull., U.S. 74:719-724.
1978. Effectiveness of escape vent shape in traps for catching legal-sized lobster, *Homarus americanus*, and harvestable-sized crabs, *Cancer borealis* and *Cancer irroratus*. Fish. Bull., U.S. 76:425-432.

KROUSE, J. S., AND J. C. THOMAS.
1975. Effects of trap selectivity and some population parameters on size composition of the American lobster, *Homarus americanus*, catch along the Maine coast. Fish. Bull.. U.S. 73:862-871.

MILLER, R. J.
In press. Saturation of crab traps: Reduced entry and escapement. J. Cons.

MUNRO, J. L.
1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. J. Cons. 35:337-350.

NULK, V. E.
1978. The effects of different escape vents on the selectivity of lobster traps. Mar. Fish. Rev. 40(5-6):50-58.

O'NEILL, D. J., AND J. S. COBB.
1979. Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). Mar. Behav. Physiol. 6:33-46.

PECCI, K. J., R. A. COOPER, C. D. NEWELL, R. A. CLIFFORD, AND R. J. SMOLOWITZ
1978. Ghost fishing of vented and unvented lobster, *Homarus americanus*, traps. Mar. Fish. Rev. 40(5-6):9-43.

SCARRATT, D. J.
1968. An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 25:2683-2690.
1973. Claw loss and other wounds in commercially caught lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 30:1370-1373.

SINODA, M., AND T. KOBAYASI.
1969. Studies on the fishery of Zuwai crab in the Japan Sea — VI. Efficiency of the Toyama Kago (a kind of crab trap) in capturing the Beni-zuwai crab. Bull. Jpn. Soc. Sci. Fish. 35:948-956.

STASKO, A. B.
1975. Modified lobster traps for catching crabs and keeping lobsters out. J. Fish. Res. Board Can. 32:2515-2520.

STEEL, R. G., AND J. H. TORRIE.
1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

STEWART, L. L.
1972. The seasonal movements, population dynamics and ecology of the lobsters, *Homarus americanus* (Milne-Edwards), off Ram Island, Connecticut. Ph.D. Thesis Univ. Connecticut, Storrs, 112 p.

TEMPLEMAN, W.
1939. Investigations into the life history of the lobster (*Homarus americanus*) on the west coast of Newfoundland, 1938. Newfoundland Dep. Nat. Resour., Res. Bull. (Fish) 7, 52 p.

THOMAS, J. C.
1973. An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-667, 57 p.

WILDER, D. G.
1945. Wider lath spaces protect short lobsters. Fish Res. Board Can., Atl. Biol. Stn. Circ. G-4, 1 p.

ACOUSTIC MEASUREMENTS OF A MIGRATING LAYER OF THE MEXICAN LAMPFISH, *TRIPHOTURUS MEXICANUS*, AT 102 KILOHERTZ

R. E. PIEPER AND B. G. BARGO[1]

ABSTRACT

Biological sampling in a migrating scattering layer recorded at 102 kilohertz resulted in collections which consisted primarily of juvenile *Triphoturus mexicanus*. The scattering from this layer was quantified. Volume scattering strengths and corresponding target strengths were determined. The rate of migration and the target strength of *T. mexicanus* changed as the layer approached the surface. Target strengths at 102 kilohertz ranged from −60.6 decibels at 284 m to −71.3 decibels at 206 m.

Initial investigations of the deep scattering layer (DSL) emphasized military and hydrographic applications and used relatively low-frequency echo sounders (20-80 kHz). Later, research was directed at the biological organisms responsible for sound scattering in the DSL but was still confined largely to low-frequency studies. Fishes and physonectid siphonophores have been identified as the major scatterers in this frequency range (Barham 1963). In addition to determining the sources of scattering, oceanographers, fishery biologists, and commercial fishermen have been using acoustics to locate and quantify fish schools and shoals. Quantitative studies require the measurement of volume scattering strengths from the water column and knowing (or measuring) the ability of the fishes to scatter sound (acoustic cross section or target strength). Recent compilations of work in these areas can be found in Farquhar (1970) and Andersen and Zahuranec (1977).

The development of high-frequency echo sounders (>50 kHz) during the past 10 yr has progressed to the point where research at frequencies up to 3.0 MHz is now practical (Holliday and Pieper[2]). Working with high frequencies has several advantages over low frequencies. As the frequency is increased, shorter pulses can be used and the resolution is increased. In addition, smaller organisms become better sound scatterers as the frequency is increased. At 102 kHz, for example, shoals of euphausiid shrimp can be detected and quantified at ranges up to 300 m (Bary and Pieper 1970; Pieper 1979).

The present paper reports on two migrating scattering layers recorded only at 12 kHz and a deeper, third layer recorded at both 12 kHz and 102 kHz. Large numbers of a single size class of juvenile Mexican lampfish, *Triphoturus mexicanus* (Gilbert 1890), were collected from the deepest scattering layer. Volume scattering strengths of this layer were measured at 102 kHz and corresponding target strengths of *T. mexicanus* were calculated. Although no directed sampling was completed in the two, shallower, 12 kHz scattering layers, the possible scatterers responsible for these layers are indicated. We discuss the advantage of using acoustic frequencies above swim bladder resonance for biomass studies and recommend the increased usage of high-frequency acoustics for biological studies in the sea.

METHODS

Three 12 kHz scattering layers were observed migrating towards the surface near sunset on an acoustic survey at the northwest end of the San Clemente basin off southern California on 25 and 26 January 1977. The deepest of these 12 kHz layers was recorded as a strong scattering layer on a 102 kHz echo sounder being used to study euphausiid distributions (Pieper 1979). Quantitative acoustic measurements at 102 kHz and biological sampling were completed in this scattering layer on 26 January. Salinity and temperature profiles were taken immediately after the tow

[1]Institute for Marine and Coastal Studies, University of Southern California, Los Angeles, CA 90007.

[2]Holliday, D. V., and R. E. Pieper. 1978. Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. Program of the 96th Meeting of the Acoustical Society of America, Honolulu, Hawaii, 25 p.

Manuscript accepted May 1979
FISHERY BULLETIN: VOL. 77, NO. 4, 1980

with a submersible salinity, temperature, and depth (STD) recorder.

Acoustic Measurements

A Ross Laboratories[3] 102 kHz echo sounder with its transducer housed in an Endeco V-fin was used in conjunction with a 12 kHz hull mounted Edo transducer triggered by an Edo model 444 transceiver and model 551 recorder. Information from the 12 kHz sounder was recorded only as qualitative echograms. Acoustic data from the 102 kHz echo sounder was recorded qualitatively as echograms, and quantitatively over specific 20 m (26.87 ms) intervals where the scattering was observed. The returned signal for this interval was electronically squared and integrated for each pulse, and the value displayed on a chart recorder. The average scattering level (RL) over this 20 m interval was then calculated and the volume scattering strength (S_v) was determined by the following (Urick 1975):

$$S_v\,(\mathrm{dB/m^3}) = RL - SL + 40\log r + 2\alpha r - 10\log V$$

where RL = average received (scattering) level
SL = source level
r = mean range of the 20 m interval
α = absoprtion loss per m^3
V = volume insonified = $(c\tau/2)(\Psi r^2)$
where c = speed of sound
τ = pulse length
Ψ = solid angle of the ideal two-way beam pattern.

Volume scattering strengths were determined at various times (and depths) as the layer migrated toward the surface.

Biological Sampling

Biological samples were collected with a 6-ft modified Tucker trawl with an acoustically controlled opening-closing sequence and a continuous depth readout on a Gifft recorder. While sampling in the migrating scattering layer, the net depth was regulated to keep pace with the movement of the layer. The samples were preserved in 10% buffered Formalin in the field and transferred to 70% ethanol in the laboratory. All fishes were identified to species and their standard length measured.

The density of fishes collected was calculated by dividing the number of animals caught by the product of ship speed (meters per minute) times the length of the tow (minutes) times the mouth area (square meters). The mouth area of the net has been calculated to be 2.36 m^2 assuming a 45° fishing angle (Davies and Barham 1969).

Swim bladders were measured from 12 *T. mexicanus* which represented the range of sizes of this species collected by the trawl in the 102 kHz scattering layer (trawl 25660[4]). Swim bladder measurements were also taken from four *Protomyctophum crockeri*, five *Argyropelecus sladeni*, and five *Vinciguerria lucetia* collected from two earlier trawls (trawls 25657 and 25658). The volume of the swim bladder was calculated by using the formula for a prolate spheroid (Capen[5]).

Calculations

The density of fishes was then used to calculate their average target strength (TS) by applying the formula:

$$TS = S_v\,(\text{fishes}) - 10\log(\text{fishes m}^{-3})$$

where S_v (fishes) = $10\log[\log^{-1} 0.1\,S_v\,(\text{total}) - \log^{-1} 0.1\,S_v\,(\text{plankton})]$.

The S_v value for plankton was calculated from an average of the two integration values recorded after the fish scattering layer had migrated out of the integration window.

The depth where the swim bladder would resonate at 12 kHz was calculated for the range of swim bladder sizes observed assuming constant swim bladder volume with depth. These calculations were determined by solving for z (depth) in the following simplified formula for resonance of an air bubble in water (Clay and Medwin 1977; equation 6.3.10):

$$f_{FR} = (3.25 \times 10^6/a)(1 + 0.1z)^{1/2}$$

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]All trawl numbers mentioned refer to ship's station numbers (*VeleroIV*, University of Southern California).

[5]Capen, R. L. 1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electronics Laboratory, San Diego, Calif., Rep. 1447, 25 p.

where f_{FR} = resonant frequency (Hz)
a = equivalent spherical radius (μm)
z = depth (m).

In the above formula, f_{FR} is 12 kHz. The a is the radius of a sphere equal in volume to that of the swim bladder at the surface.

RESULTS

The deepest of the three 12 kHz scattering layers (Figure 1) was also recorded at 102 kHz (Figure 2). The calculated volume scattering strengths at 102 kHz and at different times and depths are also shown in Figure 2. The biological sample from this layer was composed almost exclusively of juvenile *T. mexicanus* (Table 1). The movement of the scattering layer with time showed an increasing rate of migration up to a depth of around 180 m which corresponded to a change in the temperature-salinity characteristics of the water (Figure 3).

Calculated target strengths for *T. mexicanus* (Table 2) were highest at the deepest depth (−60.6 dB at 284 m) and slowly decreased as the layer migrated upwards (−71.3 dB at 206 m). The decrease in calculated target strengths corresponded to the increased migratory rate of the layer (Fig-

TABLE 1.—Biological collection from trawl 25660 taken in the 102 kHz scattering layer of San Clemente basin, southern California, 26 January 1977, 1731-1744 h.

Taxon	Total number caught	Number per 1,000 m³	Mean standard length (mm)	SE
Triphoturus mexicanus	263	114 0	24 5	0 2
Stenobrachius leucopsarus	3	1 3	24 7	1 4
Lampanyctus ritteri	1	0 4	68 5	
Argyropelecus sladeni	2	0 9	10 5	3 0
Sergestids	9	3 9	28 7	2 9
Euphausiids	105	45 0	17 4	0 7

TABLE 2.—Volume scattering strengths (S_v) for the 102 kHz scattering layer and calculated target strengths (TS) for *Triphoturus mexicanus*. Data from San Clemente basin, southern California, 26 January 1977.

Time (PST)	Type of scattering	Depth (m)	S_V (dB/m³)	Fish S_V (dB/m³)	Fish TS (dB)
1719 0	Plankton	257	−76 86	—	—
1735 0	Plankton	244	−77 31	—	—
	Average plankton	—	−77 08	—	—
1716 0	Plankton and fish	284	−69 13	−70 02	−60 6
1726 0	Plankton and fish	257	−71 13	−72 40	−63 0
1726 5	Plankton and fish	257	−71 13	−72 40	−63 0
1730 5	Plankton and fish	244	−72 83	−74 88	−65 4
1731 0	Plankton and fish	244	−73 05	−75 24	−65 8
1736 0	Plankton and fish	226	−74 48	−77 94	−68 5
1736 5	Plankton and fish	226	−74 18	−77 30	−67 9
1740 5	Plankton and fish	206	−75 23	−79 83	−70 4
1741 0	Plankton and fish	206	−75 53	−80 76	−71 3

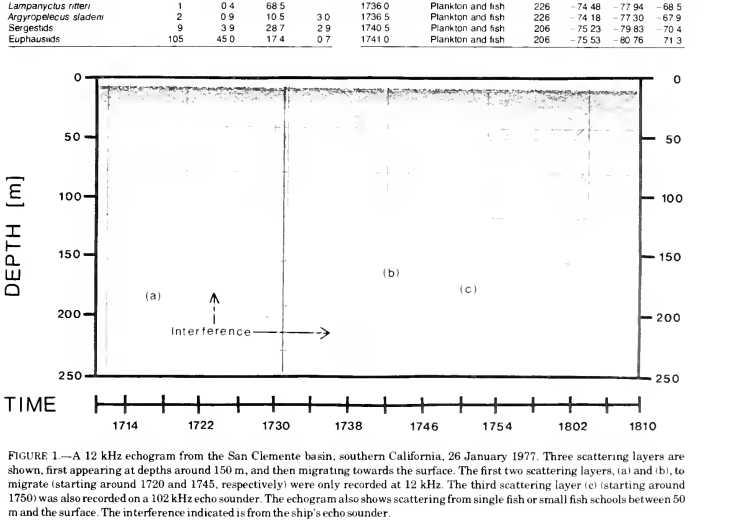


FIGURE 1.—A 12 kHz echogram from the San Clemente basin, southern California, 26 January 1977. Three scattering layers are shown, first appearing at depths around 150 m, and then migrating towards the surface. The first two scattering layers, (a) and (b), to migrate (starting around 1720 and 1745, respectively) were only recorded at 12 kHz. The third scattering layer (c) (starting around 1750) was also recorded on a 102 kHz echo sounder. The echogram also shows scattering from single fish or small fish schools between 50 m and the surface. The interference indicated is from the ship's echo sounder.

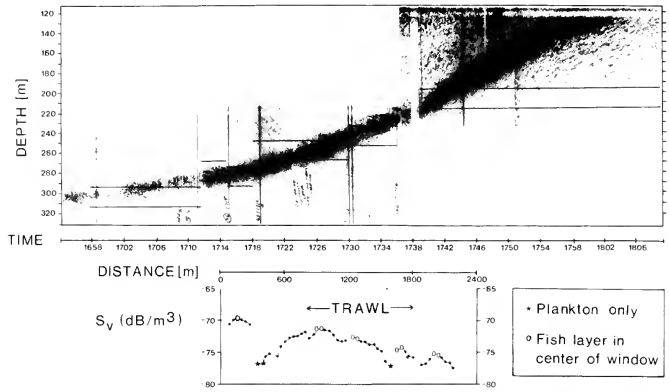


FIGURE 2.—A qualitative 102 kHz echogram showing a migrating scattering layer in San Clemente basin, southern California, 26 January 1977, and calculated volume scattering strengths (S_v) at 102 kHz for selected 20 m depth intervals (horizontal solid lines on echogram). The volume scattering strengths are shown when the scattering layer is in the center of the integration window (open circle), partially in the window (solid circle), and absent from the window (asterisk). The towing period for trawl 25660 is shown.

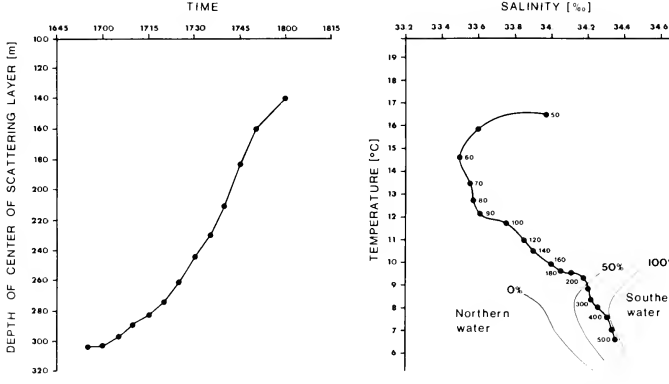


FIGURE 3.—Left: Depth of the center of the 102 kHz scattering layer plotted against time. Right: The temperature-salinity diagram for the water column immediately after trawl 25660.

ure 4). Measurements were not taken <206 m due to increased interference from surface scattering.

The organisms which were responsible for producing the two, shallower, 12 kHz scattering layers are not known since no trawls were taken from the depths of these two layers. Before the migratory period, however, two trawls were completed from depths which might correspond to the distributions of the scattering organisms. Trawls 25657 (1350-1432 h; 292-302 m) and 25658 (1514-1547 h; 267-268 m) were completed before the scattering layers became evident on either echo sounder. They were also from shallower depths than the first appearance of the 102 kHz scattering layer (1638; 315-325 m). Data from these trawls consisted of small numbers of *Argyropelecus sladeni*, *Cyclothone signata*, *Protomyctophum crockeri*, and *Vinciguerria lucetia* (Table 3). Of these four species, only *C. signata* is known not to be a vertical migrator (Rainwater 1975; Pearcy et al. 1977). Swim bladder resonance calculations for the other three species are shown in Table 4.

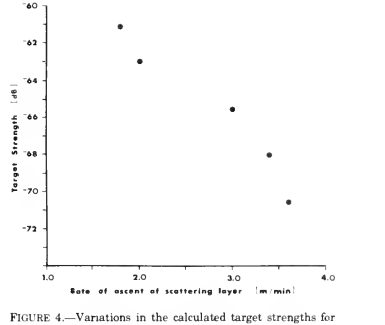


FIGURE 4.—Variations in the calculated target strengths for *Tripholurus mexicanus* at 102 kHz as a function of the rate of ascent of the 102 kHz scattering layer.

DISCUSSION

Lanternfishes (Family Myctophidae) have been implicated as the most important scatterers of scattering layers recorded at frequencies around 12 kHz, especially since many of these fishes have air-filled swim bladders of such a size as to be resonant from 1 to 30 kHz (Hersey and Backus 1962). *Triphoturus mexicanus* is a known vertical migrator off southern California (Paxton 1967) and its distribution has been previously correlated with scattering layers which showed diel migrations. Barham (1966) noted that adult *T. mexicanus* were associated with a 12 kHz scattering layer in the California Current, and Holton (1969) correlated collections of 8-10 cm long *T. mexicanus* with a strong scattering layer in the Gulf of California.

This paper reports on a scattering layer recorded at both 12 kHz (Figure 1) and 102 kHz (Figure 2). *Triphoturus mexicanus* dominated the net collection from this scattering layer (Table 1). Kleckner and Gibbs[6] suggested that lanternfishes probably regulate the gas in their swim bladders during migration to maintain constant gas volume. Assuming that calculations of swim bladder resonance can be approximated by using equations based on a free bubble in water (Hawkins 1977; Love 1978), these fish would show 12 kHz resonance only between 28 and 43 m (Table 4). In addition, a frequency of 102 kHz is too high for possible resonance effects. We suggest that the deepest 12 kHz layer and the 102 kHz layer were due to a large number of *T. mexicanus* rather than a few fishes scattering the sound at resonant frequencies.

Volume scattering strengths (Figure 2, Table 2) and target strengths (Table 2) were calculated at 102 kHz for *T. mexicanus*. Target strength values decreased as the layer migrated upwards from a

[6]Kleckner, R. C., and R. H. Gibbs, Jr. 1972. Swimbladder structure of Mediterranean midwater fishes and a method of comparing swimbladder data with acoustic profiles. Mediterranean Biological Studies Final Report to the U.S. Office of Naval Research 1(4):230-281.

TABLE 3.—Fishes collected from trawls 25657 and 25658, San Clemente basin, southern California, 26 January 1977.

Species	Trawl 25657, 1350-1432 h, 292-302 m			Trawl 25658, 1514-1547 h, 267-268 m		
	Total number caught	Number per 1,000 m³	Mean standard length (mm)	Total number caught	Number per 1,000 m³	Mean standard length (mm)
Argyropelecus sladeni	4	0.4	11.2	12	16.0	12.6
Cyclothone signata	10	0.9	16.6	5	6.5	16.5
Protomyctophum crockeri	5	0.5	22.9	1	1.3	12.5
Vinciguerria lucetia	3	0.3	24.0	4	5.2	23.2

TABLE 4.—Swim bladder size and calculated depths for 12 kHz resonance, assuming regulation of swim bladder volume for the specimens of *Triphoturus mexicanus*, *Protomyctophum crockeri*, *Argyropelecus sladeni*, and *Vinciguerria lucetia* in our collections.

Species	Standard length (mm)	Swim bladder				Depth[1] (m)
		Major axis (mm)	Minor axis (mm)	Volume (mm^3)	Equivalent spherical radius (μm)	
T. mexicanus	19	1 92	1 00	1 01	622	43
trawl 25660	21	1 83	92	81	578	36
	22	2 08	1 00	96	612	41
	23	2 09	95	99	618	42
	24	1 77	95	84	585	37
	25	1 96	89	81	578	36
	26	2 03	82	71	553	32
	27	1 65	89	68	546	31
	27	1 58	83	57	514	26
	29	2 08	75	61	526	28
	33	2 08	67	49	⅔ fat invested	—
	39	1 50	67	35	Completely fat invested	—
P. crockeri	14	1 60	1 12	1 01	622	43
trawl 25657	22	1 92	1 28	1 68	738	64
	26	2 24	1 28	1 95	775	72
	29	2 24	1 44	2 25	813	80
A. sladeni	11	1 12	64	24	385	10
trawl 25658	14	1 28	80	43	468	20
	15	1 28	80	43	468	20
	24	2 40	1 44	2 60	853	89
	29	3 36	1 92	5 83	1,117	160
V. lucetia	21	3 16	85	1 20	659	49
trawl 25657	22	3 54	92	1 56	719	60
and 25658	24	3 80	89	1 58	723	61
	26	3 86	1 14	2 63	856	90
	27	5 38	1 58	7 03	1,188	182

[1]Where swim bladder would resonate at 12 kHz, assuming constant volume at all depths

high value of −60.6 dB at 284 m to a low value of −71.3 dB at 206 m.

The change in calculated target strength with depth could be due to two factors: either the density of fishes per cubic meter decreased with time or the target strength decreased due to the changing orientation of the migrating fishes. The second explanation is more likely for two reasons. First, the thickness of the scattering layer appears to be constant over the period where target strengths were calculated (1716-1741 h, Figure 2). Second, the increase in the migratory rate of the layer over time (Figures 2, 3) implies a more rapid, upward swimming of the fishes. This would result in a more vertical orientation of the fish in the water column.

The calculated target strengths for the juvenile *T. mexicanus* at 102 kHz (Table 2, Figure 4) can only be compared with theoretical values since no measured values could be found in the literature. Love (1977) presented formulas for predicting the target strength of an individual fish at any aspect as a function of fish size and insonifying frequency. His equations are valid for the range $1 \leq L/\lambda \leq 100$ where L is the fish length and λ is the acoustic wavelength. Our data on *T. mexicanus* for a mean standard length of 24.5 mm (Table 1) and at a frequency of 102 kHz would show a L/λ ratio of 1.7. Using his formulas on our data, calculated target strengths for dorsal aspect vary from −55.6 dB to −56.6 dB and for anterior aspect from −67.1 dB to −67.7 dB. Thus, the target strength would be decreased by 10 to 12 dB as the orientation of the fish changed from dorsal aspect to anterior aspect. The change in target strength values from our data (10.7 dB) indicates that such a change in the orientation of the fish might have occurred.

The absolute values of our calculated target strengths are about 4.5 dB less than the predicted values. Since the data used by Love (1977) to determine his equations did not include myctophids, it is possible that juvenile *T. mexicanus* (and lanternfishes in general) may be poorer scatterers than the larger, nearshore, and surface fishes used for his study.

The migratory pattern shown for this layer is not unique to this study. The increased migratory rate of scattering layers during the middle of the sunset migration has been shown by a number of authors (e.g., Kampa and Boden 1954). Kampa and Boden (1954) also correlated this type of migratory pattern to a similar pattern in the isolume at the scattering layer depths. The interrelationship between isolumes, scattering layer migrations, and vertical water mass structure is not well understood. Thus, the observed change in mi-

gratory rate with change in water type around 180 m (Figure 3) may or may not reflect the reason for the observed migratory pattern.

The scatterers responsible for the two, shallower, 12 kHz scattering layers cannot be specifically determined in the present study. Of the fishes collected from two previous tows (Table 3) only *Cyclothone signata* is known not to migrate into surface waters (Pearcy et al. 1977). Since *Vinciguerria lucetia* has been collected at the surface at night, it is probably a vertical migrator (Grey 1964). The information on the vertical distribution and migration for *Argyropelecus sladeni* and *Protomyctophum crockeri* indicates that vertical migration is unlikely, but the data on these two species are sparse and incomplete. *Argyropelecus sladeni* has been collected both day and night at depths from 0 to 2,000 m (Baird 1971; Rainwater 1975; Pearcy et al. 1977), although the center of their distribution appears to be from 100 to 500 m. The information on *P. crockeri* shows similar broad distributions (Paxton 1967; Rainwater 1975; Pearcy et al. 1977), although Paxton stated that they only reach depths of 150 m at night and Wisner[7] stated that they are not caught above 100 m at night.

Since the two, shallower, 12 kHz scattering layers were not recorded on the 102 kHz echo sounder, it is likely that swim bladder resonance at 12 kHz from a small number of organisms was responsible for the scattering. Based on swim bladder measurements made at the surface and assuming regulation of swim bladder volume to maintain constant volume during migration, the depths where 12 kHz resonance would occur were calculated (Table 4) for the range of sizes of the fishes collected. These calculations indicate that *A. sladeni* and *V. lucetia* would show 12 kHz resonance at depths from 10 to 160 m and 49 to 182 m, respectively. Thus, we suggest that one or both fishes could be responsible for the shallower, 12 kHz scattering layers. The depth range for 12 kHz resonance for *P. crockeri* (43-80 m) indicates that it was probably not the source of either of the scattering layers. In addition, both shallow layers reached a depth of 40-50 m during the migration and *P. crockeri* has not been collected at depths <100 m at night (Paxton 1967; Wisner see footnote 7). It is also possible, however, that the shallower layers resulted from an organism or organisms not collected by the two net tows discussed.

The potential use of high-frequency acoustics for studying the distribution, behavior, and abundance of scattering organisms is strongly indicated. Echo sounders operated at frequencies above 30 kHz are working at frequencies above swim bladder resonance and therefore, reflect the biomass of scatterers more accurately. In addition, they generally have narrow beam angles and utilize short pulse lengths (3.5° beam angle and 1.0 ms pulse length in this study) which produce finer resolution in the scattering patterns. Calibrated, multifrequency acoustic systems used in conjunction with sophisticated net systems are needed to better define distributional patterns and interactions of these midwater organisms.

SUMMARY AND CONCLUSIONS

Triphoturus mexicanus is known to migrate vertically in the water column (Paxton 1967). We have shown that juvenile *T. mexicanus* were the major sound scatterers in a migrating scattering layer recorded at both 102 kHz and 12 kHz. Calculated target strengths for *T. mexicanus* at 102 kHz varied from −60.6 dB at 284 m to −71.3 dB at 206 m. This decrease in target strength with depth was probably due to a change in the orientation of the fish in the water column. The lowest target strength (−71.3 dB) occurred when the scattering layer was migrating towards the surface at its highest rate and, therefore, the fishes should be oriented more vertically in the water column.

Two, shallower, scattering layers were recorded at 12 kHz but not 102 kHz. We suggest that these two layers probably resulted from scattering which occurred from fishes with swim bladders which 1) resonated at 12 kHz and 2) were regulated to maintain constant swim bladder volume during migration. *Vinciguerria lucetia* and *A. sladeni* are both possible scatterers of these layers although *A. sladeni* is not known to be a vertical migrator.

The importance of using acoustics to study mesopelagic organisms is indicated. Echo sounders can be used to both qualitatively direct biological sampling and quantitatively determine distributions and biomass. High-frequency echo sounders (e.g., 102 kHz in this study) have an advantage over low-frequency echo sounders. Target strength measurements on the midwater fishes, however, are needed to better predict the

[7]Wisner, R. L. 1976. The taxonomy and distribution of lanternfishes (Family Myctophidae) of the eastern Pacific Ocean. Navy Ocean Research and Development Activity, Bay St. Louis, Miss., Rep. 3, 229 p.

concentration of such fishes by the acoustic technique.

ACKNOWLEDGMENTS

We wish to thank the many people who helped with this study. Larry Marx completed and checked most of the measurements, made the graphs, and edited the manuscript. John Chapman calibrated and ran the electronics and acoustic systems. Heidrun Mumper drafted the illustrations and Sally Womack typed the manuscript. Cheryl Chapman introduced us to the use of the computer for editing and final typing of the manuscript. We also appreciate the helpful discussions with M. Neighbors, C. Rainwater, and B. Nafpaktitis of the University of Southern California and D. V. Holliday of Tracor, Inc., San Diego. Special thanks must go to the officers and crew of the *Velero IV* and to Comdr. R. Tipper of the Office of Naval Research for their support. This work was supported by the Office of Naval Research contract N00014-75-C-0683.

LITERATURE CITED

ANDERSEN, N. R., AND B. J. ZAHURANEC (editors).
1977. Oceanic sound scattering prediction. Plenum Press, 859 p.

BAIRD, R. C.
1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (Family Sternoptychidae). Bull. Mus. Comp. Zool. 142:1-128.

BARHAM, E. G.
1963. Siphonophores and the deep scattering layer. Science (Wash., D.C.) 140:826-828.
1966. Deep scattering layer migration and composition: observations from a diving saucer. Science (Wash., D.C.) 151:1399-1403.

BARY, B. MCK., AND R. E. PIEPER.
1970. Sonic - scattering studies in Saanich Inlet, British Columbia: a preliminary report. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 601-611. Maury Center for Ocean Science, Wash., D.C.

CLAY, C. S., AND H. MEDWIN.
1977. Acoustical oceanography: Principles and applications. John Wiley & Sons, N.Y., 544 p.

DAVIES, I. E., AND E. G. BARHAM.
1969 The Tucker opening-closing micronekton net and its performance in a study of the deep scattering layer. Mar. Biol. (Berl.) 2:127-131.

FARQUHAR, G. B. (editor).
1970. Proceedings of an international symposium on biological sound scattering in the ocean. Maury Center for Ocean Science, Wash., D.C., 629 p.

GILBERT, C. H.
1890. A preliminary report on the fishes collected by the steamer ALBATROSS on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. 13:49-126.

GREY, M.
1964. *Family* Gonostomatidae. *In* H. B. Bigelow (editor), Fishes of the western North Atlantic, Part four, p. 78-240. Sears Found. Mar. Res., Yale Univ. Mem. 1.

HAWKINS, A. D.
1977. Fish sizing by means of swimbladder, resonance. *In* A. R. Margetts (editor), Hydroacoustics in fisheries research, p. 122-129. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 170.

HERSEY, J. B., AND R. H. BACKUS.
1962. Sound scattering by marine organisms. *In* M. N. Hill (editor), The Sea, Vol. 1, p. 498-539. Interscience, N.Y.

HOLTON, A. A.
1969. Feeding behavior of a vertically migrating lanternfish. Pac. Sci. 23:325-331.

KAMPA, E. M., AND B. P. BODEN.
1954. Submarine illumination and the twilight movements of a sonic scattering layer. Nature (Lond.) 174:869-871.

LOVE, R. H.
1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. 62:1397-1403.
1978. Resonant acoustic scattering by swimbladder-bearing fish. J. Acoust. Soc. Am. 64:571-580.

PAXTON, J. R.
1967. A distributional analysis for the lanternfishes (family Myctophidae) of the San Pedro basin, California. Copeia 1967:422-440.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

PIEPER, R. E.
1979. Euphausiid distribution and biomass determined acoustically at 102 kHz. Deep-Sea Res. 26A:687-702.

RAINWATER, C. L.
1975. An ecological study of midwater fishes in Santa Catalina basin, off southern California, using cluster analysis. Ph.D. Thesis, Univ. Southern California, Los Ang., 159 p.

URICK, R. J.
1975. Principles of underwater sound. 2d ed. McGraw Hill, N.Y., 384 p.

EMBRYONIC DEVELOPMENT OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, AND A FISH EMBRYO AGE ESTIMATION METHOD

STEVEN P. FERRARO[1]

ABSTRACT

Eggs of Atlantic menhaden, *Brevoortia tyrannus*, were artificially fertilized and embryos were reared in the laboratory at 12 temperature-salinity combinations (temperature: 10°, 15°, 20°, and 25° C; salinity: 10, 20, 30‰). Salinity between 10 and 30‰ had no significant effect on embryonic mortality and no noticeable effect on rate of development. Temperature had a significant effect on embryonic mortality and rate of development. Embryonic mortality was significantly greater at 10° C than at 15°, 20°, and 25° C, and significantly greater before than after blastopore closure at 15°, 20°, and 25° C. The temperature coefficient for embryonic development of *B. tyrannus* from fertilization to hatching at temperatures between 10° and 25° C is 3.89.

Age of *B. tyrannus* embryos can be estimated by the regression of age on developmental stages when incubated at constant temperature.

The Atlantic menhaden, *Brevoortia tyrannus*, is an important commerical and forage fish of the east coast of North America (geographic range: lat. 27°-46° N). Atlantic menhaden spawn in Continental Shelf waters and in bays and estuaries in the northern part of its range during a northward spring and southward fall-winter migration (Reintjes 1961, 1969; Higham and Nicholson 1964; Kendall and Reintjes 1975; Chapoton[2]). *Brevoortia tyrannus* embryos were first described by Kuntz and Radcliffe (1917), and *B. tyrannus* embryos captured at sea have been reared in the laboratory by Reintjes (1968) and Hettler (1970), but rearing conditions were not well controlled and details on development were not published.

Rapid growth and low natural survival characterize the early life history of many marine fishes. Presented in this paper are results of a laboratory experiment to determine effects of temperatures between 10° and 25° C and salinities between 10 and 30‰ on survival and development rates of *B. tyrannus* embryos. Also presented is a useful method for estimating fish embryo age from empirical relations between embryo age, stage of development, and temperature. This fish embryo age estimation method is simple and has broader practical applications than other methods. It was developed for use in ichthyoplankton research to identify cohorts, construct embryonic stage life tables, and back calculate the time of day of spawning.

MATERIALS AND METHODS

Adult Atlantic menhaden were captured by gill nets off the Shoreham Power Plant, Long Island, N.Y., at 2300 h on 14 June 1973 (lat. 40°58′ N, long. 72°52′ W; water temperature 20.5° C; salinity 23.5‰). Eggs from a sexually mature female *B. tyrannus* were artificially fertilized on shipboard with milt from five adult males. Fertilized eggs were carried in four 1 l glass jars in an insulated box to the laboratory at the Marine Sciences Research Center, State University of New York at Stony Brook, N.Y.

Laboratory rearing experiments were two-factor, 4 × 3 (temperature × salinity) factorial designs with two replicates per treatment. Twenty-five embryos were transferred to each culture dish containing 85 ml water with salinities 10, 20, or 30‰, and temperature 20° C. Distilled water or artificial sea salts were added to filtered seawater to produce the desired salinities, and loose fitting plastic covers on the culture dishes reduced evaporation. Culture dishes with embryos were placed in thermostatically controlled constant temperature Hotpoint (#535)[3] incubators

[1]Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11794.

[2]R. B. Chapoton. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 69 p. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3]Reference to trade names does not imply endorsement by the State University of New York at Stony Brook, or the National Marine Fisheries Service, NOAA.

Manuscript accepted May 1979.
FISHERY BULLETIN VOL. 77, NO. 4, 1980

which maintained temperatures within ±0.5° C of 10°, 15°, 20°, and 25° C. Before the experiments began the embryos had been reared for 5 h at 20.5° C and 23.5‰, and had reached the early blastodisc stage of development. By the time of the next observations, about 5 h later, water temperature in the culture dishes had reached the desired incubation temperatures. Development data were mathematically adjusted for the delay in attaining experimental temperatures—see Results.

Developing embryos were observed with a stereomicroscope at intervals of about 4-6 h. Dead embryos were counted and removed, and stage of development of most live embryos was recorded. The basic nine-stage staging classification (Table 1) used in this research was similar to that used by Farris (1958, 1961). I refined this staging scheme by distinguishing among an early, middle, and two late periods within the nine stages. Early and late periods within a stage of development were quantified by subtracting 0.2 from, and adding 0.3, and 0.5, respectively, to the stage number.

TABLE 1.—Fish embryo stages of development used for *Brevoortia tyrannus*.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring halfway around egg
4	Germ ring halfway around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal one-eighth of body free of the yolk
7	Caudal one-eighth of body free of yolk to caudal one-fourth of body free of yolk
8	Caudal one-fourth of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

RESULTS

Survival to hatching in the *B. tyrannus* rearing experiments was low, particularly at the 10° C incubation temperature. Temperature but not salinity had a significant effect on embryonic mortality in these experiments (Table 2). Testing by a posteriori sum of squares simultaneous test procedure (SS-STP) (Sokal and Rohlf 1969) revealed that embryonic mortality was significantly greater ($P < 0.05$) at the 10° C incubation temperature, and not significantly different ($P > 0.05$) at 15°, 20°, and 25° C.

During the experiments it became clear that most embryo deaths occurred during the first half of embryogenesis, and in particular, just prior to blastopore closure (prior to stage 5 in the staging classification used in this research) (Table 3).

TABLE 2.—Data on mortality (upper) and two-way ANOVA (lower) with replication to determine the effect of temperature and salinity on *Brevoortia tyrannus* embryos. Mortality data are the proportion of dead embryos (p). ANOVA performed on angular transformed (arc sine $p^{0.5}$) data.

	Temperature			
Salinity	10° C	15° C	20° C	25° C
10‰	0.96	0.64	0.68	0.56
	.92	.60	.92	.72
20‰	1.00	.72	.76	.64
	1.00	.56	.60	.80
30‰	1.00	.48	.56	.68
	1.00	.48	.52	.68

Source of variation	df	SS	MS	F_s
Subgroups	11	5,327.935	484.358	
Temperature	3	4,640.063	1,546.688	49.6**
Salinity	2	106.056	53.028	1.7 ns
Temp × Salinity	6	581.816	96.969	3.1 ns
Within subgroups (error)	12	373.950	31.162	
Total	23	5,701.885		

** = $P < 0.01$, ns = $P > 0.05$

TABLE 3.—Percent (cumulative) mortality of *Brevoortia tyrannus* embryos prior to and after blastopore closure (stage 5) reared at four temperatures in the laboratory.

Temperature (° C)	Mortality to stage 5 (%)	Mortality to stage 9 (%)
10	94	98
15	49	58
20	59	67
25	63	68

When the difference in frequency of embryo deaths prior to stage 5 and from stage 5 to stage 9 was tested at each of the four incubation temperatures, mortality was not significantly different throughout development at 10° C, but was significantly greater prior to stage 5 at the 15°, 20°, and 25° C incubation temperatures (Table 4).

Data on embryonic age and stage of development were virtually identical in replicate culture dishes and for embryos reared at the same temperature but different salinity. Therefore, analysis was restricted to temperature effects on development rate.

TABLE 4.—Significance of difference in deaths of *Brevoortia tyrannus* embryos prior to and after blastopore closure (stage 5) at four temperatures. Test is 2 × 2 test of independence using the G-statistic with Yates' correction.

Temperature	Development stage	Alive	Dead	Sum	% dead	G_{adj}
10° C	Prior to stage 5	9	141	150	94.0	
	Stage 5-stage 9	3	6	9	66.7	3.639 ns
15° C	Prior to stage 5	77	73	150	48.7	
	Stage 5-stage 9	63	14	77	18.2	19.922**
20° C	Prior to stage 5	62	88	150	58.7	
	Stage 5-stage 9	49	13	62	21.0	24.684**
25° C	Prior to stage 5	55	95	150	63.3	
	Stage 5-stage 9	48	7	55	12.7	42.685**

ns = $P > 0.05$, ** = $P < 0.01$

Brevoortia tyrannus embryos used in the experiments were fertilized and reared at 20.5° C and 23.5‰ for the first 5 h of embryogenesis. To adjust development data for the delay in attaining experimental temperatures, correction factors were calculated to estimate the age embryos would have been at the beginning of the experiment had the embryos been incubated at experimental temperatures from fertilization. Since at 20°±0.5° C incubation temperature was constant throughout development, the correction factor used was the ratio of development time to stage 9 for embryos reared at 10°, 15°, and 25° C relative to development time to stage 9 at 20° C. Correction factors should be approximately proportional to development rates at different temperatures if the effect of delay in attaining experimental temperatures is small relative to incubation time to stage 9, and development rates are linear, as they appear to be (experimental (unadjusted) data points in Figure 1). When the experiments began, embryos had reached the early blastodisc stage of development; the age at that stage, therefore, for each incubation temperature, was estimated by multiplying the appropriate correction factor by 5 h. Development data were adjusted by adding to or subtracting from experimental data the difference between the expected age at the early blastodisc stage at 10°, 15°, and 25° C from the age observed at 20° C. Derivations of correction factors are presented in Table 5, and adjusted data on embryonic development in Table 6.

Age was regressed on embryonic stage of development (S) by least-squares linear regression.

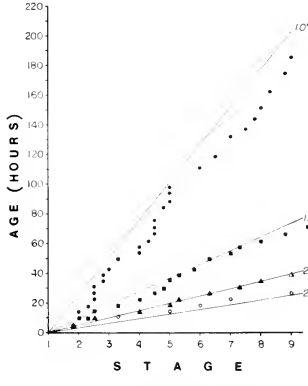


FIGURE 1.—Symbols represent age-stage relations of most *Brevoortia tyrannus* embryos in experiments (unadjusted data) at 10° C, 15° C, 20° C, and 25° C. Solid lines are regression lines of embryo age (A) on developmental stage (S) with experimental data adjusted for preexperimental time and temperature. Regression equation at 10° C is $A = 25.476(S - 1)$; 15° C, $A = 9.295(S - 1)$; 20° C, $A = 4.948(S - 1)$; 25° C, $A = 3.311(S - 1)$.

TABLE 6.—Adjusted data on the embryonic development of *Brevoortia tyrannus* incubated at four temperatures.

Temperature	Age (h)	Embryonic stage	Temperature	Age (h)	Embryonic stage
10° C	24.0	1.8	15° C	8.6	1.8
	28.5	2.0		13.0	2.3
	33.0	2.0		17.5	2.5
	36.5	2.3		21.5	3.3
	41.5	2.5		25.5	4.0
	45.5	2.5		30.0	4.5
	49.5	2.5		33.0	4.8
	53.5	2.8		38.5	5.0
	57.5	2.8		42.0	5.3
	61.5	3.0		46.0	5.8
	68.5	3.3		53.0	6.3
	72.5	4.0		57.0	7.0
	76.5	4.0		61.0	7.3
	80.5	4.3		65.0	8.0
	85.5	4.5		70.0	8.8
	89.5	4.5		74.0	9.3
	94.5	4.5	20° C	5.0	1.8
	103.0	4.8		10.0	2.5
	107.0	5.0		14.0	4.0
	113.0	5.0		18.5	5.0
	117.0	5.0		22.5	5.3
	129.5	6.0		27.0	6.3
	137.5	6.5		30.5	7.3
	151.0	7.0		35.0	8.0
	156.0	7.5		39.0	9.0
	163.0	7.8	25° C	3.5	1.8
	170.5	8.0		9.0	3.3
	181.5	8.3		13.0	5.0
	194.0	8.8		17.0	6.0
	205.0	9.0		21.0	7.0
				25.0	9.0

TABLE 5.—Derivation of correction factors to adjust development data for differences between experimental and preexperimental temperatures during the first 5 h of embryogenesis in *Brevoortia tyrannus*.

Item	10° C	15° C	20° C	25° C
Hours to stage 9 in experiment (unadjusted data)	186	67	39	27
Ratio of hours to stage 9 relative to 39 h to stage 9 at 20° C	4.77	1.72	1.00	0.69
Expected age (h) at early blastodisc stage. Line 2 × 5 h	24.0	8.6	5.0	3.5
Correction factor to unadjusted data. Line 3 − 5 h	+19.0	+3.6	0	−1.5

$$\text{Age} = B\,(S - 1). \quad (1)$$

The results (Table 7; Figure 1) showed that age stage relations were nearly perfectly linear as a function of incubation temperature, and the regressions were highly significant (Table 7). Analysis of variance of the regression coefficients showed that development rates were highly significantly different among temperatures ($F(3, 57) = 1{,}405.0$; $P < 0.001$). (Regression coefficients (B's) of Table 7 represent the "stage" development rate (units: hours/stage) of embryogensis in *B. tyrannus* and are only meaningful when used in context with the embryo staging classification in Table 1.)

The linear relationship between the logrithm of the stage development rate of *B. tyrannus* (B) and temperature (T in degrees Celsius) (Figure 2) is expressed by the following:

$$\log_{10} B = 1.923 - 0.059\,T. \quad (2)$$

The temperature coefficient (Q_{10}) for *B. tyrannus* embryonic development from fertilization to hatching at 10° to 25° C determined by Equation (2) is 3.89. The relation between the logarithm of the embryonic development rate of fish and temperature, though, is not necessarily linear (Kinne and Kinne 1962; Fonds et al. 1974), and, therefore, best predictions of stage development rates of *B. tyrannus* embryos (B) incubated at constant temperature (T in degrees Celsius) are obtained from the explicit empirical equation:

$$\log_{10} B = -0.193 + 17.193\,T^{-1} + 34.090\,T^{-2} - 461.276\,T^{-3}. \quad (3)$$

TABLE 7.—Linear regression of *Brevoortia tyrannus* embryo age (A) in hours since fertilization on morphological stage of development (S).

Temperature	Regression equation	F ratio	P	r^2
10 C	$A = 25.476\,(S - 1)$	$F(1, 29) = 7,110.8$	***	0.996
15 C	$A = 9.295\,(S - 1)$	$F(1, 15) = 6,427.6$	***	998
20 C	$A = 4.948\,(S - 1)$	$F(1, 8) = 3,386.8$	***	998
25 C	$A = 3.311\,(S - 1)$	$F(1, 5) = 1,258.6$	***	996

*** = $P < 0.001$

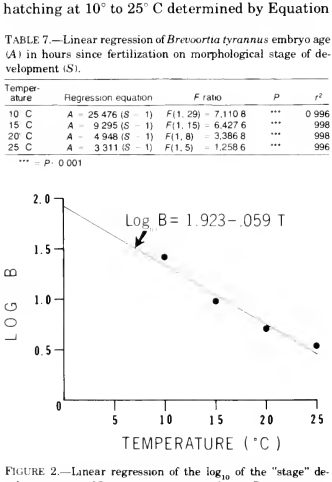


FIGURE 2.—Linear regression of the $\log_{10}$ of the "stage" development rate of *Brevoortia tyrannus* embryos (B) on temperature (T). Coefficient of determination = 0.96; SE regression coefficient = 0.0084.

DISCUSSION

The *B. tyrannus* embryo rearing experiments were mainly designed to determine effects of temperature and salinity on development rate; however, the results also have a bearing on temperature and salinity effects on embryonic survival.

Wide salinity tolerances have been reported for many marine fish embryos (Holliday 1969). *Brevoortia tyrannus* embryos have a salinity tolerance range >10-30‰, and they are, therefore, euryhaline by Kinne's (1964) criteria. Atlantic menhaden embryos have been collected in water with salinity as low as 18.15‰ (Wheatland 1956), but according to Reintjes (1967) most spawning occurs ". . . in the ocean or in inshore waters with salinities similar to those of the ocean." It would appear, therefore, that *B. tyrannus* embryos can tolerate low salinity conditions not normally encountered in nature.

Details of the salinity-development rate relation are species dependent, and they may be complicated by the influence of salinity on dissolved oxygen (Kinne and Kinne 1962; Forrester and Alderdice 1966), and the hatching process (Kinne and Kinne 1962; Alderdice and Velsen 1971); but, within limits, salinity effects on embryonic development rates tend to be small or insignificant for most marine fishes studied (e.g., McMynn and Hoar 1953; Alderdice and Forrester 1968, 1971a, b). Slight but apparently significant positive relations between embryonic development rate and salinity have been reported in some oceanic species (Forrester and Alderdice 1966; Laurence and Rogers 1976). Embryos of oceanic species are probably more sensitive to low salinity and changes in salinity than estuarine species. In the experiments presented in this paper, salinity between 10 and 30‰ had no noticeable effect on the embryonic development rate of *B. tyrannus*.

Brevoortia tyrannus embryo mortality was high at the 10° C incubation temperature. In a preliminary laboratory experiment, naturally fertilized *B. tyrannus* embryos at the blastodisc stage of development (stage 2) from field plankton collections (14.7° C, 24‰) failed to develop beyond stage 4 when the incubation temperature was lowered to 6° ± 1° C. The lowest temperatures at which Atlantic menhaden embryos have been collected in the field generally range between 10° and 13° C (Perlmutter 1939; Wheatland 1956; Richards 1959; Herman 1963), but they have been reported in water as low as 7.7° C (Mundy[4]). The available information, therefore, indicates that while spawning rarely occurs in water <10° C, the low lethal temperature of *B. tyrannus* embryos is probably about 7° C.

The temperature range in the experiments (10°-25° C) was not sufficiently wide to determine the upper temperature tolerance of *B. tyrannus* embryos, which survived equally well at 15°, 20°, and 25° C. There are no references in the literature of Atlantic menhaden embryos in nature in water >25° C.

A number of investigators have noted that high fish embryo mortalities tend to occur during gastrulation and just prior to or during hatching (McMynn and Hoar 1953; Alderdice and Forrester 1971a; Laurence and Rogers 1976; and others). High mortalities of *B. tyrannus* embryos occurred only during gastrulation.

Generally there is a linear or slightly curvilinear relationship between the logarithm of the development rate of fish embryos and temperature (see Blaxter 1969, fig. 4; Williams 1975; and others). The embryonic development rate of *B. tyrannus* followed this general rule (Figure 2).

Brevoortia tyrannus embryo age-stage relations at each of the four incubation temperatures were nearly perfectly linear (Figure 1; Table 7). These results imply a) the durations of the stages (Table 1) are approximately equal, b) the effect of the four incubation temperatures on rate of development of *B. tyrannus* embryos was relatively the same in all stages, and c) the stages of development can be used to estimate the age of embryos if the incubation temperature is known and constant.

A simple method of predicting the age of a *B. tyrannus* embryo at any stage of development from Table 1, incubated at any constant temperature (degrees Celsius) is to solve Equations (3) and (1), in succession for B and age. At low temperatures precision of the age estimate decreases because duration of stages increases. At temperatures in which menhaden commonly spawn (15°-20° C), this method yields an estimate of embryo age with an average expected error from stage duration of between 1.3 and 2.3 h (average error = ¼ × stage development rate).

Kuntz and Radcliffe (1917) and Hettler (1970) gave the incubation time of *B. tyrannus* embryos, but Kuntz and Radcliffe did not specify the incubation temperature. Hettler (1970) observed hatching within 66-74 h at an average incubation temperature of about 15.5° C (range 11.5°-19.5° C). The embryo age calculated for stage 9 at 15.5° C from the age prediction equations is 68.8 h, which compares well with Hettler's observation.

Other methods have been developed which estimate age of fish embryos. Simpson (1959) and Brown and Hassler (1973) constructed nomographs recording the influence of temperature on durations of embryonic stages of *Pleuronectes platessa* and *Morone saxatilis*, respectively. Ahlstrom (1943) and Talbot (1977) used regression analysis to describe the relationship between temperature and durations of fish egg stages, but their methods require calculating separate regressions for each development stage and temperature and does not allow interpolation of development rates between temperatures. Zweifel and Lasker (1976) applied the Laird-Gompertz growth equation to incubation times and embryonic growth (extrapolated from early posthatch growth) of fish embryos. The Laird-Gompertz equation appears to give good predictions of fish embryo growth, but its computation requires solving a multiparameter equation by iteration for each incubation temperature. The fish embryo age estimation method described in this paper is simple and has broader practical applications than the methods above. Together Equations (3) and (1) accurately describe the age-stage-temperature relations of *B. tyrannus* embryos at easily identifiable stages, during the entire embryonic development, and over a wide range of temperatures. Embryo age prediction equations can be calculated for other species in the manner described

[4]Mundy, B. C. 1974. Order Clupeiformes Family Clupeidae *Brevoortia tyrannus* (Latrobe), Atlantic menhaden. *In* H. M. Austin (editor), Preoperational ecological monitoring program of the marine environs at the Long Island Lighting Company (LILCO) nuclear power generating facility, Shoreham, Long Island, N.Y., vol. 2, sect. 5, p. 15-20. Contract SR-72-32. LILCO Community Relations, 250 Old Country Road, Mineola, NY 11501.

here for *B. tyrannus*, and, if necessary, the precision of embryo age estimates by this method can be improved by increasing the number of development stages of approximately equal duration in the embryo stage classification scheme.

ACKNOWLEDGMENTS

I thank the field research team from the New York Ocean Science Laboratory, Montauk, N.Y., for their assistance in the capture of ripe menhaden. I thank John L. McHugh, Marine Sciences Research Center, State University of New York at Stony Brook; and Herbert M. Austin, Virginia Institute of Marine Science, for reviewing an earlier draft of the manuscript. Thanks also to *Fishery Bulletin* reviewers for constructive criticism of the manuscript. Special thanks to George C. Williams, State University of New York at Stony Brook, for reviewing the manuscript and for assistance and support throughout the research.

Research for this paper was financially supported in part by NOAA, Sea Grant Project 2-35281 to G. C. Williams, and by Grant-in-Aid and University Awards from the State University of New York at Stony Brook Research Foundation, and 1977 and 1978 summer Biomedical Research Grants to the author.

LITERATURE CITED

AHLSTROM, E. H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 23, 26 p.

ALDERICE, D. F., AND C. R. FORRESTER.
1968. Some effects of salinity and temperature on early development and survival of the English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 25:495-521.
1971a. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish Res. Board Can. 28:727-744.
1971b. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 28:883-902.

ALDERDICE, D. F., AND F. P. J. VELSEN.
1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Board Can. 28:1545-1562.

BLAXTER, J. H. S.
1969. Development: Eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 177-252. Acad. Press., N.Y.

BROWN, J. T., AND W. W. HASSLER.
1973. A nomography for age determination of striped bass (*Morone saxatilis*) eggs. [Abstr.] *In* A. L. Pacheco (editor), Proc. of a workshop on egg, larval and juvenile stages of fish in Atlantic Coast estuaries, p. 66. U.S. Dep. Commer., NOAA, NMFS, Sandy Hook Lab. Tech. Publ. No. 1.

FARRIS, D. A.
1958. Jack mackerel eggs, Pacific coast, 1951-54. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 263, 44 p.
1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). U.S. Fish Wildl. Serv., Fish. Bull. 61:247-279.

FONDS, M., H. ROSENTHAL, AND D. F. ALDERDICE.
1974. Influence of temperature and salinity on embryonic development, larval growth and number of vertebrae of the garfish, *Belone belone*. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 509-525. Springer-Verlag, N.Y.

FORRESTER, C. R., AND D. F. ALDERDICE.
1966. Effects of salinity and temperature on embryonic development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 23:319-340.

HERMAN, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.

HETTLER, W. F., JR.
1970. Rearing menhaden. U.S. Fish Wildl. Serv., Circ. 350:24-26.

HIGHAM, J. R., JR., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.

HOLLIDAY, F. G. T.
1969. The effects of salinity on the eggs and larvae of teleosts. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 1, p. 293-311. Acad. Press, N.Y.

KENDALL, A. W., JR., AND J. W. REINTJES.
1975. Geographic and hydrographic distribution of Atlantic menhaden eggs and larvae along the middle Atlantic coast from RV *Dolphin* cruises, 1965-66. Fish Bull., U.S. 73:317-335.

KINNE, O.
1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Oceanogr. Mar. Biol. Annu. Rev. 2:281-339.

KINNE, O., AND E. M. KINNE.
1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. Can. J. Zool. 40:231-253.

KUNTZ, A., AND L. RADCLIFFE.
1917. Notes on the embryology and larval development of twelve teleostean fishes. Bull. [U.S.] Bur. Fish. 35:87-134.

LAURENCE, G. C., AND C. A. ROGERS.
1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.)). J. Cons. 36:220-228.

MCMYNN, R. G., AND W. S. HOAR.
1953. Effects of salinity on the development of the Pacific herring. Can. J. Zool. 31:417-432.

PERLMUTTER, A.
1939. Section I. An ecological survey of young fish and eggs identified from tow-net collections. *In* A biological survey of the salt waters of Long Island, 1938, Part II, p.

11-71. N.Y. Conserv. Dep., Suppl. 28th Annu. Rep., 1938, Salt-Water Surv. 15.

REINTJES, J. W.
1961. Menhaden eggs and larvae from M/V *Theodore N. Gill* cruises, South Atlantic coast of the United States, 1953-54. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 393, 7 p.
1967. Classification and distribution of North American menhaden. U.S. Fish Wildl. Serv., Circ. 264:14-15.
1968. Development and oceanic distribution of larval menhaden. U.S. Fish Wildl. Serv., Circ. 287:9-11.
1969 Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Circ. 320, 30 p.

RICHARDS, S. W.
1959. Pelagic fish eggs and larvae of Long Island Sound. *In* Oceanography of Long Island Sound, p. 95-124. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).

SIMPSON, A. C.
1959. The spawning of the plaice (*Pleuronectes platessa*) in the Irish Sea. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. 11, 22(8), 30 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

TALBOT, J. W.
1977. The dispersal of plaice eggs and larvae in the Southern Bight of the North Sea. J. Cons. 37:221-248

WHEATLAND, S. B.
1956. Pelagic fish eggs and larvae. *In* Oceanography of Long Island Sound, 1952-54, p. 234-314. Bull. Bingham Oceanogr. Collect., Yale Univ. 15.

WILLIAMS, G. C.
1975. Viable embryogensis of the winter flounder *Pseudopleuronectes americanus* from -1.8° to 15° C. Mar Biol. (Berl.) 33:71-74.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

DISTRIBUTION AND MOVEMENTS OF RISSO'S DOLPHIN, *GRAMPUS GRISEUS*, IN THE EASTERN NORTH PACIFIC

STEPHEN LEATHERWOOD,[1] WILLIAM F. PERRIN,[2] VICKY L. KIRBY,[3] CARL L. HUBBS,[4] AND MARILYN DAHLHEIM[5]

ABSTRACT

Records of occurrence are summarized from 22 strandings/collections and 210 sighting records from miscellaneous sources. When available, levels of effort have been identified and utilized to interpret the trends in distribution and movement apparent from the data. Risso's dolphins occur from at least the Equator (southern end of area examined) north to approximately latitude 50° N, with regions of apparently very low density centering at about latitude 20° and 43° N. Records from northern and inshore portions of the range were most numerous during late spring through early fall. Both within and among years, periods of greatest abundance for the species north of latitude 43° N, near Monterey Bay, California, and over the southern California continental borderland appear to correspond with protracted periods of warm water. Groups contained from 1 to an estimated 220 animals, about a geometric mean of 10.7. An estimated 76.4% of the groups contained fewer than 20 animals.

The Risso's dolphin or gray grampus, *Grampus griseus*, is widely distributed in tropical and temperate waters around the world. It occurs on the western side of the Atlantic Ocean from at least Newfoundland (approximately lat. 50° N, Leatherwood et al. 1976) south to Cape Horn (approximately lat. 53° S, Norris[6]), and in the Gulf of Mexico (True 1885; Gunter 1954; Paul 1968) and the Caribbean (Caldwell et al. 1971). On the eastern side of the Atlantic it occurs from the Shetland Islands, Scotland (Turner 1892), south to the Cape of Good Hope (approximately lat. 34° S, Barnhard 1954), including the North Sea (Schultz 1970), and throughout the Mediterranean Sea complex (Bazzauti 1910; Tamino 1953; Pilleri and Gihr 1969), including the Adriatic (Trois 1883; Ninni 1901; Carrucio 1906; Riedl 1965; Pilleri and Gihr 1969). It also occurs in the Red Sea (Hershkovitz 1966) and in the Indian Ocean (Ellerman et al. 1953; Weber 1923), at least to the Indo-Australian Archipelago, and on the west side of the Pacific Ocean from the Commander Islands (approximately lat. 55° N, Sleptsov 1961) south to New Zealand (Hector 1873; Parker 1934; Alpers 1960; Gaskin 1968; Baker 1974), including the South China Sea, the Philippine Sea (Baker 1974), and the waters around the New Hebrides (Maxwell 1952), the Solomon Islands (Dawbin 1966), and New Guinea (Gaskin 1972). On the eastern side of the Pacific it has been reported from the Bering Sea (Clark 1945) and British Columbia (Guiguet and Pike 1965) south to Valparaiso, Chile (Aguayo 1975), and Cape Horn (Norris see footnote 6), including the Gulf of California (Leatherwood et al. 1979). That Risso's dolphins are present in Hawaiian waters as well is indicated by three sightings and a stranding on Maui in 1977 (E. W. Shallenberger[7]). Davies (1963) remarked on the species' overall distribution that it is basically tropical but extends its ranges poleward to overlap the ranges of temperate forms, though they generally do not penetrate so far into high latitudes. In all areas, the species' distribution is known only from infrequent stranding records and at-sea sightings, and published accounts continue to restate those records, often without adding substantial new data. Details of the animal's distribution and movements are not reported. This paper reviews the information available through 1975 on Risso's

[1]Biomedical Branch, Naval Ocean Systems Center, San Diego, Calif.; present address: Hubbs/Sea World Research Institute, 1700 South Shores Road, San Diego, CA 92109.

[2]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3]Department of Biology, San Diego State University, San Diego, CA 92115.

[4]Scripps Institution of Oceanography, La Jolla, CA 92037. Deceased.

[5]Department of Biology, San Diego State University; present address: Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[6]Norris, K. S. 1968. Cruise report of the R/V *Hero*, November 12-December 11, Valparaiso-Puntarenas, Chile, 11 p. Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[7]E. W. Shallenberger, Curator, Sea Life Park, Waimanalo, HI 96795, pers. commun. to Leatherwood September 1977.

Manuscript accepted May 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980

dolphins in the portion of the eastern Pacific from the Equator and long. 145° W north and east respectively, from strandings, collections, and sighting records, and examines the data for patterns in distribution, movement, and seasonal occurrence.

METHODS

Inherent in the approach to this paper is the opinion that for this as for other areas, there are numerous scientists and organizations which have small amounts of information of little significance alone, but when the data are combined, they can yield a better understanding of what is known about a given cetacean species (e.g., see Leatherwood and Walker (1979) on *Lissodelphis borealis*).

We reviewed previously published records of at-sea sightings of Risso's dolphins in the study area (Table 1). We then examined over 250 previously unpublished reports of sightings of the species in the area from 1958 to 1975[8] for reliability of identification. Interviews with observers and photos assured us of the accuracy of most records. Descriptions of animals with slate gray to nearly all-white coloration, extensive scarring, a bifurcated melon, and a prominent dark dorsal fin, all distinctive characteristics of Risso's dolphins (Figure 1), aided in verification of the remainder. We discarded questionable records.

Many of the reports included estimates of herd size. Since many of these were stated as ranges (e.g., 30-40 animals), we used the midpoint of each estimate. If the estimate was such that the midpoint was a half number (e.g., an estimate of 10-15 animals) we took the lower of the numbers (e.g., 12).

Some records also included measurements of sea surface temperature at or near the location of the observation. The few of those most important to interpreting apparent trends in the more northern portions of the study area were used, along with annual summaries of temperature trends.

Incidental sighting records alone cannot be used to reliably determine trends in distribution, movements, or abundance. Data on sighting effort are essential. Although a few major marine surveys have been conducted in the study area, effort is difficult to quantify for most other sources of

[8]A summary of verified records of observations of *Grampus griseus* in the northeast Pacific is available from Leatherwood or Perrin.

TABLE 1.—Previously published at-sea sightings of Risso's dolphins in the eastern North Pacific. In the few cases where collections were reported, as in Orr (1966), herds from which animals were collected are not included as sight records.

Source	Date	Location	Number in school
Hubbs (1960)	? 1960	Isla Guadalupe, Mexico	Unreported
Fiscus and Niggol (1965)	18 Mar 1958	38 30' N, 124 15' W	'Many animals'
Guguet and Pike (1965)	22 July 1958	50 00' N, 145 00' W	1
Fiscus and Niggol (1965)	27 Jan 1959	36 45' N, 122 33' W	3
Fiscus and Niggol (1965)	4 Feb 1959	35 12' N, 122 05 W	50 +
Fiscus and Niggol (1965)	8 Feb 1959	35 44 N, 122 43' W	2
Fiscus and Niggol (1965)	18 Mar 1959	41 42' N, 125 53' W	10 +
Fiscus and Niggol (1965)	28 Mar 1959	40 52' N, 125 19' W	5
Guguet and Pike (1965)	11 Oct 1959	50 00' N, 145 00' W	6
Guguet and Pike (1965)	15 Aug 1960	50 00' N, 145 00' W	5
Guguet and Pike (1965)	4 Sept 1960	50 00' N, 145 00' W	4
Daugherty (1972)	? 1971	Midway between San Diego (Pt Loma) and San Clemente Island, Calif	50
Leatherwood et al (1972)	? 1971	05 00 N, 87 04 W	Unreported
Leatherwood et al (1972)	? 1971	11 00' N, 109 30' W	Unreported
Leatherwood et al (1979)	13 Feb 1974	24 52' N, 108 58' W	5-10
Leatherwood et al (1979)	13 Feb 1974	28 21' N, 112 30' W	2

FIGURE 1.—Risso's dolphins off southern California, 1973. The animal's distinctive whitish head (in adults), scarring, and high subtriangular dorsal fin enhance the reliability of "incidental" observational records. (Photo by G. E. Lingle, courtesy Naval Oceans Systems Center, San Diego, Calif.).

data. The following information on effort, from which we feel reliable trends may be determined, exists for the survey programs in the study area.

From San Diego to Equator—National Marine Fisheries Service (NMFS) observers, aboard tunaboats working primarily out of San Diego, Calif, surveyed the area from San Diego south to the Equator from 1966 through 1975. The majority of effort was concentrated in January and February, declining rapidly through April to no effort in the Commission Yellowfin Regulatory Area (CYRA) of the Inter-American Tropical Tuna Commission by the third quarter (Figure 2). It is evident that there has been very little effort in the nearshore portion of the tropical CYRA during the third and fourth quarters, although there were six chartered cruises between September and December. Far-offshore fishing and research activity continued throughout the year. Because the vessels return north to San Diego, running anywhere from 12 mi offshore to beyond the continental shelf off Baja California, effort appears to have been adequate throughout that area to detect major seasonal changes in composition of marine mammal fauna. This is the only program for the area for which extensive and quantified data on effort and sightings were available.

Since 1968, cruises of the Naval Ocean Systems Center, San Diego (NOSC, formerly Naval Undersea Center), have examined the continental shelf area off northwestern Baja California during winter and spring (October-December and February-April). Vessels of the Scripps Institution of Oceanography with marine mammal observers aboard have cruised extensively among the San Diego-Guadalupe Island-Cedros Island triangle for over 30 yr.

Southern California Continental Borderland—Survey effort has been extremely heavy over the continental shelf from Ensenada north to Point Conception. Norris and Prescott (1961) reported on activities of Marineland of the Pacific, primarily between Catalina and Santa Barbara Islands and the mainland shore near Los Angeles. Leatherwood (1974), Evans (1975), and Leatherwood and Walker (1979) summarized NOSC aerial

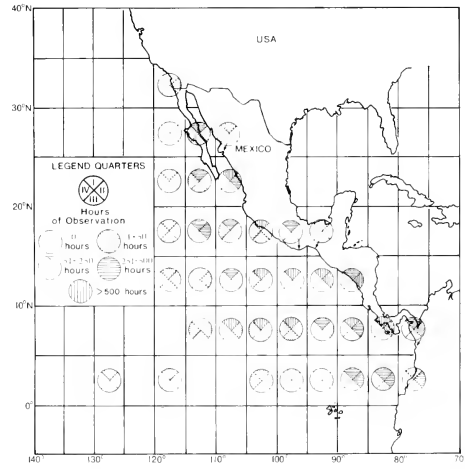


FIGURE 2.—Relative numbers of hours of observation by NMFS/SWFC observers aboard tunaboats in the eastern tropical Pacific by quarter of year, 1974-75.

and ship survey effort in this area for 1968-75. Norris et al.[9] summarized Bureau of Land Management (BLM) aerial and ship surveys during 1975 and 1976. Although variable by month, we consider this combined effort adequate at all seasons to have detected trends in composition of marine mammal fauna for the borderland and adjacent continental slope. Coverage was particularly thorough for the area in 1975, when NOSC and BLM programs overlapped.

Offshore Southern and Central California—During 1967 and 1968, cruises of the Smithsonian Institution's Pacific Ocean Biological Survey program surveyed the outer California Channel Islands and the area from lat. 29° to 37° N and seaward to long. 126° W during all quarters of the year. Marine mammal observations by experienced personnel were logged for all cruises (R. L. Brownell, Jr.[10]).

Offshore Baja California North to Washington—More recent coverage of the area from lat. 25° N to Washington State, primarily offshore, has been provided by NMFS observers out of the Southwest Fisheries Center (SWFC) placed on commercial albacore boats. In 1971-75, observers aboard 15 working albacore boats reported marine mammal observations made between May and September from lat. 25° to 46° N (Table 2). Although the time and location of their activities varied annually with the albacore migration, coverage was generally restricted to summer and generally moved north as the season progressed.

Nearshore Central California—Recent aircraft and ship surveys by the University of California at Santa Cruz have examined the area from about Point Conception north, with the most extensive sampling effort in Monterey Bay. Coverage near Monterey Bay has been year-round (J. D. Hall[11]). Infrequent cruises by personnel from Hopkins Marine Station and Moss Landing Marine Laboratory have examined the same area (A. Baldridge[12]).

Oregon and North—With one important exception, recorded survey effort begins to decline as one moves north from California. NMFS albacore-boat observer programs conducted in the summer have extended north of Point Conception (Table 2), and one NOSC marine mammal cruise was conducted from San Diego to Kodiak, Alaska, in April 1971. The primary effort, however, including extensive coverage of the area from Seattle north through the Gulf of Alaska and northwest to the Aleutian Islands and the Bering Sea, has been that by cruises of the NMFS Northwest and Alaska Fisheries Center (NWAFC) Pelagic Fur Seal Research Program. Over the past 10 yr, these cruises have primarily spanned the fall and winter months (C. H. Fiscus[13]). Other research cruises by NWAFC have begun in the Seattle area and worked south to southern California in January, February, and March (Fiscus and Niggol 1965), while still others beginning in San Francisco have worked south to the Revillagigedo Islands in winter and spring (Rice 1963a, b).

The remainder of the sighting effort for the northeastern Pacific is difficult to assess, though it

[9]Norris, K. S., T. P. Dohl, R. C. Guero, L. J. Hobbs, and M. W. Honnig. 1976. Cetaceans; numbers, distribution, and movements in the southern California Bight. 192 p. Draft report to Bureau of Land Management, OCSEAP, from Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[10]R. L. Brownell, Jr., U.S. National Museum of Natural History, National Fisheries and Wildlife Laboratory, Wash., DC 20560, pers. commun. to Leatherwood June 1975.

TABLE 2.—Months during 1961-75 in which marine mammal watches were maintained aboard one or more albacore vessels (×) in the eastern Pacific (1971-75), by 5° increments of latitude. A total of 15 vessels were involved.[1-4]

Lat. (° N)	May	June	July	August	September
45-50				·	·
40-45		×	×	·	×
35-40		×	×	·	
30-35	·	×	×		
25-30	·	·	×		

[1]Laurs, R. M., and Associates. 1972. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1971 and 1972. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif. 76 p.

[2]Laurs, R. M., and Associates. 1973. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1973. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

[3]Laurs, R. M., and Associates. 1974. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1974. Admin. Rep. 25-74-47, SWFC, NMFS, NOAA, La Jolla, Calif.

[4]Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1975. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

[11]J. D. Hall, U.S. Fish and Wildlife Service, Office of Biological Services, 800 A Street, Suite 110, Anchorage, AK 99501, pers. commun. to Leatherwood August 1975.

[12]A. Baldridge, Library, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Fla.; present address: Hopkins Marine Station, Pacific Grove, CA 93950, pers. commun. to Leatherwood 1975.

[13]C. H. Fiscus, Northwest and Alaska Fisheries Center Marine Mammal Division, NMFS, NOAA, 7600 Sand Point Way NE Seattle, WA 98115, pers. commun. to Leatherwood June 1976.

is clearly sporadic and has concentrated on coastal regions near population centers.

The areas of coverage of the most important programs considered in this report are summarized in Figure 3. (The expanded area coverage of the SWFC tunaboat-observer program is shown in Figure 2).

RESULTS

Strandings and Collections

As nearly as we can determine, 22 strandings and/or collections of specimens of *G. griseus* have been recorded in the northeastern Pacific since about 1872 (Figure 4).

1. (Published). In the late 19th century, probably in 1872, although the exact date is undeterminable, Charles M. Scammon obtained two lower jaws from Monterey, Calif. (Scammon 1874). Dall (1874) used these two lower jaws as the basis for his description of *G. sternsii*, later rejected as a species by True (1889) because it was indistinguishable from *G. griseus* (G. Cuvier 1812). One lower jaw and two teeth were deposited in the U.S. National Museum (USNM 13021), though True could not make his measurements agree with Dall's and tentatively said that it was "apparently neither the No. 1 nor the No. 2 of Mr. Dall's description" (True 1889). The whereabouts of the second mandible or, if True's

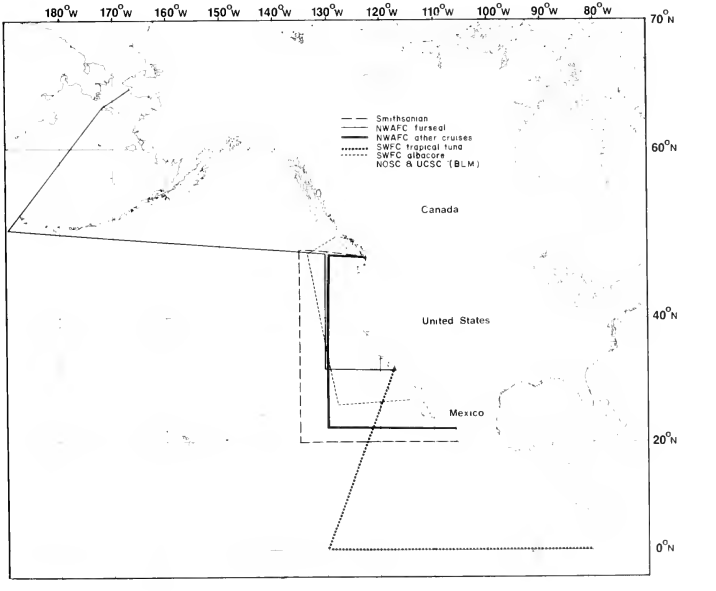


FIGURE 3.—The eastern North Pacific north of lat. 15° N, showing areas surveyed by major marine mammal survey programs (1958-75). See text for details of documentation.

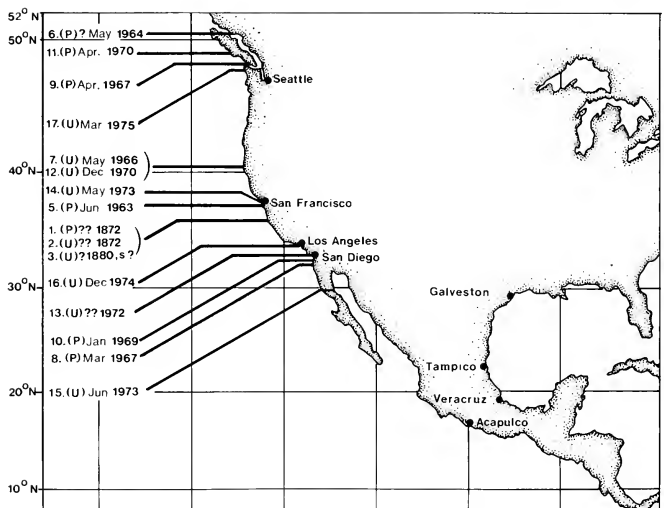


FIGURE 4.—Dates and approximate locations of strandings and collections of Risso's dolphins in the eastern North Pacific (1972-75) numbered in chronological order. The letters in parentheses indicate whether the record has (P) or has not (U) been previously published.

observations are correct, both mandibles described by Dall, are unknown, as is the identity of USNM 13021.

2. (Unpublished). During the same period, exact date also undeterminable, Scammon collected a second specimen which he also forwarded to True at the U.S. National Museum (USNM 21163). Like the first, this specimen was reportably taken in Monterey Bay, Calif. (C. H. Gilbert[14]).

3. (Unpublished). There are three remaining specimens from the Pacific coast of North America in the collection of the U.S. National Museum. One (USNM 28066) was purchased from fishermen in Monterey; one (USNM 49895) was taken from an unidentified locality in California; and the third (USNM 49347) was collected by C. H. Gilbert, presumably also in Monterey. Interestingly, in referring to this last specimen in his correspondance with Dall, Gilbert (see footnote 14) wrote "In addition to that, I have the complete skeleton of a calf about 6 months old. The species is abundant in Monterey

[14]C. H. Gilbert undated letter to W. Dall, in possession of Hubbs

Bay and additional specimens could be secured for you if you desire."

4. (Unpublished). In 1959, a single lower jaw identifiable as that of a Risso's dolphin was brought to Hubbs from Isla de Coco ("Cocos Island"), lat. 05°32′ N, long. 87°04′ W. The location of the specimen is currently unknown.

5. (Published). On 11 June 1963, a 325.0 cm male apparently dead from gunshot wounds stranded on the beach 0.9 km from Princeton by the Sea, San Mateo, Calif. The account of the stranding and its workup includes a description of the specimen, analysis of stomach contents, miscellaneous external measurements and organ weights, and some cranial measurements (Orr 1966). The specimen was deposited in the collection of the California Academy of Sciences, San Francisco (CAS 13461, Orr 1966). This account represents the first continental eastern Pacific record of the species published since the late 19th century.

6. (Published). In May 1964, a single 11-ft (334.0 cm) Risso's dolphin was observed alive in Big Bay on the west side of Stuart Island, British Columbia (approximately lat. 50°20′ N, long. 125°00′ W). The animal was shot, dissected, and discarded. The caudal peduncle and flukes were later recovered and placed in the collection of the British Columbia Provincial Museum (BCPM 9077). The animal was reported by the collectors to have been feeding on squid and to have had a heavy intestinal parasite load (Guiget and Pike 1965).

7. (Unpublished). On 13 May 1966, Robert E. Jones (Museum of Vertebrate Zoology, Berkley, Calif.) found a long dead but complete carcass of a stranded male approximately 10 km south of Cape Mendocino, Humbolt County, Calif. The total length of the specimen was 9 ft 7.5 in (293.9 cm). The skull and left flipper were collected and deposited at the Humboldt State University (HSC-66-4).

8. (Published). On 18 March 1967, an adult male stranded alive at Cantomar (Rosarita Beach), 42 km south of Tijuana, Baja California, Mexico (approximately lat. 32°18′ N, long. 117°00′ W). It was taken to Sea World in San Diego, Calif., where it survived for a short time. A photo of this animal appeared in the *San Diego Union* 28 March 1967 on page B-5. This specimen was 307.0 cm long (Harrison et al. 1969) and weighed 850 lb (386 kg) (measured by Hubbs). Although the specimen was reportedly deposited in the San Diego Natural History Museum, the Museum has no record of the specimen and its whereabouts are unknown.

9. (Published). On 20 April 1967, a 258 cm male apparently dead from a gunshot wound in the head was found stranded at Makkaw Bay, Wash. (lat. 48°19′ N, long. 124°40′ W). The dolphin had been dead an estimated 1 mo. Its stomach contained squid beaks and fragments. The skull and postcranial skeleton were preserved in the collection of NWAFC, NMFS, NOAA, Seattle, Wash. (Stroud 1968).

10. (Unpublished). On 21 January 1969, a 309 cm adult male stranded alive at Imperial Beach, San Diego County, Calif. The animal was taken to Sea World, San Diego, where it died the night of 21-22 January 1969. The complete skeleton was collected by Raymond M. Gilmore and deposited in the San Diego Natural History Museum (SDNHM 21554) (R. M. Gilmore[15]).

11. (Published). On 17 April 1970, a 266 cm male washed ashore on the east side of Vargas Island, British Columbia (lat. 49°10′ N, long. 125°58′ W). The skull, axial skeleton, and bones from one pectoral appendage were collected and placed along with a complete photo series (Photofile No. 51) in the collection of the Vertebrate Museum, Department of Zoology, University of British Columbia (UBC 9464). The report of the stranding includes external measurements, organ weights, and an analysis of stomach contents (Hatler 1971).

12. (Unpublished). On 26 December 1970, a male neonate was collected from the beach in Shelter Cove, Humboldt County, Calif. The entire specimen (Field No. WJH 71-1) was deposited at the Humboldt State University (HSU 1620) (W. J. Houck[16]).

13. (Unpublished). In August of 1970, responding to a radio call from local fishermen, F. Brocata and B. Falcone of Marineland of the Pacific investigated a call about an "albino" pilot whale which had been harpooned by fishermen between Santa Cruz and Santa Rosa Islands, Calif. When Marineland's research boat, the MV *Geronimo*, approached the whale, which turned out to be a Risso's dolphin, the animal managed to

[15]R. M. Gilmore, Research Associate, San Diego Natural History Museum, San Diego, CA 92112, pers commun. to Leatherwood 1975.

[16]W. J. Houck, Humboldt State University, Arcata, CA 95521, pers. commun. to Leatherwood 1975.

pull out the harpoon and swim away (W. A. Walker[17]).

14. (Unpublished). On 20 May 1973, an immature female was found stranded on southeast Farallon Island, off San Francisco, Calif. (approximately lat. 37°42′ N, long. 123°00′ W). The available measurements for the specimen are as follows: total length 270 cm, dorsal fin 27.5 cm, axilla-tip of flipper 5 cm, origin of flipper to tip of lower jaw 46.5 cm, anus-tip of lower jaw 178 cm, width of flukes 62 cm. The specimen was not collected (R. L. Brownell, Jr. see footnote 10).

15. (Published). On 18-19 June 1973, four females and a fifth animal of undetermined sex, all about 13 ft long (400 cm) and weighing 500-600 lb (73-77 kg) stranded alive at Punta Buffeo, Baja California, about 100 mi (160 km) south of San Felipe on the northwest coast of the Gulf of California (approximately lat. 29°55′20″ N, long 114°26′20″ W). All five animals were towed out to sea (dead), and no materials were retrieved (Leatherwood et al. 1979).

16. (Unpublished). On 8 December 1974, a female stranded alive at the Manhattan Beach Pier, Los Angeles, Calif. (approximately lat. 33°55′ N, long. 118°25′ W). The animal was alive when it was collected by Marineland of the Pacific but died almost immediately after collection. It was photographed, measured, and necropsied at the Los Angeles County Museum of Natural History, where it is currently held as specimen LACM 47145. Detailed findings will be reported elsewhere (W. F. Samaras and D. R. Patten[18]).

17. (Unpublished). On 10 March 1975, a 348 cm female stranded alive at Port Discovery, Wash., in the Strait of Juan de Fuca (about lat. 48°02′ N, long. 122°52′ W), perhaps driven ashore by killer whales. The animal was recovered alive and taken to Seattle Marine Aquarium where it died on 11 March. The complete skeleton is in the collection of the NWAFC (No. 1975-1).

At-Sea Sightings

We found 16 previously published records of at-sea sightings of Risso's dolphins for the study area (Table 1) and 194 additional previously unpublished reliable records (see footnote 8) (Figure 5). When examined by latitude (Figure 5), the distribution of sightings falls into three major groups—those from the Equator to approximately lat 20° N (Zone I); those thence north to approximately lat. 43° N (Zone II); and those north of lat. 43° N (Zone III). Zones I and II are separated by a broad region characterized by very few sightings, centering at about lat. 20° N and extending from lat. 14° to 29° N. All except two sightings in that area of low density were within 60 mi of the Mexican coast, though seaward of the continental shelf. The separation between Zones II and III is less pronounced, centering at lat. 43° N and extending from lat. 38° to 45° N.

Regarding seasonality, records in Zone I are almost exclusively limited to first and second quarters, and the majority of those from Zone III are from the period July through October. Both of these apparent seasonal fluctuations result from the biases in observation effort discussed above. Those from Zone II are distributed throughout the year. Records from north of Point Conception (lat. 35° N) are most numerous in the third quarter (Figure 6).

Off southern California (approximately lat. 31°-35° N), records from 1959 to 1975 were sporadic, reaching a peak of 11 in 1974 (Table 3). Until 1971 the majority of sightings for the area were seaward of the 100-fathom curve; however, beginning in 1971 and increasing in frequency through 1974 (9 of 11) and 1975 (3 of 3), most sightings were over the continental shelf.

Although surface water temperatures were not reported for most sightings, Risso's dolphins have been sighted in waters ranging from 28° to 10° C. Sightings in Zone I cover the full range of temperatures reported for the area. Sightings off southern California in 1974 and 1975 were associated with water temperatures above 19° C. Of the 22

TABLE 3.—Summary of sightings of Risso's dolphins off southern California (about lat. 31°-36° N), 1959-75, showing the frequency of encounter over and seaward of the continental shelf.

Year	Total no sightings	Over continental shelf	Seaward of continental shelf
1959	1	1	0
1960	1	1	0
1965	1	0	1
1966	3	0	3
1967	9	0	9
1968	3	1	2
1971	4	4	0
1972	4	4	0
1973	3	2	1
1974	11	10	1
1975	3	3	0

[17] W. A. Walker, 21 Barkentine Road, Rancho Palos Verdes, CA 93704, pers. commun. to Leatherwood 1975.

[18] W. F. Samaras, Research Associate, and D. R. Patten, Curator, Department of Mammals, Los Angeles County Museum of Natural History, Los Angeles, CA 90007, pers. commun. to Leatherwood 1975.

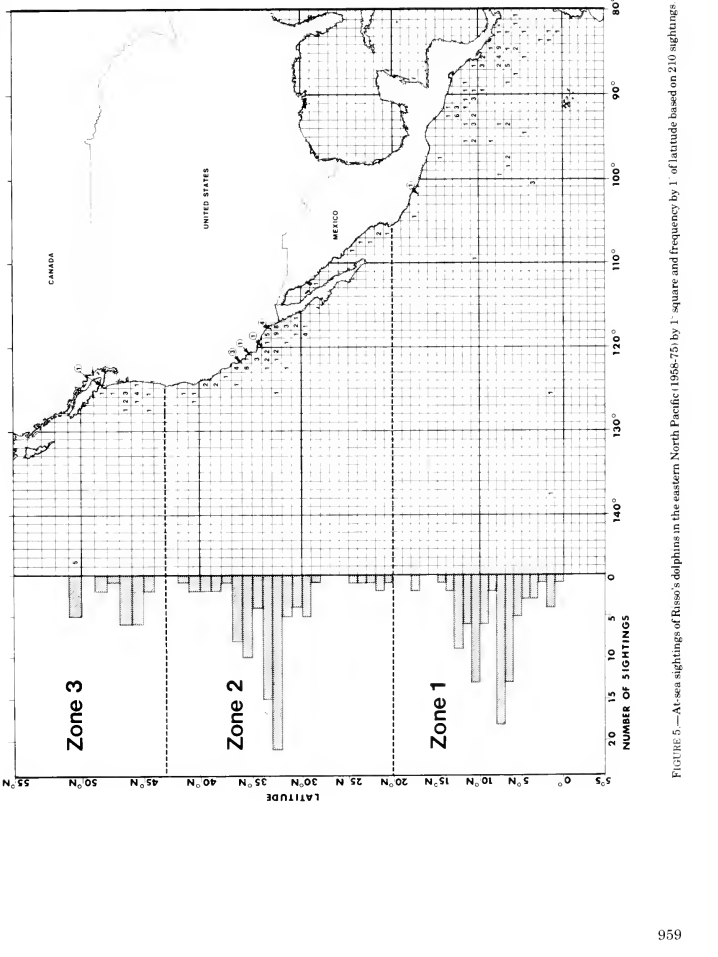


FIGURE 5.—At-sea sightings of Risso's dolphins in the eastern North Pacific (1958-75) by 1° square and frequency by 1° of latitude based on 210 sightings

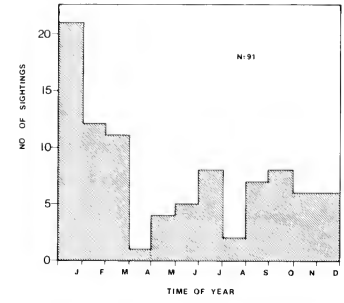


FIGURE 6.—Frequency of sightings of Risso's dolphins by month in Zone II in the eastern North Pacific (defined in Figure 5).

most northern records, the 4 from February to April were associated with water temperatures of 12° and 13°C, unusually high temperatures for the season.

Of the records, 12 published and 191 unpublished provided usable estimates of herd sizes. Numbers of animals sighted ranged from 1 to 220, about a geometric mean of 10.65. About 75% of the groups contained fewer than 20 animals (Figure 7). No statistically significant differences could be demonstrated among herd sizes from different zones (I, II, III) or different seasons (Mann-Whitney U Test, $\alpha = 0.05$).

SUMMARY AND DISCUSSION

Risso's dolphins are clearly abundant and widely distributed year-round in tropical and warm temperate waters of the northeastern Pacific.

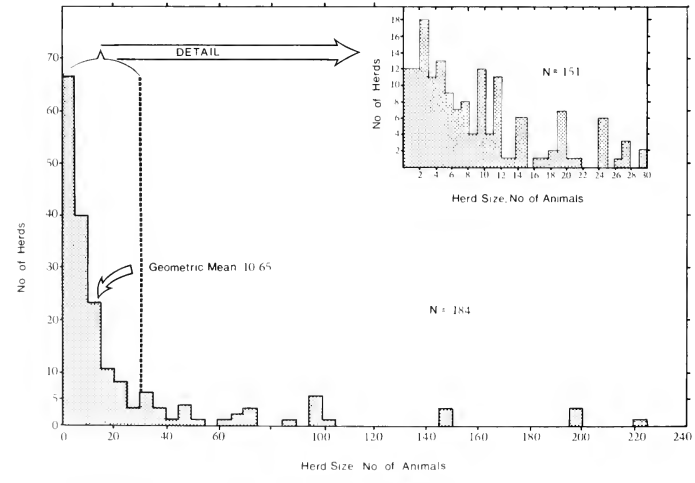


FIGURE 7.—Distribution of estimated "herd" sizes of Risso's dolphins, in the eastern North Pacific (1958-75). Inset gives detail for herd sizes with ≤ 30 animals.

The rather dramatic decrease in the number of sightings north of about lat. 13° N and the very limited number of offshore sightings in the broad belt from about the latitudes of Cedros and Guadalupe Islands south to approximately Acapulco, appear to reflect an area of apparent very low density in the species' distribution, since survey effort in the area was heavy even where no sightings were reported. Pronounced distributional gaps in portions of the same ocean area have been documented for *Delphinus delphis* (Evans 1975) and *Stenella* spp. (Perrin 1975).

Risso's dolphins appear to occur year-round in offshore waters from about central Baja California northward to about San Francisco. Movements onto the continental shelf of southern California are seasonal and appear to be related to surface temperatures. For example, records of Risso's dolphins over the continental shelf were more numerous in 1974 than in previous years since 1968, despite an equal effort, and more numerous than in 1975, despite increased survey effort in that year. In 1974 and 1975, surface temperatures were unusually high (California Cooperative Oceanic Fisheries Investigations[19]).

A poorly defined area of apparent low density in distribution, centering at about lat. 43° N, probably reflects generally poor sampling in the area from about San Francisco north to the latitude of Seattle and not any real change in the species' density there.

Records from lat. 45° to 51° N are most abundant during summer and are primarily off the continental shelf. Like the movements onto the southern California continental borderland and those into more northern latitudes, this change appears to relate to warming of surface waters.

The reports of abundance near Monterey in the late 19th century seem inconsistent with modern records of low abundance in the area. It may well be that this indication of the common occurrence of the species in Monterey Bay in the 1870's and 1880's represents a holdover of the occurrence of tropical animals in central California in the 1850's (Hubbs 1948). This being the case, the movement of Risso's dolphins north and inshore in some abundance during that period is consistent with behavior in 1974 and 1975 off southern California. Southward movements of the Dall's porpoise, *Phocoenoides dalli*, into southern California (Norris and Prescott 1961) and seasonal movements of the right whale dolphin, *Lissodelphis borealis* (Leatherwood and Walker 1979), and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens* (Leatherwood and Reeves 1978), in the eastern North Pacific have been similarly linked to seasonal changes in water temperature.

Despite extensive survey effort in the northern temperate and Arctic eastern Pacific, Risso's dolphins have not been reported north of lat. 51° N. Therefore, since it provided no new data, the summary report of the species' occurrence in the Bering Sea (Clark 1945) is of doubtful accuracy.

Considered together, these records tend to support Davies' (1963) summary of the species' distribution, at least in the northeast Pacific. It appears, as he contended, to be primarily tropical, extending its range poleward to overlap with temperate forms, though not penetrating as far into high latitudes. Perhaps the most important point supported by these records is the dynamic nature of distribution of this (and probably other) marine mammal species. In addition to well-documented short-term and seasonal movements, there appears to have been a long-term fluctuation in the boundries of species' ranges, apparently in responses to long-term environmental changes.

ACKNOWLEDGMENTS

The authors thank all the following institutions and individuals for contributing unpublished data: Fisheries Research Board of Canada (MaCaskie from Pike's records); University of Southern California (Capt. F. Zeischenhene); Moclips Cetological Society (K. C. Balcomb); Northwest and Alaska Fisheries Center, NMFS, NOAA (C. H. Fiscus, R. L. DeLong, and D. W. Rice); University of California, Santa Cruz (T. P. Dohl, J. D. Hall, and L. J. Hobbs); U.S. Fish and Wildlife Service (R. L. Brownell, Jr.); Museum of Vertebrate Zoology, Berkeley (R. E. Jones); Humboldt State College (W. J. Houck; San Diego Natural History Museum (R. M. Gilmore); Los Angeles County Museum (W. A. Walker, D. R. Pattern, and W. A. Samaras); Hopkins Marine Station (J. E. Vandevere); University of Oregon (T. Wahl); USA/USSR Marine Mammal Cooperative Program (D. W. Rice and W. E. Evans); and Hubbs-Sea World Research Institute (W. Evans and J. Jehl, Jr.). J. D. Hall, F. G. Wood, M. Schaeffer, and D. W. Rice critically reviewed the manuscript.

[19]California Cooperative Oceanic Fisheries Investigations. Unpublished data in files of CalCOFI at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

LITERATURE CITED

AGUAYO, A.
1975. Progress report of small cetacean research in Chile. J. Fish. Res. Board Can. 32:1123-1143.

ALPERS, A.
1960. A book of dolphins. J. Murray, Lond., 147 p.

BAKER, A. N.
1974. Risso's dolphin in New Zealand waters, and the identity of "Pelorus Jack." Rec. Dom. Mus. Wellington 8:267-276.

BARNARD, K. H.
1954. A guidebook to South African whales and dolphins. S. Afr. Mus., Cape Town, Guide 4:1-3.

BAZZAUTI, A.
1910. *Grampus griseus* (G. Cuv.). Monit. Zool. Ital. 21:85-95.

CALDWELL, D. K., M. C. CALDWELL, W. F. RATHJEN, AND J. R. SULLIVAN.
1971. Cetaceans from the Lesser Antillean Island of St. Vincent. Fish. Bull., U.S. 69:303-312.

CARRUCCIO, A.
1906. Sovra un raro delfino (*Grampus grıseus* G. Cuvier) di recente cattbrata presso lo spiaggia di S. Vincenzo Boll. Soc. Zool Ital., Ser. II-VII, p. 207-214.

CLARK, A. H.
1945. Animal life of the Aleutian Islands. Smithson. Inst., War Background Stud. 21:48-54, 75-76.

DALL, W. H.
1874. Catalogue of the Cetacea of the North Pacific Ocean, with osteological notes, and descriptions of some new forms; with special reference to the forms described and figured in the foregoing monograph of Pacific Cetacea, by Captain C. M. Scammon, U.S.R.M. *In* C. M. Scammon, The marine mammals of the north-western coast of North America, described and illustrated· together with an account of the American whale-fishery, p. 281-307. John H. Carmany and Co., San Franc.

DAUGHERTY, A. E.
1972. Marine mammals of California. Calif. Dep. Fish Game, Sacramento, Calif., 87 p.

DAVIES, J. L.
1963. The antitropical factor in cetacean speciation. Evolution 17:107-116.

DAWBIN, W. H.
1966. Porpoises and porpoise hunting in Malaita. Aust. Nat. Hist. 15:207-211.

ELLERMAN, J. R., T. C. S. MORRISON-SCOTT, AND R. W. HAYMAN.
1953. Southern African mammals, 1758-1951. Br. Mus. (Nat. Hist.) Lond., 363 p.

EVANS, W. E.
1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph D. Thesis, Univ. California, Los Ang., 145 p.

FISCUS, C. H., AND K. NIGGOL.
1965. Observations of cetaceans off California, Oregon, and Washington. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 498, 27 p.

GASKIN, D. E.
1968. The New Zealand cetacea. N.Z. Fish. Res. Div., Fish. Res. Bull. 1, 92 p.

1972. Whales dolphins and seals. Heinemann Educ. Books, N.Y., 200 p.

GUIGUET, C. J., AND G. C. PIKE.
1965. First specimen record of the gray grampus or Risso dolphin, *Grampus griseus* (Cuvier) from British Columbia. Murrelet 46:16.

GUNTER, G.
1954. Mammals of the Gulf of Mexico. *In* P. S. Galtsoff (coordinator), Gulf of Mexico; its origin, waters, and marine life, p. 543-551. U.S. Fish Wildl. Serv., Fish. Bull. 89.

HARRISON, R. J.
1969. Reproduction and reproductive organs. *In* H. T. Andersen (editor), The biology of marine mammals, p. 253-348. Academic Press, N.Y.

HATLER, D. F.
1971. A Canadian specimen of Risso's dolphin. Can. Field-Nat. 85:188-189.

HECTOR, J.
1873. Notes on the whales and dolphins of the New-Zealand seas. Ann. Mag. Nat. Hist., Ser. 4, 11:104-112.

HERSHKOVITZ, P.
1966. Catalog of living whales. Bull. U.S. Natl. Mus. 246, 259 p.

HUBBS, C. L.
1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res. 7:459-482.
1960. The marine vertebrates of the outer coast. *In* Symposium: The biogeography of Baja California and adjacent seas. Part II, Marine biotas, p. 134-147. Syst. Zool. 9.

LEATHERWOOD, J. S.
1974. Aerial observations of migrating gray whales, *Eschrichtius robustus*, off southern California, 1969-72. Mar. Fish. Rev. 36(4):45-49.

LEATHERWOOD, S., D. K. CALDWELL, AND H. E. WINN.
1976. Whales, dolphins, and porpoises of the western North Atlantic. A guide to their identification. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 396, 176 p.

LEATHERWOOD, S., W. E. EVANS, AND D. W. RICE.
1972. The whales, dolphins, and porpoises of the eastern North Pacific. A guide to their identification in the water. Nav. Underseas Cent. Tech. Publ. 282, 175 p.

LEATHERWOOD, S., C. L. HUBBS, AND M. FISHER.
1979. First records of Risso's dolphin *Grampus griseus* from the Gulf of California with detailed notes on a mass standing. Trans. San Diego Soc. Nat. Hist. 19:45-52.

LEATHERWOOD, S., AND R. R. REEVES.
1978 Porpoises and dolphins. *In* D. Haley (editor), The marine mammals of eastern North Pacific and Arctic waters, p. 96-111. Pac. Search Press, Seattle.

LEATHERWOOD, S., AND W. A. WALKER.
1979. The northern right whale dolphin, *Lissodelphis borealis* Peale, in the eastern North Pacific. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Vol. III, Natural history of cetaceans, p. 85-141. Plenum Press, N.Y.

MAXWELL, G.
1952. Harpoon venture. The Viking Press, N.Y., 304 p.

NINNI, E.
1901 Sulle catture di alcuni cetacei nel mare adriatico ed in particolare Delphinus Lursio. Neptunia 8:1-9.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool. 63:291-402.

ORR, R. T.
1966. Risso's dolphin on the Pacific Coast of North America. J. Mammal 47:341-343.

PARKER, W. R.
1934. 'Pelorus Jack.' Proc. Linn. Soc. Lond. 146:2-3.

PAUL, J. R.
1968. Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico. J. Mammal. 49:746-748.

PERRIN, W. F.
1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.

PILLERI, G., AND M. GIHR.
1969. On the anatomy and behaviour of Risso's dolphin (*Grampus griseus* G. Cuvier). Invest. Cetacea 1:74-93.

RICE, D. W.
1963a. Pacific coast whaling and whale research. Trans. 28th North Am. Wildl. Nat. Resour. Conf. 28:327-335.
1963b. The whale marking cruise of the *Sioux City* off California and Baja California. Nor. Hvalfangst-Tidende. 52:153-160.

RIEDL, A.
1965. Fauna d'Italia. Bologna Ed. Calderina 3, 647 p.

SCAMMON, C. M.
1874. The marine mammals of the north-western coast of North America, described and illustrated: together with an account of the American whale-fishery. John H. Carmany and Co., San Franc., 319 p.

SCHULTZ, W.
1970 Ueber das Vorkommen von Walen in der Nord-und Ostsee (Ordn. Cetacea). Zool. Anz. 185:172-264

SLEPTSOV, M. M.
1961. Observations on the small cetacea of the far eastern seas and northwestern parts of the Pacific Ocean. [In Russ.] Akad. Nauk SSSR, Inst. Morfol. Zhivotn. 34:136-143.

STROUD, R. K.
1968. Risso dolphin in Washington State. J. Mammal. 49:347-348.

TAMINO, G.
1953. Ricupero di un *Grampus griseus* arenata sue lido di Ladispoli (Roma) ie 5 April de 1953. Boll. Zool. 20:45-48.

TROIS, E. F.
1883. *Grampus rissoanus* - Notes on a specimen caught in the Adriatic. Atti Ist. Veneto Schieze, Lett. Arti. Venice, Ser. 6, 1:735-740.

TRUE, F. W.
1885. A provisional list of the mammals of North and Central America, and the West Indian Islands. Proc. U.S. Natl. Mus. 7:587-611.
1889. Contributions to the natural history of the cetaceans, a review of the family Delphinidae. U.S Natl. Mus. Bull. 36, 191 p.

TURNER, W.
1892. Notes on some of the viscera of Risso's dolphin (*Grampus griseus*). J. Anat. Physiol. 26:258-270.

WEBER, M.
1923. Die cetaceen der Siboga-Expedition. Siboga-Exped. Monogr., Bull. 97(58), 38 p.

DESCRIPTION OF LARVAL AND JUVENILE RED SNAPPER, *LUTJANUS CAMPECHANUS*[1]

L. Alan Collins, John H. Finucane, and Lyman E. Barger[2]

ABSTRACT

Identification and description of the red snapper, *Lutjanus campechanus*, family Lutjanidae, were based upon the general morphology, meristic characters, head spination, and pigmentation of 18 larval and 6 juvenile specimens, 4.0-22.4 mm standard length. These 24 specimens were selected from a total of 226 larval and juvenile *L. campechanus* which were collected mainly along the Texas coast from 1975 to 1977. Lutjanids <4.0 mm lacked presently recognizable characters that are diagnostic at the species level. The key to the development of the series was a unique meristic count. Some other useful diagnostic characters were: small serrations on the anterior margin of the pelvic spine in specimens of 4.8-12.4 mm, and a long unbroken soft ray immediately adjacent to the pelvic spine in specimens of 4.8-10.6 mm. A brief comparison was made between *L. campechanus* and other lutjanid larvae and juveniles.

The red snapper, *Lutjanus campechanus* (Poey), family Lutjanidae, is one of the most important commercial and recreational fish species in the Gulf of Mexico (Bradley and Bryan 1975; Beaumariage and Bullock 1976). Numerous biological and fisheries publications concern the adult of this species. Apparantly only one short publication has dealt with the early life history of *L. campechanus* however. Arnold et al. (1978) described the spawning of this species in captivity. The primary purpose of the present paper is to describe the larval and juvenile development of *L. campechanus*.

METHODS

A total of 226 larvae and juveniles (4.0-22.4 mm SL, standard length) of the species were captured by four different methods, which are listed in Table 1. The bongo and neuston net sampling was done according to Marine Resources Monitoring, Assessment and Prediction specifications (Jossi et al. 1975) and was made at a vessel speed of 2.8 km/h (1.5 kn).

The largest specimen was preserved in 40% isopropyl alcohol. Other larvae and juveniles were preserved in buffered 5% Formalin.[3] Some larval and juvenile specimens were stained with alizarin-red to aid in measuring and in counting body parts.

A dissecting microscope with an ocular micrometer was used to make standard measurements (Laroche 1977) on 24 specimens. The level of accuracy for micrometer measurements was 0.01 mm for measurements <1 mm and 0.1 mm for measurements >1 mm. All measurements of body length refer to standard length unless otherwise noted. Standard length was defined as the distance from the tip of the snout to the posterior tip of the notochord (before hypural formation) and the tip of the snout to the posterior margin of the hypurals (after hypural formation posterior to the notochord tip).

Larvae were defined as individuals which had absorbed the yolk sac but which had not completed differentiation of adult fin spine and ray complements. Juveniles were defined as sexually immature individuals having adult fin complements of spines and rays.

We used the serial or dynamic method of tracing certain characters back from juvenile to larval specimens (Moser and Ahlstrom 1970).

IDENTIFICATION

The genus *Lutjanus* is the most speciose in the family Lutjanidae. *Lutjanus campechanus* is 1 of 10 species of that genus which occur in U.S. waters <200 m deep (Bailey et al. 1970). *Lutjanus campechanus* occurs along the continental shelf of the

[1]Contribution No. 79-32PC, Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA.

[2]Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, 3500 Delwood Beach Road, Panama City, FL 32407.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted May 1979.
FISHERY BULLETIN VOL. 77, NO. 4, 1980

TABLE 1.—Catch data arranged chronologically for larval and juvenile *Lutjanus campechanus* from the Gulf of Mexico and adjacent waters.

Location	Depth range (m)	Latitude (N)	Longitude (W)	Period	Gear/tow	No. collected	Size (mm SL)	Temp (°C)	Salinity (‰)
St. Andrew Bay, Fla.	6	30°09'	85°41'	July 1973	10.7 headrope otter trawl, 2.5 cm stretched mesh in cod end/bottom tow	1	22.4	27.0	33.7
South Texas continental shelf	42-131	27°54' to 26°57'	96°19' to 96°48'	Sept. 1975	1 m diameter plankton net, 0.250 mm mesh; single oblique tow	59	4.0-12.4	19.7-29.2	33.7-36.4
		27°17' to 26°10'	96°23' to 96°24'						
	42-183	27°54' to 26°57'	96°19' to 96°48'	July-Sept. 1976	61 cm diameter bongo nets, 0.505, 0.333 mm mesh; double oblique tow	57	4.1-10.6	17.4-29.7	34.7-37.5
		27°15' to 26°10'	96°18' to 96°39'						
	49-131	27°30' to 27°17'	96°44' to 96°23'	May, July-Sept., Nov. 1977	As above.	17	4.2-5.8	17.3-29.8	33.4-36.5
		26°10'	96°24'						
Buccaneer Oil Field, near Galveston, Tex.	17	28°52'	94°40'	July 1977	As above, also 1.0 × 0.5 m, 0.505 mm mesh neuston net	92	4.0-7.3	23.0-26.0	32.8-35.5

Atlantic coast of the United States and in the Gulf of Mexico (Rivas 1966). The taxonomy of this species has undergone several revisions. Three specific names have been used for the Gulf of Mexico red snapper in recent literature: *L. campechanus*, *L. aya*, and *L. blackfordii* (Anderson 1967). We used the American Fisheries Society (Bailey et al. 1970) nomenclature.

To date, the only lutjanid that has had its larval stages described in the literature is *Rhomboplites aurorubens* (Laroche 1977). Identification of lutjanid larvae is difficult unless a series of the larvae and juveniles is available for study.

Juveniles of only three Atlantic species of *Lutjanus* and one specimen of *Symphysanodon* have been illustrated. Illustrations of 10.5, 14.4, 19.9, and 48.5 mm juvenile *L. griseus* have been presented by Starck (1971). A 17.8 mm *L. synagris* or *L. mahogoni* was described and partially sketched by Heemstra (1974). A 14.4 mm fork length juvenile identified as *Lutjanus* sp. was illustrated by Fahay (1975). A 20 mm juvenile *Symphysanodon* was partially illustrated in Fourmanoir (1973).

Identification of the present series of *L. campechanus* is based upon the meristic characters of the juveniles. Six juveniles (8.0-22.4 mm) had the meristic complement of adult *L. campechanus* and formed the key to the series. These counts included 24 myomeres; X, 14 dorsal fin spines and rays; III, 9 anal fin spines and rays; 9 + 8 principal caudal fin rays; 16-18 pectoral fin rays; I, 5 pelvic fin spine and rays. These counts have also been reported for *L. analis* and *L. aya* (Miller and Jorgenson 1973). However, Anderson (1967) reported that *L. analis* has a maximum of 8 anal fin soft rays. Rivas (1966) reviewed the *L. campechanus* complex of "red snappers" and stated that the species described as *Bodianus aya* by Bloch in 1790 was probably not a lutjanid. Rivas recognized only two species in the complex commonly referred to as red snappers: *L. campechanus*, from the Gulf of Mexico and the South Atlantic coast of the United States, and *L. purpureus*, from the Caribbean Sea and southeastward along the coast of the Guianas, and probably to Brazil. Rivas (1966) synonymized *L. blackfordii* with *L. campechanus*. Therefore, *L. campechanus* is the only species occurring in the northern Gulf of Mexico which has the meristic complements observed in our specimens.

DESCRIPTION

Although we collected many lutjanid larvae, only those ≥4.0 mm were identifiable as *L. campechanus*. Lutjanids <4.0 mm lacked presently recognizable characters diagnostic at the species level and, therefore, were not described. This gen-

eral lack of development has also been observed in laboratory-reared larvae of *L. campechanus* <4.0 mm (Rabalais[4]).

Pigmentation

Diagnostic melanophores occurred on various regions of the specimens (Table 2). The first melanophore to appear on the head was on the dorsal midline over the midbrain. The dorsal surface of the peritoneum was nearly covered by large melanophores in all specimens. The presence and amount of pelvic fin pigment was variable. Fading of the pigment in some specimens was probably due to the preservation and/or handling. When pelvic fin pigment was present in specimens <7.3 mm, it was located only on the fin membrane. Our undamaged specimens ≥7.3 mm had pelvic fin melanophores primarily on the most anterior soft ray (Figure 1D) and/or in the fin membrane (Figure 2B).

The largest juvenile had the most pigmentation (Figure 2C). Four vertical bars made up of small melanophores were located between the head and the caudal section. All fin membranes between the 2d and 10th posteriormost spinous dorsal rays had three melanophores between each spinous ray. The soft dorsal fin had five melanophores on the fin membranes between the 7th and 13th posteriormost rays. An additional melanophore was present near the distal end of the dorsal principal caudal rays. Unfortunately, specimens were not available to link the development of pigmentation between 12.4 and 22.4.

Fin Formation

Dorsal and pelvic fins were the first to begin development in *L. campechanus* (Figure 1A), followed by caudal, anal, and pectoral fins. The adult complement of fin spines and rays was completed in the following order: caudal (principal rays only), pelvic, pectoral, dorsal, and anal (Table 3).

Dorsal Fin

The smallest illustrated specimen had developed only the five anteriormost dorsal spinous rays (Figure 1A). Most dorsal soft rays seemed to develop simultaneously, with the exception of the posteriormost soft rays which developed last. The total adult number of dorsal fin rays (24) was present at 4.9 mm, with the 2 posteriormost dorsal

[4]N. Rabalais, University of Texas Marine Laboratory, Port Aransas, TX 78373, pers. commun. October 1978.

TABLE 2.—Number of melanophores on regions of larval and juvenile *Lutjanus campechanus*. When available, several larvae of a given size were used in determining the number of melanophores.

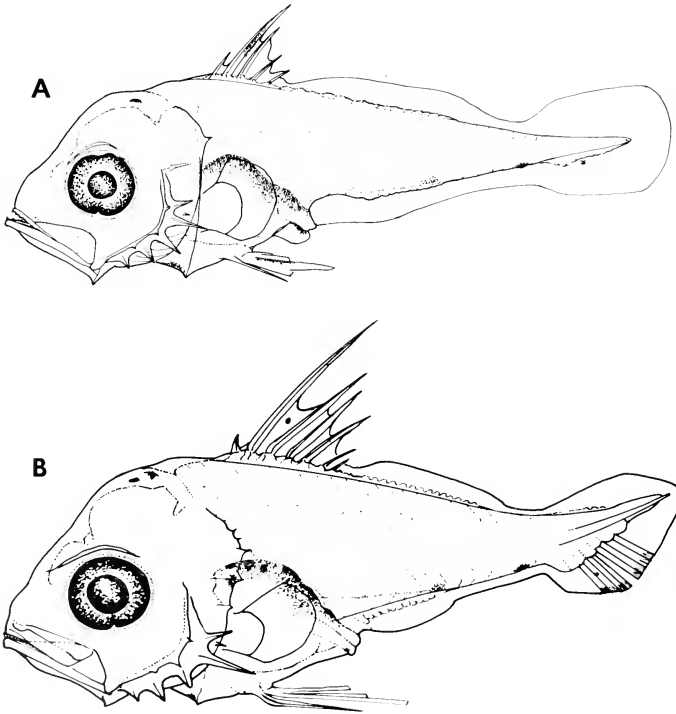
	Head				Gut		Dorsal and pelvic		Caudal			
SL (mm)	Over fore-brain	Over mid-brain	On oper-culum	On ventral midline anterior to ventral tip of cleithrum	Internal, over dorsal surfaces of peritoneum	On ventral midline just anterior to anus	Fin membrane between 2d and 3d dorsal spines	On anterior portion of pelvic fin	Internal, near posterior base of anal fin	On ventral midline of myomere no. 22-25	On ventral principal caudal rays	Internal, lateral to notochord and anterior to point of flexion
4.0	0	1	0	1	5-10	1	1-2	1-2	1	1	1	0
4.2	0	1-2	0	1	5-10	1	1-2	0-2	1	1	1	0
4.6	0	1	0	1	5-10	1	2	0-2	1	1	1	0
4.7	0	2	0	1	5-10	1	2	0-2	1	1	1	0
4.8	0	2	0	1	5-10	1	3-7	1-2	1	1	1	0
4.9	0	1-2	0	1	5-15	0-1	3-6	0-2	1	1	1	0
5.4	0	1	0	1	5-15	0-1	1-8	0-1	1	1	1	0
5.5	0	1-2	0	1	5-15	0	3-5	0-3	1	1	1	0
6.1	0	2-3	0	1	5-15	0	2-8	2-3	1	1	1	0-1
6.2	0	3-5	0	1	5-15	0	3-8	1-2	1	1	1	0-1
6.3	0	1-2	0	1	5-15	0	3-8	1-2	1	1	1	0-1
6.4	0	1-6	0	1	5-15	0	3-8	0-2	1	1	1	0-1
6.5	0	1-3	0	1	5-15	0	3-8	1-3	1	1	1	(1)
6.6	0	3-4	0	1	5-15	0	1-8	0-8	1	1	1	0-1
7.3	0	2	0	1	5-15	0	12-20	14	1	1	1	1
7.4	1	6	2	1	5-15	0	2	(1)	1	1	1	1
7.5	3	9	2	1	5-15	0	1	3	1	1	1	1
7.6	(1)	(1)	(1)	(1)	5-15	0	3-8	(1)	1	1	1	1
[2]8.0	1	13	1	1	5-15	0	3	(1)	1	1	1	1
[2]9.0	3	17	2	0	5-15	0	3-8	(1)	1	1	1	1
[2]9.5	6	30	2	0	5-15	0	3-8	3-8	1	1	1	1
[2]10.6	3	34	3	0	5-15	0	3-8	3-8	1	1	1	1
[2]12.4	7	36	1	0	5-15	0	10	6	1	1	1	1
[2]22.4	ca. 30	ca. 100	2	0	ca. 20	0	3	(1)	1	3	4	2

[1]Specimen was damaged and no count was taken
[2]Juvenile

spines represented by 2 soft rays (Table 3). At 5.4 mm the anteriormost soft ray became a spine. All specimens ≥7.5 mm had X, 14 dorsal fin spines and rays. The second dorsal spine was the longest ray in the dorsal fin in specimens 4.0-12.4 mm. In the 22.4 mm specimen, all dorsal fin rays except the first spine were about equal in length (Figure 2C). Serrations did not appear on the dorsal spines of *L. campechanus* between 4.0 and 22.4 mm.

Pelvic Fin

The smallest larva had not yet developed pelvic fin soft rays but had developed the pelvic spine (Figure 1A). The pelvic spine was smooth on the anterior margin on 4.0 and 4.7 mm specimens. Between 4.7 and 4.8 mm this spine developed ~30 fine serrations along its anterior margin. All larvae and juveniles 4.8-12.4 mm had these serrations. The number of serrations generally in-



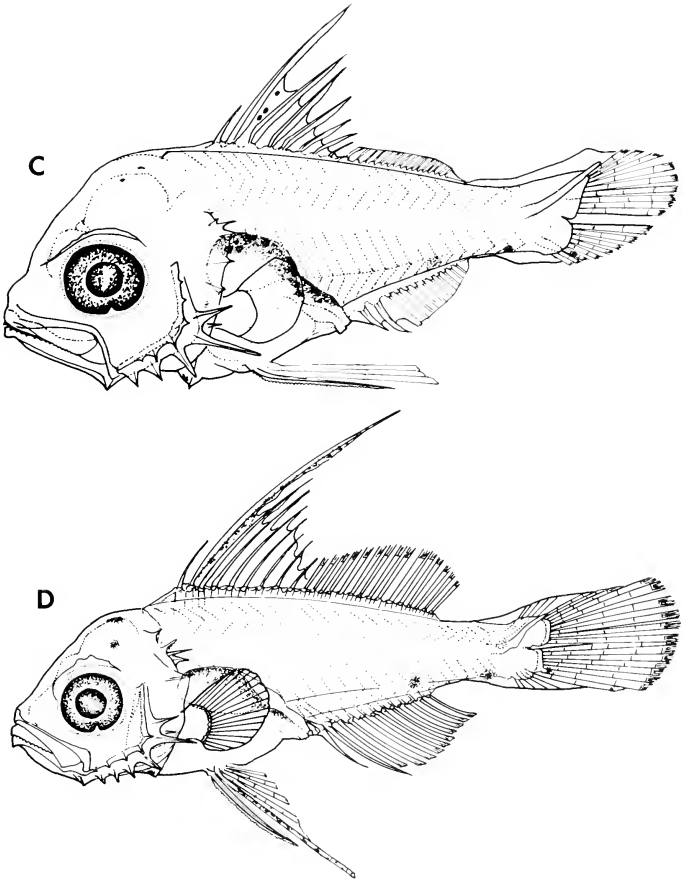


FIGURE 1.—Developmental stages of the red snapper, *Lutjanus campechanus*, larvae drawn using a camera lucida: A, 4.0 mm SL; B, 4.2 mm; C, 4.9 mm; D, 7.3 mm.

creased with specimen size between 4.8 and 12.4 mm. The 12.4 mm juvenile had ~60 fine serrations on the anterior margin of each of its pelvic spines. Between 12.4 and 22.4 mm these serrations were lost.

Three distinct pelvic rays appeared on the 4.2 mm larva in the anterior portion of the previously undifferentiated finfold (Figure 1B). Between 4.6 and 5.5 mm the pelvic fin attained the adult complement of 1 spine and 5 soft rays (Table 3).

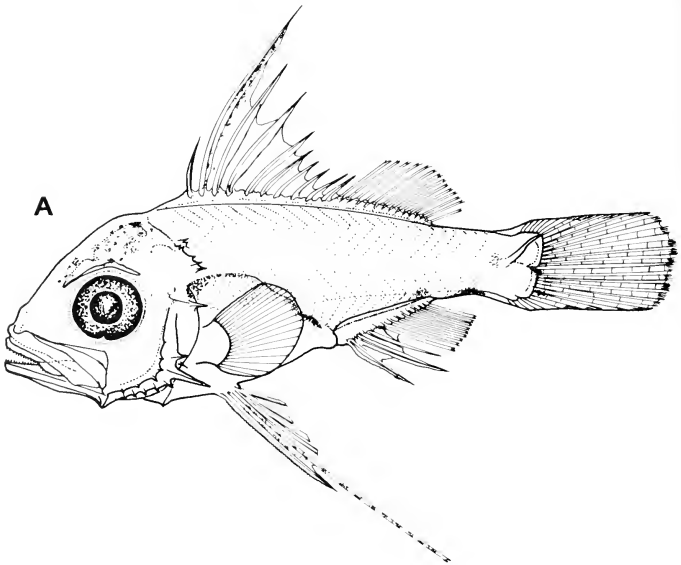
The pelvic spine was long. It extended to or beyond the anus in all but the smallest and largest specimens, 4.0 and 22.4 mm, respectively (Figures 1, 2). The pelvic soft ray closest to the pelvic spine was always the longest pelvic fin ray. Apparently this longest ray may be easily broken off during collection and handling. Approximately half of all specimens had this ray broken off. The unbroken, anteriormost pelvic ray in specimens 4.8-10.6 mm extended at least to the center of the anal fin base (Figure 1C). Specimens of 6.4, 7.3, and 9.5 mm had an unbroken ray that extended posteriorly beyond the center of the anal fin base (Figures 1D, 2A).

Caudal Fin

Caudal fin formation began at ~4.2 mm (Figure 1B, Table 3). The most ventral principal rays and those near the tip of the urostyle were the last to develop. Between 4.2 and 4.7 mm the adult complement of 17 (9 dorsal and 8 ventral) principal caudal rays developed. Notochord flexure occurred between 4.7 and 4.9 mm (Table 3).

Anal Fin

At 4.7 mm, 8 anal rays were present as 2 spines and 6 soft rays in the anteriormost part of the fin (Table 3). The posteriormost rays formed last. By 4.9 mm the adult complement of 12 rays was pres-



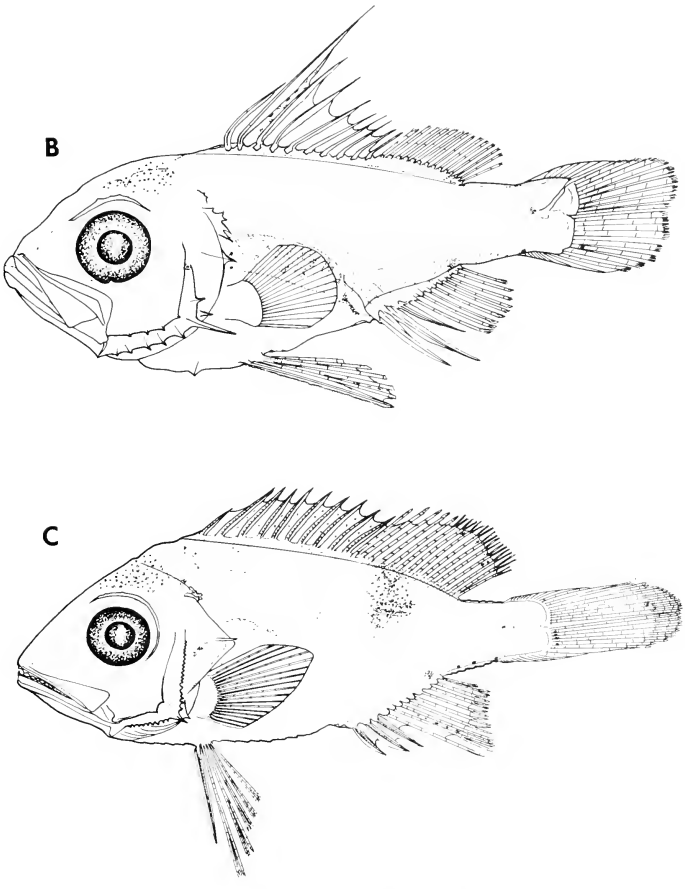


FIGURE 2.—Developmental stages of the red snapper, *Lutjanus campechanus*, juveniles drawn using a camera lucida: A, 9.5 mm SL; B, 12.4 mm; C, 22.4 mm.

TABLE 3.—Meristic characters and notochord flexure of larval and juvenile *Lutjanus campechanus*.

SL (mm)	Principal caudal fin rays		Dorsal fin		Anal fin		Pectoral fin	Pelvic fin		Notochord
	Upper	Lower	Spines	Rays	Spines	Rays	Rays	Spines	Rays	
4.0	0	0	V	0	0	0	0	I	0	Straight
4.2	4	4	VII	0	0	0	(1)	I	3	Straight
4.6	5	5	VI	0	0	0	(1)	I	3	Straight
4.7	9	8	VII	8	II	6	(1)	I	4	Flexed
4.8	9	8	VIII	11	II	8	(1)	I	4	Straight
4.9	9	8	VIII	16	II	10	(1)	I	(1)	Flexed
5.4	9	8	IX	15	II	10	(1)	I	(1)	Flexed
5.5	9	8	IX	15	II	10	(1)	I	5	Flexed
6.1	9	8	IX	15	II	10	(1)	I	5	Flexed
6.2	9	8	IX	15	II	10	(1)	I	5	Flexed
6.3	9	8	IX	15	II	10	(1)	I	5	Flexed
6.4	9	8	IX	15	II	10	(1)	I	5	Flexed
6.5	9	8	IX	15	II	(1)	(1)	I	5	Flexed
6.6	9	8	IX	15	II	10	14	I	5	Flexed
7.3	9	8	IX	15	II	10	16	I	5	Flexed
7.4	9	8	IX	15	II	10	17	I	5	Flexed
7.5	9	8	X	14	II	(1)	16	I	5	Flexed
7.6	9	8	X	14	II	10	17	I	5	Flexed
[2]8.0	9	8	X	14	III	9	17	I	5	Flexed
[2]9.0	9	8	X	14	III	9	18	I	5	Flexed
[2]9.5	9	8	X	14	III	9	18	I	5	Flexed
[2]10.6	9	8	X	14	III	9	18	I	5	Flexed
[2]12.4	9	8	X	14	III	9	18	I	5	Flexed
[2]22.4	9	8	X	14	III	9	17	I	5	Flexed

[1]An accurate count was not possible
[2]Juvenile

ent in the form of 2 spines and 10 soft rays (Figure 1C). The transformation of the anteriormost soft ray into the third anal spine occurred between 7.6 and 8.0 mm and marked the end of the larval period. Anal spines were not serrated.

Pectoral Fin

The 4.0 mm larva had only a pectoral finfold (Figure 1A). Between 4.0 and 6.5 mm ray development began, but ossification was not completed and the exact number of rays was difficult to determine. The 6.6 mm larva had 14 pectoral rays, and 2 more rays were added by 7.3 mm. The 16 rays on the 7.3 mm specimen were within the 16-18 range for adult pectoral rays (Rivas 1966). The number of pectoral rays on specimens 7.3-22.4 mm varied from 16 to 18 (Table 3).

Squamation

Scales were present on the 22.4 mm specimen only. An accurate lateral line scale count was not possible.

Head

The head of the larval and juvenile *L. campechanus* was large, ranging between 32.5 and 44.9% SL (Table 4). Head size (head length as percent of SL) generally increased in larvae and decreased in juveniles. The smallest and largest specimens had the smallest head proportions, 32.5% on the 4.0 mm larva and 34.8% on the 22.4 mm juvenile. The head was proportionally largest, 44.9 and 44.4%, on the 4.9 and 5.4 mm larvae, respectively. Head length was about equal to body depth in all specimens. Head length ranged from 32.5 to 44.9% SL and body depth from 32.5 to 43.9% SL.

TABLE 4.—Measurements and body part proportions for larval and juvenile *Lutjanus campechanus*.

SL (mm)	Head length (mm)	Head length (% SL)	Snout to anus length (mm)	Snout to anus length (% SL)	Body depth (mm)	Body depth (% SL)	Eye diameter (mm)	Eye diameter (% SL)
4.0	1.3	32.5	1.9	47.5	1.3	32.5	0.44	11.0
4.2	1.6	38.1	2.3	54.8	1.5	35.7	0.51	12.1
4.6	1.7	37.0	2.3	50.0	1.5	32.6	0.53	11.5
4.7	1.9	40.4	2.6	55.3	1.6	38.3	0.59	12.6
4.8	1.8	37.5	2.8	58.3	1.9	40.0	0.66	13.8
4.9	2.2	44.9	3.0	61.2	2.0	40.8	0.56	11.4
5.4	2.4	44.4	3.3	61.1	2.3	42.6	0.77	14.3
5.5	2.3	41.8	3.4	61.8	2.1	38.2	0.70	12.7
6.1	2.4	39.3	3.6	59.0	2.3	37.7	0.78	12.8
6.2	2.6	41.9	3.9	62.9	2.4	38.7	0.79	12.7
6.3	2.6	41.3	3.8	60.3	2.5	39.7	0.79	12.5
6.4	2.4	37.5	3.8	59.4	2.6	40.6	0.79	12.3
6.5	2.6	40.0	4.1	63.1	2.7	41.5	0.83	12.8
6.6	2.8	42.4	4.3	65.1	2.9	43.9	0.87	13.2
7.3	2.7	37.0	4.3	58.9	2.8	38.4	0.95	13.0
7.4	3.1	41.9	4.7	63.5	3.1	41.9	0.93	12.6
7.5	3.0	40.0	4.7	62.7	3.1	41.3	0.97	12.9
7.6	3.1	40.8	4.7	61.8	3.0	39.5	0.98	12.9
[1]8.0	3.2	40.0	5.1	63.8	3.3	41.3	0.99	12.4
[1]9.0	3.3	36.7	5.8	64.4	3.3	36.7	1.2	13.3
[1]9.5	3.5	36.8	5.9	62.1	3.4	35.8	1.2	12.6
[1]10.6	4.0	37.7	6.7	63.2	4.0	37.7	1.2	11.3
[1]12.4	4.8	38.7	7.9	63.7	4.7	37.9	1.4	11.3
[1]22.4	7.8	34.8	15.1	67.4	8.1	36.2	2.7	12.1

[1]Juvenile

Spines were found on the preopercle, posterodorsal margin of the operculum, posttemporal, and supracleithrum. Serrations developed on the supraocular crest.

The preopercular spines developed in two rows, one anterior to the preopercular margin and one along the preopercular margin (Figures 1, 2). Both rows had vertical and horizontal segments. The vertical segments were situated approximately perpendicular to the body midline, and the horizontal segments were situated approximately parallel to the body midline of the fish. The anteriormost row had 3-6 spines (1-3 vertically and 2-3 horizontally) in the 4.0-22.4 mm specimens. The number of anterior row spines decreased in the largest specimens. The row along the preopercular margin had 5-27 spines (2-18 vertically and 3-9 horizontally) in the 4.0-22.4 mm specimens. The number of both vertical and horizontal preopercular margin spines increased between 12.4 and 22.4 mm. Vertical spines increased by 16 and horizontal spines increased by 4 along the preopercular margin between these two lengths.

A small spine was present on the interopercle of all specimens. A larger spine was also present on the posterodorsal margin of the opercle of all specimens. (Figures 1, 2). The spine at the angle of the preopercle was the largest spine on the head. No serrations developed on this or any other preopercular spine.

A spine on the posttemporal was first present on the 7.3 mm larva. A second spine developed on this bone by 9.5 mm. These 2 posttemporal spines were greatly reduced in the two largest specimens. A supracleithral spine was present on the smallest larva (4.0 mm). Three spines were present by 4.2 mm, and 5 spines had developed by 9.5 mm (Figures 1A, B; 2A). The 2 most ventral supracleithral spines were longer in the 12.4 mm specimen than in smaller specimens. The 22.4 mm juvenile had all of the supracleithral spines, but these spines were much smaller (Figure 2C).

Two serrations developed on the supraocular crest by 7.3 mm (Figure 1D), and two more by 12.4 mm. The 22.4 specimen had no serrations on the supraocular crest (Figure 2C).

Eye diameter was 11.0-14.3% SL (Table 4). The eye was almost spherical, and the iris had a ventral cleft in all but the largest specimen (Figures 1, 2).

Teeth were present in all specimens on the dentary and premaxillary bones. In addition, the two largest specimens (12.4 and 22.4 mm) had vomerine and palatine teeth. The vomerine teeth in these two specimens were arranged in a V-shaped pattern with the angle pointed anteriorly.

TABLE 5.—Predictive linear regressions of body measurements on standard length for 24 larval and juvenile *Lutjanus campechanus* over the size range 4.0-22.4 mm SL.

Measurement	Slope	Intercept	$S_{y \cdot x}$	r
Head length	0.341	0.350	0.177	0.991
Body depth	0.699	-0.601	0.159	0.998
Snout to anus length	0.359	0.197	0.181	0.992
Eye diameter	0.118	0.050	0.054	0.993

Body Growth

Measurements of four body parts are given in Table 4. The growth of these parts in relation to standard length is described by linear regressions (Laroche 1977; Sokal and Rohlf 1969), the statistics for which are presented in Table 5. All relationships have high correlation coefficients of ≥ 0.991.

Comparison With Other Lutjanid Larvae and Juveniles

As stated earlier, *R. aurorubens* is the only lutjanid to have previously had its larval and juvenile stages described. The two snappers are easily separated as follows: In specimens ≥ 4.0 mm, *R. aurorubens* has serrations on the largest spine at the preopercular angle. Figure 1A in Laroche (1977) did not show the serrations on this spine, however, the text stated that, "A large, stout, and serrated spine occurs at the preopercular angle in all specimens." Laroche[5] confirmed this. In addition, large serrations develop on the anterior and posterior margins of the dorsal and pelvic spines in larval *R. aurorubens* ≥ 4.7 mm. None of the 4.0-4.7 mm *L. campechanus* had serrated preopercular, dorsal, or pelvic spines. Both species have serrated pelvic spines in specimens >4.8 mm, but *R. aurorubens* has large serrations on the anterior and posterior margins while *L. campechanus* has small serrations on just the anterior margin. The total number of rays in the dorsal and anal fins also separates these two snappers at sizes ≥ 5.0 mm. *Rhomboplites aurorubens* has 22 or 23 dorsal and 11 anal rays while *L. campechanus* has 24 dorsal and 12 anal rays. *Rhomboplites aurorubens* is the only lutjanid to have an adult complement of

[5]W. A. Laroche, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. June 1978.

12 dorsal spines. All other members of the Lutjanidae have 10 spines. Finally, the head length of *R. aurorubens* is greater than the body depth (Laroche 1977), while in *L. campechanus* head length is about equal to body depth (Table 4).

Identification of the larvae and juveniles of other lutjanid species is more difficult than that of *L. campechanus* and *R. aurorubens*, since the meristic characters are very similar in most other species of lutjanids. At the present time, field-collected lutjanid larvae <4.0 mm can be identified only to family. Laboratory rearing presents the most likely solution to the larval and juvenile lutjanid taxonomic problem.

ACKNOWLEDGMENTS

We thank Suzanne Christoff for making the illustrations and Barbara Y. Sumida and William J. Richards for furnishing information on illustrating techniques. We are indebted to Arthur W. Kendall, Jr., both for assistance in the identification of all but the largest specimen and for the preliminary review of most of our illustrations. We are grateful to Larry H. Ogren who collected and identified the largest specimen. We thank William D. Anderson, Jr., Edward D. Houde, G. David Johnson, Wayne A. Laroche, William J. Richards, and Bruce W. Stender for reviewing the manuscript.

LITERATURE CITED

ANDERSON, W. D., JR.
1967. Field guide to the snappers (Lutjanidae) of the western Atlantic. U.S. Fish Wildl. Serv., Circ. 252, 14 p.

ARNOLD, C. R., J. M. WAKEMAN, T. D. WILLIAMS, AND G. D. TREECE
1978. Spawning of red snapper (*Lutjanus campechanus*) in captivity. Aquaculture 15:301-302.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc., Spec. Publ. 6, 149 p.

BEAUMARIAGE, D. S., AND L. H. BULLOCK.
1976. Biological research on snappers and groupers as related to fishery management requirements. *In* H. R. Bullis, Jr. and A. C. Jones (editors), Proceedings: Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean, p. 86-94. Fla. Sea Grant Rep. 17. FSUS-76-R-17.

BRADLEY, E., AND C. E. BRYAN.
1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970-1974. Gulf Caribb. Fish. Inst., Proc. 27th Annu. Sess., p. 77-106.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

FOURMANOIR, P.
1973. Notes ichthyologiques (V). Cah. O.R.S.T.O.M. Ser. Oceanogr. 11:33-39.

HEEMSTRA, P. C.
1974. On the identity of certain eastern Pacific and Caribbean postlarval fishes (Perciformes) described by Henry Fowler. Proc. Acad. Nat. Sci. Phila. 126:21-26.

JOSSI, J. W., R. R. MARAK, AND H. PETERSON, JR.
1975. At-sea data collection and laboratory procedures. MARMAP survey I manual. National Marine Fisheries Service, Wash., D.C., 115 p.

LAROCHE, W. A.
1977. Description of larval and early juvenile vermilion snapper, *Rhomboplites aurorubens*. Fish. Bull., U.S. 75:547-554.

MILLER, G. L., AND S. C. JORGENSON.
1973. Meristic characters of some marine fishes of the western Atlantic Ocean. Fish. Bull., U.S. 71:301-312.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

RIVAS, L. R.
1966. Review of the *Lutjanus campechanus* complex of red snappers. Q. J. Fla. Acad. Sci. 29:117-136.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freemen and Co., San Franc., 776 p.

STARCK, W. A., II.
1971. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. *In* W. A. Starck II and R. E. Schroeder, Investigations on the gray snapper, *Lutjanus griseus*, p. 11-150. Stud. Trop. Oceanogr. (Miami) 10.

ISOLATION OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, POPULATIONS OFF SOUTHERN CALIFORNIA

MILTON S. LOVE[1]

ABSTRACT

Movements of the olive rockfish, *Sebastes serranoides*, off Santa Barbara, California, were investigated, using mechanical and parasite tags. The movements were restricted over shallow reefs though somewhat less so around deeper oil platforms. Highly restricted movements may cause greater vulnerability of populations to overfishing—comparisons of olive rockfish size frequencies between two reefs indicated that fishing pressure had reduced olive rockfish populations to almost all prereproductive individuals on the more heavily fished site.

Rockfishes, genus *Sebastes* (Family Scorpaenidae), form a most diverse fish group along the California coast. Some 57 species are found in these waters (Miller and Lea 1972), inhabiting virtually every marine habitat from estuarine (occasionally) and intertidal waters to depths of more than 610 m (Miller and Lea). Rockfish are very important to both sport and commercial fishing industries; in California waters in 1974, rockfish ranked third in the commercial fishery (poundage landed) and first in the sport fishery (numbers landed) (McAllister 1976).

California species can be roughly divided into two bathymetric groups: shallow species that inhabit subtidal areas of reef and kelp, and those that live in relatively deep water (deeper than about 70 m). All species are ovoviviparous, producing pelagic larvae. There is some evidence that the shallow water species may remain within a relatively small area of reef or kelp (Miller and Geibel 1973).

A species that consists of relatively sedentary, reef-oriented aggregations would present potential problems in management, as certain management strategies presuppose movements of this fish (Harden Jones 1968; Cushing 1968). If the exploited species inhabits reefs, for example, it might soon be decimated at a heavily fished reef if individuals were parochial and did not move from an unexploited site to repopulate the depleted one. Obviously, a management strategy to protect this type of segregated reef species would differ from that for a species whose individuals move between sites. Many rockfish species grow very slowly (Phillips 1964; Chen 1971: Westrheim and Harling[2]). Thus, even if a depleted reef were densely settled by a successful year class, it would not harbor adults for a number of years. Before then, the subadults would probably be caught before the age of first maturity, so the reef would effectively be lost as a site of propagation for the species. If this process continued through all available reef sites, the fisheries would be endangered.

On the other hand, a rockfish species whose individuals move freely from reef to reef may be less vulnerable to such perturbations. Even a locally depleted reef could be sufficiently repopulated by adults during breeding season because of the typically high fecundity of females (Phillips 1964) and great dispersability of pelagic larvae. Thus the fishery might be effectively managed by conventional procedures of establishing catch limits, etc.

The olive rockfish, *Sebastes serranoides*, inhabits reefs and kelp beds from San Benito Island, Baja California, north to Redding Rock, Del Norte County, northern California, and from intertidal waters (juveniles) to 146 m (Miller and Lea 1972). The species is most common in southern and central California from surface waters to depths of about 75 m. It is a major sport fish throughout much of the state (Miller and Gotshall 1965), particularly in southern and central California. Objectives of the present study were to determine whether individuals move from reef to reef and if average size was smaller at heavily fished reefs.

[1]Department of Biological Science, University of California, Santa Barbara, Calif.; present address: Department of Biology, Occidental College, 1600 Campus Road, Los Angeles, CA 90041.

[2]Westrheim, S. J., and W. R. Harling. 1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Fish. Mar. Serv. (Can.), Res. Dev. Dir. Tech. Rep. 565, 12 p.

Manuscript accepted May 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980

METHODS

Artificial Tagging

Between 26 October 1973 and 17 October 1976, 1,847 olive rockfish (19-43 cm total length, TL) were tagged and released upon capture at 18 sites off southern California (Figure 1, Table 1). Generally, sites were selected either on the basis that they were reefs regularly fished by partyboats or private vessels, which maximized the opportunity to recapture tagged animals; or that sites had to be within 2 km of another regularly fished reef that harbored olive rockfish, which maximized the opportunity to recover fish that move short distances. The exception was Naples Reef, which had no other suitable site within 2 km. Naples Reef was included because its fish fauna was being studied intensively by other scientists. Only a few fish were tagged at some sites, such as Anacapa Island, Platform Holly, and Avila, either because olive rockfish were infrequent there or because the sites were relatively remote from Santa Barbara.

The tags (yellow Floy[3] anchor type FD-67c) consisted of a plastic tube 42 mm long with a 15 mm nylon stem and a 10 mm cross bar attached to the stem and were inserted with a Floy tagging gun, FDM 68, with a heavy-duty needle 2 cm long. My name, Department of Biology, UCSB, and a number were printed on each tag. The anchor was injected into the dorsal musculature between the second and third dorsal spines, leaving the brightly colored end free. Even though bryozoan growth completely obscured the legend within a few months, this growth was easily rubbed off by a person's finger when the tag was read.

Fish were caught by hook and line aboard research vessels and sportfishing partyboats, then measured, tagged, and returned to the water. Because of expanded gas in their swim bladders, fish taken at depths greater than about 20 m had to be deflated before they could return to depth. Perhaps 10% of all fish tagged required deflation, using a technique modified slightly from Gotshall (1964). A 3.8 cm, 18 gage hypodermic needle was inserted through the body wall into the swim bladder. However, instead of placing both fish and needle underwater, then waiting for the gas bubbles to stop emanating from the needle, gas was sucked from the bladders to speed the process, and if needed, the fish's everted stomach was pushed back into place. About 20% of the inflated fishes died either before or immediately after being returned to the water. Undoubtedly others that swam downward also died; of six fish placed in a tank after deflation, two died within 1 day and the rest survived for 2 wk, to the end of the test. Eliminated were all fish whose eyes were everted by gas expansion in the choroid plexa. Experience with *S. caurinus*, *S. paucispinis*, and *S. serranoides* indicates that this condition frequently leads to blindness and/or death, whether or not pressure is released.

Tagging mortality in fish that did not have to be deflated was probably low. Ten of 12 tagged olive rockfish lived for 2 mo in an aquarium, two dying after about 1 mo, apparently of a fungal infection. I saw none of the extensive hemorrhaging previously observed in Floy-tagged Pacific mackerel, *Scomber japonicus* (Gregory[4]).

TABLE 1.—Descriptions and locations of tagging sites for olive rockfish near Santa Barbara, Calif. For locations of sites see Figure 1 also.

Site and description
Diablo Canyon, Avila—11 km west of Avila Harbor, 9 m reef in 33 m, 0.3 km offshore
Naples Reef—24 km west of Santa Barbara, 1.6 km offshore, in 8-10 m, surrounded by 16-20 m deep sand flats
Oil Platform Holly—18 km southwest of Santa Barbara, in 60 m, about 3.2 km offshore
1 Mile Reef—2 km southeast of Santa Barbara, 2-6 m reef in 30-35 m
Horseshoe Reef—10 km east of Santa Barbara. Average depth 8-10 m, surrounded by 12-13 m
Oil Platform Hilda—8.7 km east of Santa Barbara, 3.1 km offshore in 34 m
4 Mile Reef—6.4 km southeast of Santa Barbara, 6-8 m pinnacle in 40 m
Oil Platform Hillhouse—10.4 km southeast of Santa Barbara, 8.9 km offshore in 58 m
Oil Platforms Houchin, Hogan, Hope—About 14.0 km southeast of Santa Barbara, about 7 km offshore in 50 m
Talcott Shoals, Santa Rosa Island—64.0 km southwest of Santa Barbara, 2-15 m pinnacles in 4-45 m
Fraser Pt., Santa Cruz Island—46 km south of Santa Barbara, 2-6 m reefs in 12-15 m
Smugglers Cove, Santa Cruz Island—40 km southeast of Santa Barbara
Anacapa Island—43 km southeast of Santa Barbara
Rincon Oil Island—19 km east of Santa Barbara (not figured)
Deephole Reef—68 km east of Santa Barbara, 2-6 m reefs in 24-28 m, about 1.8 km offshore (not figured)

Biological Tagging

I analyzed the parasite mix of olive rockfish to determine the feasibility of using parasites as "biological tags." Differences in parasite infection

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Gregory, P. A. 1977. Results of tagging mortality experiments on Pacific mackerel, *Pneumatophorus japonicus*. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 40, 21 p.

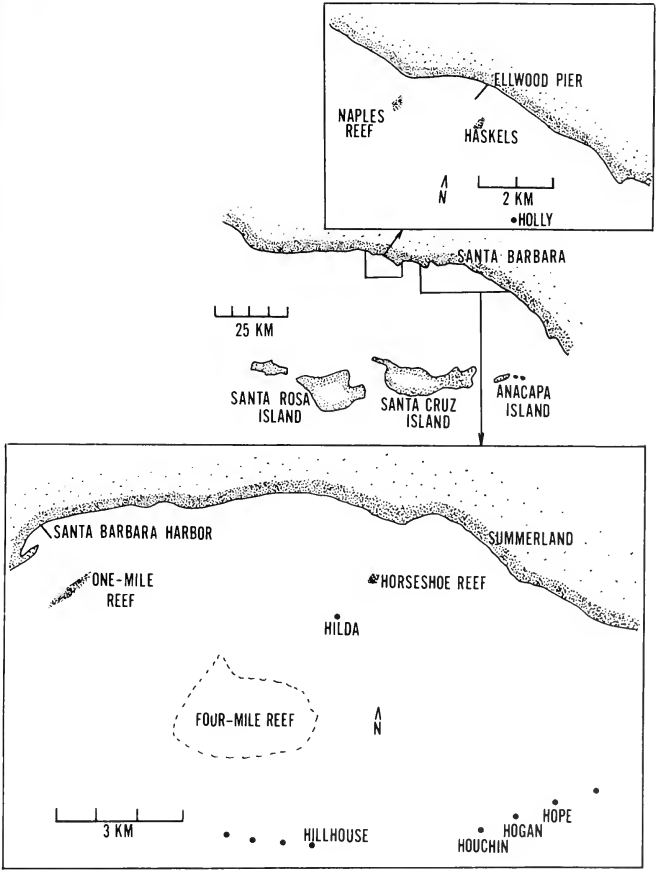


FIGURE 1.—Location of tagging and sampling sites for olive rockfish near Santa Barbara, Calif. Specific sites are described in Table 1. Deep Hole Reef (68.6 km east of Santa Barbara) and Rincon Oil Island (19 km east of Santa Barbara) are not included.

rates between host groups within a species can indicate reduced movement of fish between populations (Kabata 1963). Twenty olive rockfish from each of six sites (Naples Reef, Ellwood Pier, Horseshoe Reef, 4 Mile Reef, and oil platforms Houchin and Hillhouse—Figure 1) were sampled quarterly by hook and line or spear, between June 1976 and March 1977, placed on ice and frozen for later dissection. After thawing, fish were measured and were examined for parasites on the external surfaces as well as the gills, gill cavities, mouth, mesentery, heart, gallbladder, stomach, intestine, and muscle. Initially, copepods and monogenetic and digenetic trematodes were fixed in an alcohol-formaldehyde-acetic acid (AFA) solution and the trematodes were stained with Harris' hematoxylin, cleared with xylene, and mounted. Protozoans were studied unpreserved after thawing. Because most of the parasites recurred frequently, only those not readily indentifiable were preserved in the latter parts of the study.

After a year of sampling, it was apparent that the Ellwood Pier population was the only one not infected with the gill monogenean, *Microcotyle sebastis*. To test whether environmental conditions precluded *M. sebastis* from the site, 21 tagged, infected fish from the Horseshoe Reef were introduced into the Ellwood site. Specimens were collected after 1 and 6 mo.

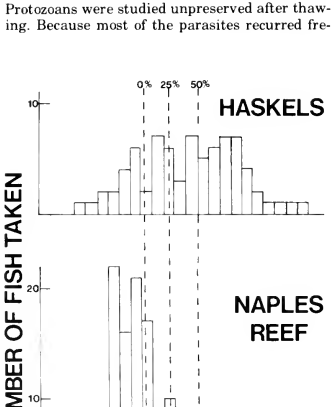


FIGURE 2.—Size frequencies of olive rockfish taken by partyboat at a heavily fished (Naples Reef) and lightly fished (Haskels) site (Naples Reef—N = 121, $\bar{x}$ = 27.3, SD = 2.5; Haskels—N = 76, $\bar{x}$ = 32.8, SD = 4.4). Dashed lines indicate size at which 0%, 25%, and 50% of the fish were mature.

Size Variation

To test whether heavy fishing pressure altered the size composition of olive rockfish on reefs, I compared size frequencies of fish taken by a sport fishing partyboat at Naples Reef (13 trips) and at a portion of the mainland bed called "Haskels" (four trips), which lies inshore and east of Naples Reef. A 4-yr study of partyboat operations indicated that Haskels had been fished by partyboats no more than four times in 5 yr.

Data on size and maturity of olive rockfish (Figure 2) was taken from Love (1978), who examined 365 individuals from off Santa Barbara. The gonads of mature olive rockfish undergo marked annual changes, similar to those in the Pacific ocean perch, *Sebastes alutus*, (Westrheim 1975) and mature individuals are readily distinguished from immature specimens, based on gonad size and color.

RESULTS

Of the 1,847 fish artificially tagged, 216 were recovered, an 11.2% return (Table 2), and 9 were recaptured twice. Recaptured fish were at large 1-514 days. Highest return rates were from Horseshoe Reef (34.6%), Naples Reef (23.7%), and the

TABLE 2.—Percentage recapture of tagged olive rockfish at the study sites off Santa Barbara, Calif.

Site	Number tagged	Median time at large (days)	Percentage recovered
Horseshoe Reef	75	309	34 6
Naples Reef	177	156	23 7
Platforms Houchin, Hogan, Hope	513	172	15 2
Talcott Shoals, Santa Rosa Island	159	371	9 4
Fraser Pt , Santa Cruz Island	81	302	7 4
Deephole Reef	369	42	6 5
Rincon Oil Island	17	18	5 8
1 Mile Reef	240	291	5 0
4 Mile Reef	99	112	3.0
Other sites[1]	117	—	0 0
Total	1,847		11 2

[1]Platform Hilda, Platform Holly, Anacapa Island, Smuggler's Cove

three oil platforms off Summerland (15.2%), all of which were heavily fished by partyboats. Eighty-one percent of all returns were made by partyboat fishermen.

Only the fish tagged around the Summerland oil platforms showed any movements; here nine moved from one platform to another (about 0.8 km).

Regarding biological tags, only the incidence of infection of *Microcotyle sebastis* (Table 3) differed significantly among study sites. Naples Reef and Ellwood Pier differed significantly from the other four sites: a G-test of independence (Sokal and Rohlf 1969) was significant when all six sites were included ($G = 186.45$, $P<0.005$), but not significant when only the oil platforms, 4 Mile Reef, and Horseshoe Reef were included ($G = 1.14$, $0.9>P>0.5$). Naples Reef also differed significantly from Ellwood Pier ($G = 16.8$, $P<0.005$).

There was no seasonality in incidence of infection, as G-tests of independence among four seasons were not significant for any site (Table 3).

To test whether environmental conditions at Ellwood Pier were suitable for the monogenetic trematodes, tagged fish from Horseshoe Reef infected with *M. sebastis* were introduced into the site. Untagged fish were collected 1 and 6 mo later. After 1 mo 2 of 20 untagged fish (10%) were infected and after 6 mo 7 of 20 (35%) were infected (not a significant difference, $G = 3.6$, $0.1>P>0.05$). The presence of *M. sebastis* in the population seems to indicate that conditions were suitable for the trematode.

Fish lengths averaged significantly shorter ($t = 9.3$, $P<0.001$) at the heavily fished Naples Reef than at the lightly fished Haskels site (Figure 2). Most fish taken from Naples Reef were prereproductive, while mature individuals made up about 45% of the Haskels catch.

DISCUSSION

Kabata (1963) lists five criteria which should ideally be met if a parasite is to be useful as a tag: 1) the parasite should be common in one population and rare or absent in another; 2) the parasite should have a direct life cycle, infecting only one host species during its life; 3) the parasitic infection should be of fairly long duration; 4) the incidence of infection should stay relatively stable; 5) environmental conditions throughout the study site(s) must be within the physiological tolerance of the parasite.

Compared with artificial tags, biological tags have both advantages and disadvantages. Artificial tags may alter the normal behavior of the tagged animal, whereas, in most cases, parasites do not. Moreover, the parasite mix of a population is usually the result of long-term processes, and may be a more accurate indicator of movements than short-term tagging studies. On the other hand, parasite tags will not indicate individual movements. Over the past 20 yr, studies using parasites as tags have delineated nursery grounds (Olson and Pratt 1973), spawning grounds (Margolis 1963; Hare and Burt 1976), and discrete or semidiscrete populations (Sindermann 1961; Kabata 1963).

Results of both artificial and biological tagging indicated that olive rockfish rarely moved between shallow water reefs. A good example of this was the apparent lack of movement between Naples Reef and Ellwood Pier. Though only about 2 km apart, no tagged Naples Reef fish were taken at Ellwood Pier or anyplace else, nor were any of the *M. sebastis* found to be infecting Ellwood Pier fish before I introduced it, though they infect Naples Reef fish.

Like other monogeneans, *M. sebastis* has a direct (one host) life cycle. The maximum distance the infective oncomiricidium larval stage can travel before finding a host is not known, though it is probably limited to a few meters (Llewellyn 1972). Apparently, Ellwood fish were not parasitized because they were sufficiently isolated

TABLE 3.—Incidence of parasite *Microcotyle sebastis* in 80 olive rockfish sampled 20/mo from each of six sites off Santa Barbara, Calif. P values reflect G-tests of independence (Sokal and Rohlf 1969) for incidence of infections among four seasons.

Site	Number infected (1976-77)				Total	P	Percent
	June-Aug	Sept-Nov	Dec-Feb	Mar-May			
Ellwood Pier	0	0	0	0	0	—	0.0
Naples Reef	4	3	3	4	14	$0.9>P>0.5$	17.5
Platform Houchin	12	12	14	15	51	$0.5>P>0.1$	63.8
Platform Hillhouse	10	14	13	15	52	$0.9>P>0.5$	65.0
Horseshoe Reef	14	11	15	15	55	$0.9>P>0.5$	68.8
4 Mile Reef	17	13	15	12	57	$0.9>P>0.5$	71.2

from others to escape exposure to infected fish, even pelagic larvae.

Yet, neither tagging nor parasite data indicated whether fish move offshore from the Ellwood area to Naples Reef. However, size-frequency data of fish taken on Naples Reef and at Haskels (adjacent to the Ellwood Pier) (Figure 2), are evidence that there was probably little movement from Ellwood to Naples. Naples Reef harbors primarily juvenile and preadult olive rockfish (Love and Ebeling 1978) and adults are rarely observed (Ebeling[5]). Apparently, fishing pressure removes fish before they can mature. However, adults were abundant at the lightly fished Ellwood Pier, and limited sampling along a 16 km stretch of kelp inshore of Naples Reef indicated that mature fish were common throughout the bed. Apparently, few of these fish move across the sandy stretch between Naples Reef and the inshore bed.

Though inshore movements seem to be inhibited by stretches of sandy bottom, movement from one oil platform to another obviously is not: tagged fish must traverse at least 0.8 km over sandy bottom with a depth of about 50 m to reach the adjacent site. Miller and Geibel (1973) observed a similar greater mobility in deep waters for blue rockfish, *S. mystinus*.

Olive rockfish off Santa Barbara feed primarily on midwater organisms (nekton and plankton) rather than substrate-oriented prey (Love and Ebeling 1978). It is not known whether these prey are less abundant at the platforms compared with inshore waters. However, if they are less abundant, olive rockfish might be more likely to leave the platform to follow prey. I have noted olive rockfish feeding on anchovies as much as 300 m away from the platforms. Perhaps in these instances some fish may not return to the original platform.

This study emphasized movements of fish that inhabit isolated reefs. Little work was done on fish from the extensive area of continuous kelp forest which grows mostly on sandy bottom and parallels most of the Santa Barbara coast, because sampling is more time consuming in such areas of low rockfish densities. Moreover, much of the tagging was done aboard partyboats which rarely fish these extensive beds. It is quite possible that olive rockfish in kelp beds move about considerably more than those on isolated reefs. I suspect that the limited movements observed may be due to the lack of cover on the relatively barren bottom surrounding the reeflike study sites. Olive rockfish have been rarely taken over sand, either in otter trawls (Ebeling et al.[6]), or seen in underwater transects in kelp beds over a sand bottom (Quast 1968), and seem to be strongly attracted to high-relief substrate, such as that of platforms and rocky reefs. Kelp beds may provide "bridges" from one reef to another.

Previous studies (Table 4) indicate that many other shallow water rockfish exhibit limited movements. The two most extensively investigated benthic species, *S. carnatus* and *S. chrysomelas*, defend small feeding territories and shelter holes (Larson 1977; Hallacher 1977). Also, agonistic displays by *S. serriceps* (Feder et al. 1974; Haaker 1978) and long-term residence in particular crevices by *S. nebulosus* (McElderry[7]) indicate that these benthic species may also be territorial. Thus, it seems likely that most or all benthic reef rockfish may move relatively little.

Similarly, some midwater rockfishes that live over these shallow reefs, seem to stay within a fairly small area. In particular, tagging of *S. mystinus* (Miller and Geibel 1973) indicated restricted movements, and tagging of *S. flavidus* (Carlson and Haight 1972) showed that this species has a strong homing tendency. However, movements of tagged *S. melanops* (Coombs 1979), along with pelagic capture (Dunn and Hitz 1969) indicate that it probably moves about extensively.

Relatively parochial midwater rockfish, such as *S. mystinus*, *S. serranoides*, and *S. flavidus*, do not appear to be territorial, in the sense that a territory is a "defended" (Noble 1939) or "exclusive" (Schoener 1968) area. Indeed, these species often form single or multispecies aggregations of thousands of individuals, which show little or no agonistic behavior. The sizes of rockfish home ranges have not been estimated, though Miller and Houk[8] believed that *S. mystinus* aggrega-

[5]Ebeling, Alfred W. Department of Biological Sciences, University of California, Santa Barbara, CA 93106, pers. commun. February 1978.

[6]Ebeling, A. W., W. Werner, F. A. Dewitt, Jr., and G. M. Cailliet. 1971. Santa Barbara oil spill: short-term analysis of macroplankton and fish. EPA, Water Qual. Off. Doc. no. 15080EA02/71, 68 p.

[7]H. McElderry Department of Biology, University of Victoria, Victoria, B.C. pers. commun. January 1978.

[8]D. Miller and J. Houk, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. January 1978.

TABLE 4.—Summary of published observations on rockfish, *Sebastes* spp., movements in the northeast Pacific.

Species	Location	Method	Results	Source
S. alutus	Northeast Pacific Ocean	Analysis of fish catch data	Seasonal bathymetric movements of many kilometers and 100 m in depth	Review in Gunderson (1977)
S. atrovirens	Monterey, Calif.	Tagging	No movement	Miller and Geibel (1973)
S. auriculatus	Monterey	Tagging	No movement	Miller and Geibel (1973)
	Humboldt Bay, Calif.	Tagging	No movement	DeWees and Gotshall (1974)
S. carnatus	Santa Barbara Channel, Calif.	Underwater observation, tagging	Has home range, no evidence of extensive movement	Larson (1977)
	Monterey region, Calif.	Underwater observation, tagging	No movement	Hallacher (1977)
S. caurinus	Monterey Bay, Calif.	Tagging, underwater observation	Limited movement, farthest 2.4 km	Miller and Geibel (1973)
	Monterey region	Tagging	No movement	Hallacher (1977)
	Humboldt Bay	Tagging	No movement	Dewees and Gotshall (1974)
	Puget Sound, Wash.	Underwater observation	Fewer individuals seen in shallow water during summer	Dewees and Gotshall (1974) Patten (1973)
	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
S. chrysomelas	Santa Barbara Channel	Underwater observation, tagging	Species has home range, no evidence of extensive movement	Larson (1977)
	Monterey region	Underwater observation, tagging	No movement	Hallacher (1977)
	Monterey Bay	Tagging	No movement	Miller and Geibel (1973)
S. flavidus	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
	Alaska	Tagging	Homing study: species homed up to 22.5 km	Carlson and Haight (1972)
S. melanops	Monterey	Tagging	No movement	Miller and Geibel (1973)
	Humboldt Bay	Tagging	No movement	DeWees and Gotshall (1974)
	Oregon	Tagging	Limited number of recoveries, 2 of the 10 recovered fish moved, one 619 km, other 24 km	Coombs (1979)
	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
	Gulf of Alaska	Capture	Review of pelagic captures	Dunn and Hitz (1969)
S. miniatus (Juv.)	Redondo Beach, Calif.	Tagging	Movement of 8-9.6 km	Turner et al. (1969)
(Juv.?)	Monterey	Tagging	No movement	Miller and Geibel (1973)
S. mystinus	Southern to northern Calif.	Tagging	Generally little or no movement, slight movement in deeper water	Miller and Geibel (1973)
	Monterey Bay	Tagging	Restricted movement	
S. pinniger	Monterey Bay	Tagging	No movement	Miller and Geibel (1973)
S. rosaceus	Monterey region	Underwater observation	No movement	Hallacher (1977)
S. ruberrimus	Oregon	Tagging	No movement	Coombs (1979)
S. serranoides	Santa Monica Bay, Calif.	Tagging	No movement	Turner et al. (1969)
	Santa Barbara Channel	Tagging	No movement in shallow water, limited movement in deeper water	Present paper

tions are quite patchy within a kelp bed and some fish may remain within a very limited area for extended periods. In kelp beds, individuals of *S. serranoides* may move about more than those of *S. mystinus*. Miller and Houk noted that *S. serranoides* individuals were not seen as consistently as those of *S. mystinus* in kelp-bed transects in Monterey Bay. As *S. mystinus* preys primarily on plankton and animals on plant surfaces (Gotshall et al. 1965; Hallacher 1977; Love and Ebeling 1978), it seems likely that this species spends much of its time waiting for prey to drift by. *Sebastes serranoides* feeds somewhat more on moving prey (Love and Ebeling 1978) and so may forage more widely.

Some seasonal movement of rockfish may also occur, at least north of Pt. Conception. A number of studies report that rockfish numbers on shallow water reefs seem to decrease during winter (Miller and Geibel 1973; Moulton 1977; Burge and Schultz[9]). Increased turbulence may drive the fish into deeper water or into reef shelters where they are less visible. Ebeling (see footnote 5) observed no winter decrease in rockfish abundance at Naples Reef. The waters of the Santa Barbara Channel are considerably less turbulent

[9]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

than those above Pt. Conception; perhaps here fish can remain on the reefs despite winter storms. Miller and Geibel (1973) noted a sharp winter decrease in *S. mystinus* numbers on a reef in Monterey Bay. Yet despite extensive tagging at this site and intensive sampling and underwater observation of surrounding reefs during winter, no tagged individuals were found at other reefs (Miller and Houk see footnote 8). Factors other than turbulence may account for a winter exodus. Some rockfish species may leave inshore reefs to spawn. If fish do leave the reef, the extent of their movement is, in general, not known. Moulton (1977) found that during winter rockfish on Puget Sound reefs retreated only short distances, into slightly deeper water.

The between site difference in mean fish length found between Naples Reef and Haskels probably reflects a difference in fishing pressure. The more heavily fished site averaged smaller fish and fewer mature ones because larger fish were selectively angled, or have been subjected to fishing effort for a longer period and are thus more likely to be caught.

As heavily fished sites contain primarily prereproductive individuals (as, in general, does Naples Reef), reproduction of mature fish at lightly fished sites could account for much of the recruitment for all areas.

Based on data from mechanical and parasite tags, olive rockfish off Santa Barbara exhibit very restricted movements on shallow water reefs, but may be somewhat more mobile around deeper water oil platforms. The species' parochialism in shallow water makes it susceptible to overexploitation as interchange of individuals from other reefs is rare.

ACKNOWLEDGMENTS

I thank Alfred W. Ebeling, Alice Alldredge, Bruce Robison, and Elmer Noble for critically reading the manuscript and their suggestions. Norm Lammer provided technical help with boating operations. Fred Benko of Sea Landing Sportfishing graciously allowed me space on partyboats for sampling. I particularly thank partyboat operators Chet Phelps, Irv Grisbeck, Frank Hampton, George Kelly, and Dick Clift for making sampling possible and pleasurable.

Dave Laur, Lew Haldorson, Tony Hampton, Merritt McCrea, Ken Du Mong, and Dennis Evans assisted in specimen collections, and three anonymous reviewers made helpful suggestions. I thank my wife, Regina Paull-Love, for typing the manuscript and for her support and assistance, and Sara Warschaw and Jessica Schulz for typing successive drafts.

This work was sponsored by NOAA, Office of Sea Grant, U.S. Department of Commerce, under grant no. 04-7-158-44121 (Project r/f-39) and NSF Grant OCE 76-23301.

LITERATURE CITED

CARLSON, H. R., AND R. E. HAIGHT.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011-1014.

CHEN, L.-C.
1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus Sebastomus (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. Univ. Calif. 18, 115p.

COOMBS, C.
1979. Reef fishes near Depoe Bay, Oregon: movement and the recreational fishery. M.A. Thesis, Oregon State Univ., Corvallis, 39 p.

CUSHING, D. H.
1968. Fisheries biology. Univ. Wis. Press, Madison, 200 p.

DEWEES, C. M., AND D. W. GOTSHALL.
1974. An experimental artificial reef in Humboldt Bay, California. Calif. Fish Game 60:109-127.

DUNN, J. R., AND C. R. HITZ.
1969. Oceanic occurrence of black rockfish (*Sebastodes melanops*) in the central North Pacific. J. Fish. Res. Board Can. 26:3094-3097.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

GOTSHALL, D. W.
1964. Increasing tagged rockfish (genus *Sebastodes*) survival by deflating the swim bladder. Calif. Fish Game 50:253-260.

GOTSHALL, D. W., J. G. SMITH, AND A. HOLBERT.
1965. Food of the blue rockfish *Sebastodes mystinus*. Calif. Fish Game 51:147-162.

GUNDERSON, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull., U.S. 75:369-403.

HAAKER, P. L.
1978. Observations of agonistic behavior in the treefish, *Sebastes serriceps* (*Scorpaenidae*). Calif. Fish Game 64:227-228.

HALLACHER, L. E.
1977. Patterns of space and food use by inshore rockfishes (Scorpaenidae:*Sebastes*) of Carmel Bay, California. Ph.D. Thesis, Univ. California, Berkeley, 115 p.

HARDEN JONES, F. R.
1968. Fish migration. Edward Arnold, Lond., 325 p.

HARE, G. M., AND M. D. B. BURT.
1976. Parasites as potential biological tags of Atlantic salmon (*Salmo salar*) smolts in the Miramichi River sys-

tem, New Brunswick. J. Fish. Res. Board Can. 33:1139-1143.

KABATA, Z.
1963. Parasites as biological tags. Int. Comm. Northwest Atl. Fish., Spec. Publ. 4:31-37.

LARSON, R. J.
1977. Habitat selection and territorial competition as the causes of bathymetric segregation of sibling rockfishes (*Sebastes*). Ph.D. Thesis, Univ. California, Santa Barbara, 170 p.

LLEWELLYN, J.
1972. Behaviour of monogeneans. *In* E. U. Canning and C. A. Wright (editors), Behavioural aspects of parasite transmission, p. 19-30. Academic Press, N.Y.

LOVE, M.
1978. Aspects of the life history of the olive rockfish, *Sebastes serranoides*. Ph.D. Thesis, Univ. California, Santa Barbara, 184 p.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MARGOLIS, L.
1963. Parasites as indicators of the geographical origin of sockeye salmon, *Oncorhynchus nerka* (Walbaum), occurring in the North Pacific Ocean and adjacent seas. Int. North Pac. Fish. Comm. Bull. 11, 156 p.

MCALLISTER, R.
1976. California marine fish landings for 1974. Calif. Dep. Fish Game, Fish Bull. 166, 53 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MILLER, D. J., AND D. GOTSHALL.
1965. Ocean sportfish catch and effort from Oregon to Point Arguello, California. Calif. Dep. Fish Game, Fish Bull. 130, 135 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MOULTON, L. L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. Thesis, Univ. Washington, Seattle, 181 p.

NOBLE, G. K.
1939. The role of dominance in the social life of birds. Auk 56:263-273.

OLSON, R. E., AND I. PRATT.
1973. Parasites as indicators of English sole (*Parophrys vetulus*) nursery grounds. Trans. Am. Fish. Soc. 102:405-411.

PATTEN, B. G.
1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412-416.

PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

QUAST, J.
1968. Estimates of the populations and the standing crop of fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 57-79. Calif. Dep. Fish Game, Fish Bull. 139.

SCHOENER, T. W.
1968. Sizes of feeding territories among birds. Ecology 49:123-141.

SINDERMANN, C. J.
1961. Parasite tags for marine fish. J. Wildl. Manage. 25:41-47.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

TURNER, C. H., E. E. EBERT, AND R. R. GIVEN.
1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

WESTRHEIM, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

TRENDS TOWARD DECREASING SIZE OF BROWN SHRIMP, *PENAEUS AZTECUS*, AND WHITE SHRIMP, *PENAEUS SETIFERUS*, IN REPORTED ANNUAL CATCHES FROM TEXAS AND LOUISIANA[1]

CHARLES W. CAILLOUET, FRANK J. PATELLA, AND WILLIAM B. JACKSON[2]

ABSTRACT

An exponential model adequately characterized the size composition (expressed as a regression of transformed cumulative percentage of weight on size category) of reported annual catches of brown and white shrimp in Texas and Louisiana from 1959 to 1976. Louisiana catches contained considerably greater proportions of small shrimp than did Texas catches. For both species and States, there was a significant trend toward increase in proportion of small shrimp in the catches over the period.

The size composition of a stock has long been used as a simple criterion for assessing the status of a fishery (Henderson 1972; Ricker 1975). Decreasing average size of individuals can be an indication of increasing mortality (usually equated with increased fishing mortality) or decreasing growth (usually attributed to overcrowding). This paper develops a new and simple approach to assessing size composition of catches, and uses it to detect differences and trends in size composition of brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, catches in Texas and Louisiana.

We chose to compare Texas and Louisiana shrimp fisheries because 1) they are regulated by substantially different laws (Christmas and Etzold 1977), resulting in different size distributions of shrimp harvested within the two States, and 2) they are adjacent States which together produced the bulk (75%) of the reported shrimp catch from inshore and offshore waters of the U.S. coast of the Gulf of Mexico in 1975. Inshore refers to estuarine or bay waters landward of barrier islands, and offshore refers to waters seaward of barrier islands.

Texas shrimp laws provide for licenses, limits on number and size of trawls used per boat inshore, limits on trawl mesh size, daily limits on inshore catch, and size limits on food shrimp (not on bait shrimp) during the fall (15 August-15 December) open season inshore and during all open seasons offshore. No size limits are imposed on food shrimp during the spring (15 May-15 July) open season inshore. All offshore areas are closed to shrimping from 1 June to 15 July, and offshore areas within 7 fathoms are closed from 16 December to 1 February. No nighttime shrimping is allowed inshore. These laws lead to a fishing strategy emphasizing the harvest of larger shrimp offshore, with considerable restriction of harvest of smaller shrimp inshore.

Louisiana shrimp laws provide for licenses, limits on number and size of trawls used per boat inshore, limits on trawl mesh size, and size limits during the fall open season (third Monday in August to 21 December), with the exception that size limits are removed for brown shrimp after 15 November. No size limits are imposed during the spring open season (opened not later than 25 May and extending 50 days thereafter unless closure is warranted to protect young white shrimp). Nighttime shrimping with "butterfly nets" (wing nets) is allowed inshore. These laws encourage a fishing strategy emphasizing harvest of considerable quantities of small shrimp inshore as well as harvest of larger shrimp offshore.

Brown and white shrimp spend the juvenile and subadult phases of their life cycles inshore, and the adult and larval phases offshore (Caillouet and Patella 1978), thus recruitment to the fishery begins in the juvenile or subadult phases. The entire life cycle is completed within a year, therefore the shrimp crop in a given year depends upon recruitment in that year. Environmental

[1]Contribution No. 79-21G from the Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA.

[2]Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

Manuscript accepted April 1979
FISHERY BULLETIN VOL. 77, NO. 4, 1980

factors affecting maturation and spawning of adults and survival of larvae, juveniles, and subadults apparently have pronounced influences on recruitment. While some maturation and spawning takes place year around, peaks occur in spring and fall.

The size composition of the reported annual catches of brown and white shrimp greatly affects the value of these catches. For the years 1959-75, Caillouet and Patella (1978) estimated that the ex-vessel value (expressed in dollar units based upon 1975) of reported annual catches of brown shrimp in Texas was 1.6 times greater than that in Louisiana, for a given weight of catch. For white shrimp, it was 1.2 times greater in Texas than in Louisiana. They attributed these differences in value of the catches to differences in size composition of the catches because larger shrimp command higher prices than do smaller shrimp on the market. In addition, they were impressed that the size composition of reported catches of brown and white shrimp had remained remarkably constant within each State despite wide variations in weight of the annual catch from year to year in response to fluctuations in recruitment.

DESCRIPTION OF DATA

This paper deals with combined inshore and offshore reported annual catches of brown shrimp and white shrimp from the Texas coast (statistical areas 18-21) and Mississippi River to Texas (statistical areas 13-17), representing the Texas coast and that part of the Louisiana coast west of the Mississippi River, respectively (Figure 1), and from 1959-76 (U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78).

The annual catches reported in the Gulf Coast Shrimp Data (U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78) represent only a portion of the total annual catches; those landed by United States craft at U.S. ports along the coast of the Gulf of Mexico. Portions not reported include some of the commercial landings (including those of foreign fishing craft), undersized shrimp that are discarded, and landings by domestic sport fishermen. The proportion of the total annual catch that is not reported is unknown, and we do not know what effect its inclusion would have on size composition of the annual catch. However, we believe that the reported catch represents the bulk of the total catch and that the reported catch is a reasonably good reflection of the combined effects of shrimp population characteristics (growth and natural mortality) and removals by fishing (or fishing mortality).

Size composition of the reported catches was examined in units of pounds (as reported in catch statistics) caught in eight "count" or size categories representing number of shrimp per pound, heads-off ($\geq$68, 51-67, 41-50, 31-40, 26-30, 21-25, 15-20, and $<$15). These categories are approximately equivalent to the following number of shrimp per kilogram (heads-off), respectively: $\geq$150, 112-148, 90-110, 68-88, 57-66, 46-55, 33-44, and $<$33. The use of count (number per pound) as a measure of shrimp size amounts to a reciprocal transformation of the weight (W) per shrimp (in pound):

$$\text{Count} = \frac{1}{W}$$

The same would be true if count and weight per shrimp were expressed in metric units. Kutkuhn (1962) described biases associated with determination of size composition of reported shrimp catches, including those resulting from interview sampling methods, from prevailing practices of catch culling, grading or sorting, and from catch sampling practices. Because the methods used to determine size composition of catches have remained essentially unchanged from 1959 to 1976 (Farley[3]), we believe that the biases would have

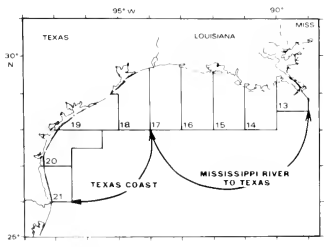


FIGURE 1.—Statistical areas used in reporting Gulf Coast Shrimp Data for Mississippi River to Texas and Texas coast.

[3]Orman Farley, National Marine Fisheries Service, NOAA, Galveston, Tex., pers. commun. December 1978.

more or less constant effects on comparisons between Texas and Louisiana and over the period from 1959 to 1976, and therefore would have only minor if any effects upon our conclusions. We further recognize that each size category may include representatives of more than one peak of recruitment, since they include catches taken over the period of 1 calendar year. Therefore, it is likely that any differences or trends in the time phasing of peak fishing activity within Texas and Louisiana within a year could contribute to the observed differences and trends in size composition of the respective catches in the two States.

ANALYTICAL METHODS

Percentage (by weight, heads-off) was determined for each size category in reported annual catches of brown and white shrimp from Texas coast and Mississippi River to Texas for each of the years from 1959 through 1976 (see Caillouet and Patella 1978). Cumulative percentage (F) for each size category was then determined for catches of both species, from Texas coast and Mississippi River to Texas, and for each year. Percentages were summed from the smallest shrimp (highest count, ≥68) to the largest (lowest count, <15).

An exponential model was chosen to represent the relationship between cumulative percentage, F, and size category, C, for brown and white shrimp, for Texas coast and Mississippi River to Texas, and for the years 1959-76 as follows:

$$F_i = ae^{bC_i}$$

where F_i = cumulative percentage (by weight, heads-off) of catch in ith size category
C_i = lower limit of ith size category ($C_1 = 15, C_2 = 21, \ldots, C_7 = 68$)
$i = 1, 2, \ldots, 7$
a = constant
b = exponent
e = base of natural logarithm.

The cumulative percentages, F, were transformed to natural logarithms, and the logarithmic form of the model was used to estimate parameters by least squares:

$$\ln F_i = \ln(a) + bC_i = \epsilon$$

where ϵ = residual (deviation from regression).

Thus, the logarithmic form of the model describes the relationship between transformed cumulative percentage and size category, and represents size composition of the reported annual catches. Note that this linear relationship describing size composition of the reported annual catches is achieved by transforming both the cumulative percentage to ln F and the weight per shrimp (in pound, heads-off) to count (number per pound).

Midpoints of size categories were not used because the size categories have unequal intervals, an unavoidable result of using data based on size categories developed by the shrimping industry. Upper limits of size categories were not used, because we could not determine the upper limit of the ≥68 category, and this category represented a significant proportion of the catches. Also, we did not use the <15 size category because we could not determine its lower limit (zero was not realistic), and this category represented a very small fraction of the catches. Apparently, total mortality (natural and fishing combined) is such that relatively small portions of the shrimp populations survive to be caught at sizes as large as <15/pound. Because lower limits of size categories were used for regression analyses, and because the <15 size category was not used in the analysis, the magnitude of the ordinate intercept, $\ln(a)$, is of no particular use. It is the slope, b (= exponent of the exponential model) that is of most interest and use as an index showing the rate of change in ln$F$ with C. Extrapolation below 15 count is not advised, because the linear relationship does not apply beyond this point.

In order to determine whether size composition of the reported annual catches changed with time, the slopes, b, of the regressions of transformed cumulative percentage on size category were plotted against years, and straight lines were fitted to points b and x (= last two digits of each year) by least squares, for brown and white shrimp from the Texas coast and Mississippi River to Texas, 1959-76 (Figures 2, 3).

RESULTS AND DISCUSSION

Slopes, b, of the regressions of transformed cumulative percentage versus size category, all differed significantly from zero at the 99.9% level of confidence, showing that the linear fit was good (Tables 1, 2). The slopes changed with time as

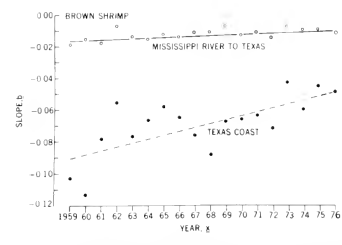


FIGURE 2.—Trends in slope (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown shrimp in Mississippi River to Texas (solid line, circles) and Texas coast (dashed line, dots) 1959-76 (data from Tables 1, 2).

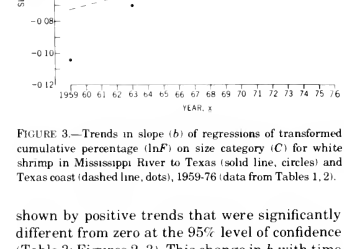


FIGURE 3.—Trends in slope (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for white shrimp in Mississippi River to Texas (solid line, circles) and Texas coast (dashed line, dots), 1959-76 (data from Tables 1, 2).

shown by positive trends that were significantly different from zero at the 95% level of confidence (Table 3; Figures 2, 3). This change in b with time indicated that the size composition of the reported annual catches of brown and white shrimp shifted during 1959-76 toward greater proportions of shrimp of smaller size in the catches. This shift was more pronounced in Texas, but the Louisiana catches contained considerably greater proportions of small shrimp than did those of Texas. Points for 1959 and 1960 may be less reliable than those for later years because the Gulf Coast Shrimp Data reports were released for the first time in 1956, and by 1961 the data collection methods had been greatly refined. Elimination of data points for 1959 and 1960 decreased all the

TABLE 1.—Linear regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Mississippi River to Texas (based on U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78).[1]

	Brown shrimp			White shrimp		
Year	ln(a)	b	r^2	ln(a)	b	r^2
1959	4 881	−0 0196	0 962	5 508	−0 0537	0 992
1960	4 767	−0 0154	0 978	5 468	−0 0496	0 988
1961	4 842	−0 0180	0 976	5 097	−0 0301	0 990
1962	4 696	−0 0077	0 994	5 005	−0 0222	0 968
1963	4 823	−0 0144	0 980	5 273	−0 0336	0 960
1964	4 817	−0 0156	0 927	5 101	−0 0318	0 998
1965	4 749	−0 0126	0 992	4 849	−0 0206	0 996
1966	4 795	−0 0144	0 988	5 003	−0 0248	0 952
1967	4 786	−0 0119	0 992	4 928	−0 0273	0 994
1968	4 730	−0 0117	0 982	4 849	−0 0207	0 986
1969	4 654	−0 0079	0 947	4 922	−0 0207	0 998
1970	4 747	−0 0135	0 988	4 884	−0 0227	0 986
1971	4 746	−0 0118	0 994	4 936	−0 0230	0 996
1972	4 795	−0 0152	0 992	4 818	−0 0179	0 992
1973	4 601	−0 0080	0 872	4 852	−0 0184	0 996
1974	4 657	−0 0101	0 910	4 767	−0 0171	0 980
1975	4 657	−0 0105	0 910	4 760	−0 0165	0 968
1976	4 712	−0 0112	0 964	4 889	−0 0232	0 980

[1] F = Cumulative percentage of weight caught in each of seven size categories, C = lower limit of each of seven size categories, all b's were significantly different from zero at the 99 9% level of confidence, r^2 = coefficient of determination

TABLE 2.—Linear regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Texas coast (based on U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78.).[1]

	Brown shrimp			White shrimp		
Year	ln(a)	b	r^2	ln(a)	b	r^2
1959	6 651	−0 1039	0 965	6 848	−0 1042	0 895
1960	6 961	−0 1140	0 957	6 008	−0 0635	0 899
1961	6 069	−0 0790	0 972	5 448	−0 0521	0 990
1962	5 525	−0 0558	0 977	5 369	−0 0436	0 993
1963	5 936	−0 0771	0 986	5 875	−0 0704	0 990
1964	5 743	−0 0669	0 995	5 697	−0 0625	0 994
1965	5 626	−0 0588	0 991	5 268	−0 0449	0 998
1966	5 692	−0 0655	0 984	5 478	−0 0541	0 995
1967	6 016	−0 0764	0 980	5 171	−0 0455	0 991
1968	6 420	−0 0883	0 964	5 462	−0 0440	0 946
1969	5 901	−0 0680	0 969	5 808	−0 0643	0 983
1970	5 737	−0 0661	0 986	5 412	−0 0502	0 994
1971	5 784	−0 0629	0 973	5 302	−0 0476	0 998
1972	6 010	−0 0722	0 979	5 470	−0 0522	0 992
1973	5 427	−0 0437	0 978	5 140	−0 0283	0 976
1974	5 690	−0 0603	0 989	5 023	−0 0343	0 984
1975	5 432	−0 0460	0 991	4 995	−0 0259	0 992
1976	5 457	−0 0478	0 990	5 032	−0 0278	0 995

[1] F = Cumulative percentage of weight caught in each of seven size categories, C = lower limit of each of seven size categories, all b's were significantly different from zero at the 99 9% level of confidence, r^2 = coefficient of determination

trends in b, and the trend for brown shrimp from Mississippi River to Texas was no longer different from zero at the 95% level of confidence (Table 3). However, elimination of points for the first 2 yr from the trends also reduced the degrees of freedom from 16 to 14 for the test of significance of trends, so the test was less sensitive in this case. Whether or not the apparent trend was real for brown shrimp from Mississippi River to Texas could be determined by examination of data for years beyond 1976, as they become available.

TABLE 3.—Trends in slopes (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Mississippi River to Texas and Texas coast, 1959-76 vs. 1961-76 (based on data from Tables 1, 2; Figures 2, 3).

	Brown shrimp				White shrimp			
	Mississippi R.-Texas		Texas coast		Mississippi R.-Texas		Texas coast	
Item	1959-1976	1961-1976	1959-1976	1961-1976	1959-1976	1961-1976	1959-1976	1961-1976
Trend[1]	0.00036*	0.00026	0.00244*	0.00141	0.00148*	0.00077*	0.00255*	0.00183*
Trend coefficient of determination	0.332	0.172	0.492	0.289	0.574	0.496	0.542	0.448

[1]Equals slope of the regression of b on x where x is the last two digits of each year
*The change in slope (b) per year was significantly different from zero at the 95% level of confidence

There was a positive correlation ($r = 0.702$) between the slopes of regressions of transformed cumulative percentage on size category for brown and white shrimp from Mississippi River to Texas in 1959-76, that was significantly different from zero at the 99% level of confidence. The same was true ($r = 0.742$) for brown and white shrimp from the Texas coast. This indicated that the direction of the shift in size composition of reported catches within a given year was usually in the same direction for both species in a given State (Tables 1, 2).

For a given weight of reported annual catch, the ex-vessel value of shrimp harvested in Louisiana is considerably less than that in Texas (Caillouet and Patella 1978), and this is largely a function of the size composition of the respective catches in the two States. Our analysis cannot distinguish whether the observed differences and trends in size composition of the reported catches are due to differences and trends in fishing mortality, natural mortality, or growth, but we suggest that the predominant causes of the observed differences and trends are differences and trends in fishing mortality. There is no evidence to indicate that separate shrimp stocks exist in these two States, or that natural mortality or growth differ between the two States (see Christmas and Etzold 1977). On the other hand the number and size of shrimp fishing craft and other indices of fishing effort are different in the two States and have increased over time (Christmas and Etzold 1977; Caillouet and Patella 1978). Also, differences and trends in time phasing of peak fishing activity in Texas and Louisiana within a year could have contributed to the differences and trends in size composition reported herein. Regardless of the cause or causes, continued shifts in size composition toward greater proportions of smaller shrimp in the catches can be expected to weaken the ex-vessel value of the catches.

LITERATURE CITED

CAILLOUET, C. W., AND F. J. PATELLA.
1978. Relationship between size composition and ex-vessel value of reported shrimp catches from two Gulf Coast States with different harvesting strategies. Mar. Fish. Rev. 40(2):14-18.

CHRISTMAS, J. Y., AND D. J. ETZOLD (editors).
1977. The shrimp fishery of the Gulf of Mexico United States: A regional management plan. Gulf Coast Res. Lab., Ocean Springs, Miss., 128 p.

HENDERSON, F.
1972. The dynamics of the mean-size statistic in a changing fishery. FAO Fish. Tech. Pap. 116, 16 p.

KUTKUHN, J. H.
1963. Gulf of Mexico commercial shrimp populations—trends and characteristics, 1956-59. U.S. Fish. Wildl. Serv., Fish. Bull. 62:343-402.

NATIONAL MARINE FISHERIES SERVICE.
1970-78. Gulf coast shrimp data, annual summary 1967-annual summary 1976. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 5412, 5721, 5925, 6126, 6425, 6725, 6925, 7225.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

U.S. FISH AND WILDLIFE SERVICE.
1960-69. Gulf coast shrimp data, annual summary 1959—annual summary 1966. U.S. Fish. Wildl. Serv., Curr. Fish. Stat. 3 unnumbered publ., 3358, 3515, 3784, 4111, 4411, 4781, 5107.

NOTES

STAGE I ZOEAE OF A CRANGONID SHRIMP, *CRANGON FRANCISCORUM ANGUSTIMANA*, HATCHED FROM OVIGEROUS FEMALES COLLECTED IN KACHEMAK BAY, ALASKA

Information on the larval stages of crangonid shrimp of the North Pacific Ocean is meager. Needler (1941) described the first zoeal stage of *Crangon septemspinosa* (as *Crago septemspinosus* Say) hatched in the laboratory from ovigerous females and the remaining four zoeal stages from plankton collected near Prince Edward Island, Canada. Kurata (1964) described the larval stages of *C. affinis* de Haan and various larval stages of six unidentified *Crangon* spp. from Japanese waters. He obtained the first zoeal stage of *C. affinis* from known parentage, but the remaining stages were collected from plankton. Makarov (1967) briefly described larvae of *C. dalli* Rathbun and *C. septemspinosa* (Say) which were collected from plankton along the western Kamchatka shelf. He suggested that *C. dalli* was an analog of *C. allmani* Kinahan and *C. septemspinosa* was an analog of *C. crangon* (Linnaeus). *Crangon allmani* and *C. crangon* are eastern Atlantic species. He assumed that the *C. affinis* larvae described by Kurata (1964) were actually larvae of *C. septemspinosa*. Loveland (1968) described larvae of *C. alaskensis* Rathbun reared in the laboratory from females collected near Anacortes, Wash.

Morphology of Stage I larvae is closely related to Caridean development and can be used to estimate the number of larval stages, classify species, categorize larvae for identification purposes, and identify subsequent larval stages (Needler 1938; Pike and Williamson 1961, 1964; Kurata 1964; Ivanov 1971; and others). In this report I describe and illustrate the first zoeal stage of *C. franciscorum angustimana* Rathbun from ovigerous females and compare these zoeae with Stage I zoeae of crangonids described by other authors. Also, I show that the criterion of the absence of exopodites on the second pair of pereopods for distinguishing larvae of *Crangon* from other genera of the Crangonidae is invalid for Crangonidae of the North Pacific Ocean.

Methods

Ovigerous *C. franciscorum angustimana* were caught at 30 m (16 fathoms) in shrimp pots in early May 1976 in Kachemak Bay, Alaska. Four females were kept in seawater in a plastic bucket for about ½ h and then each female was put into a 4 l glass jar containing filtered, aerated seawater. The water was about 35‰ salinity, about 6°C, and was changed daily until zoeae were released, about 5 days later. Most zoeae were released at night. I did not determine whether the larvae were hatched as prezoeae.

Terms used in the text, nomenclature of gills and appendages, and techniques of measurement and illustration are given by Haynes (1976). As an aid to the study of segmentation and setation, some larvae were cleared in 10% KOH and the exoskeleton stained with Turtox[1] CMC-S (acid fuchsin stain mountant). Only the left number is figured because the paired appendages of the larvae are symmetrical; except, the mandibles are drawn as a pair. There was no morphological variation, except variation in total length, among the zoeae used for the description.

Stage I Zoea

Mean total length of Stage I zoeae (Figure 1A) was 3.1 mm (range 2.8-3.3 mm; 10 specimens). Rostrum slender, spiniform, without teeth, about one-third length of carapace. Carapace with small rounded prominence near posterior margin. Two distinct denticles immediately posterior to pterygostomian spine; no supraorbital or antennal spines. Eyes sessile.

ANTENNULE (Figure 1B).—First antenna, or antennule, an unsegmented peduncle (inner flagellum) bearing a conical projection and a setulose spine. Conical projection bears a simple seta and three aesthetascs of about equal length.

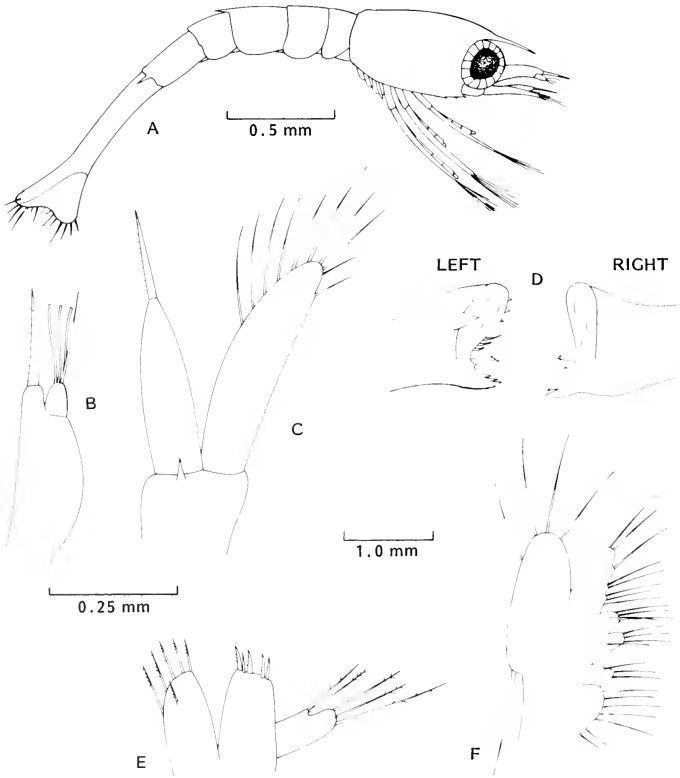
ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

shorter than scale, bears a setulose spine. Antennal scale not distally segmented, fringed with nine heavily plumose setae and subterminal plumose seta on outer margin. Protopodite bears spine at base of flagellum but not at base of scale.

MANDIBLES (Figure 1D).—Without palps; well developed. Incisor process of left mandible bears three teeth in contrast to biserrate incisor process of right mandible. Left mandible bears a movable premolar denticle (lacinia mobilis) adjacent to incisor process and large subterminal tooth on truncated molar process.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an



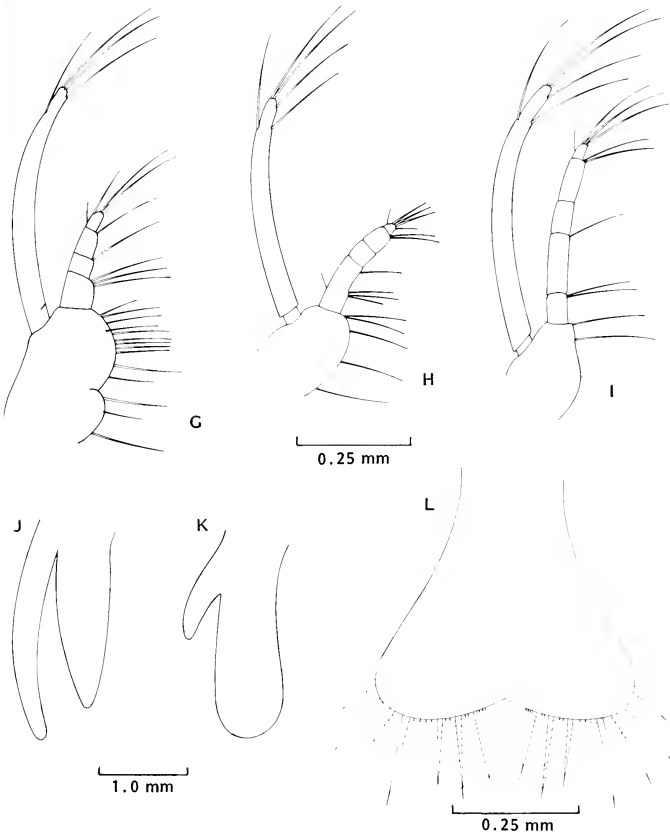


FIGURE 1. — Stage I zoeae of *Crangon franciscorum angustimana*. A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral, F, maxilla, dorsal; G, first maxilliped, dorsal; H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, first pereopod, right side; K, second pereopod, right side; L, telson, dorsal. Setules on setae are omitted for clarity; spinulose setae are shown.

endopodite. Proximal lobe (coxopodite) bears six spinulose setae. Median lobe (basipodite) bears five spinulose spines terminally. Unsegmented endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal spinulose setae. No outer seta on maxillule.

MAXILLA (Figure 1F).—Exopodite (scaphognathite) bears four long plumose setae and a proximal seta; proximal end not projected posteriorly. Endopodite unsegmented; bears eight setae. Both basipodite and coxopodite bilobed. Basipodite bears eight setae, four on each lobe. Coxopodite bears 10 setae, three on distal lobe and seven on proximal lobe. Most setae on basipodite and coxopodite spinulose.

FIRST MAXILLIPED (Figure 1G).—Unsegmented protopodite bilobed; bears 14 setae. Endopodite four-segmented; setation formula 4, 1, 1, 3. Exopodite bears four natatory setae. No epipodite.

SECOND MAXILLIPED (Figure 1H).—Unsegmented protopodite not lobed; bears five setae. Endopodite four-segmented; setation formula 5, 2, 0, 5. Exopodite bears five natatory setae.

THIRD MAXILLIPED (Figure 1I).—Unsegmented protopodite not lobed; bears two setae. Endopodite nearly as long as exopodite; five-segmented; setation formula 4, 2, 0, 1, 2. Exopodite bears five natatory setae.

PEREOPODS (Figure 1J, K).—Only pairs one to four present; pairs one and two (Figure 1J, K) biramous, pairs three and four uniramous. All pereopods poorly developed, unsegmented, and compacted tightly under cephalothorax.

PLEOPODS.—Absent.

ABDOMEN AND TELSON (Figure 1A, L).—Abdomen consists of five somites (somite six is fused with telson in Stage I). Third somite bears a dorsal spine on posterior margin; fifth somite bears pair of spines on posterolateral margin that extend posteriorly about one-fourth length of fifth abdominal somite. Telson emarginated distally; bears 7 + 7 pairs of densely plumose setae. Minute spinules at base of each seta, except possibly last pair, and along posterior margin of telson to fourth setal pair and on setae themselves. No anal spine.

Comparisons of Zoeal Stage I With Descriptions by Other Authors

Of the published descriptions of Stage I zoeae of *Crangon* spp. from the North Pacific Ocean, Stage I zoeae of *C. franciscorum angustimana* are most similar to Stage I zoeae of *C. alaskensis*, *C. affinis*, *C. septemspinosa*, and Kurata's (1964) "Species A" and "Species D." These examples are characterized by a median dorsal spine on the posterior margin of the third abdominal somite and by posterolateral spines on the fifth abdominal somite.

Stage I zoeae of *C. alaskensis* can be distinguished from Stage I *C. franciscorum angustimana* by the rostrum and pereopods. In Stage I *C. alaskensis* the rostrum does not extend beyond the eyes and the pereopods are absent (Loveland 1968), but in Stage I *C. franciscorum angustimana* the rostrum extends beyond the eyes and the larvae bear undeveloped pereopods 1-4.

Stage I zoeae of *C. affinis* and "Species A" are distinguished from Stage I zoeae of *C. franciscorum angustimana* by the presence in Stage I zoeae of *C. affinis* and "Species A" of a shallow transverse groove in the carapace and two subterminal setae along the outer margin of the antennal scale. Also in Stage I *C. affinis* and "Species A," the endopodite of the third maxilliped is four segmented. In Stage I zoeae of *C. franciscorum angustimana*, the carapace does not have a shallow transverse groove; there is only one subterminal seta along the outer margin of the antennal scale; and the endopodite of the third maxilliped is five segmented.

Stage I zoeae of Kurata's "Species D" are distinguished from Stage I zoeae of *C. franciscorum angustimana* by the presence in Stage I zoeae of "Species D" of a five-segmented endopodite on the second maxilliped and pleopods that occur as distinct buds. In Stage I zoeae of *C. franciscorum angustimana*, the endopodite of the second maxilliped is four segmented and there are no pleopod buds.

Stage I zoeae of *C. septemspinosa* are like Stage I zoeae of *C. franciscorum angustimana* with some exceptions: the antennal scale of *C. septemspinosa* bears five plumose setae and the endopodite of the first maxilliped is unsegmented (Needler 1941); whereas, the antennal scale of *C. franciscorum angustimana* bears 10 plumose setae and the endopodite of the first maxilliped is four segmented.

Tesmer and Broad (1964) described nine zoeal stages of *C. septemspinosa* reared in the laboratory from ovigerous females obtained off Beaufort, N.C. They found distinct morphological differences between their zoeae and zoeae of the same species as described by Needler, especially in the later stages. Based on Tesmer and Broad's descrip-

tion, Stage I zoeae of *C. septemspinosa* can be distinguished from Stage I zoeae of *C. franciscorum angustimana* by the exopodites of the maxillipeds. The exopodites of the maxillipeds are jointed in Stage I zoeae of *C. septemspinosa* and are not jointed in Stage I zoeae of *C. franciscorum angustimana*. Also, the fifth pair of telson spines are distinctly shorter than the fourth or sixth pair in *C. septemspinosa*; whereas, in my Stage I zoeae of *C. franciscorum angustimana*, the fifth pair of telson spines are about equal in length to the fourth and sixth pairs.

The occurrence in later zoeal stages of functional exopodites on the first pair of pereopods but not on pereopodal pairs 2-5 has been used as a criterion for distinguishing larvae of the genus *Crangon* from larvae of other genera of the family Crangonidae (Williamson 1960).

I found buds of exopodites on both the first and second pair of pereopods in Stage I zoeae of *C. franciscorum angustimana*. Assuming zoeae of *C. franciscorum angustimana* undergo typical development for crangonid larvae, these buds will become functional exopodites at Stage III or IV (Needler 1941; Kurata 1964; Makarov 1967). The criterion of the absence of exopodites on the second pair of pereopods for distinguishing larvae of *Crangon* from other genera of the Crangonidae, therefore, is invalid for the North Pacific Ocean. Unfortunately, larvae are described for only a few species of crangonids from the North Pacific Ocean, including the genus *Crangon*, and confirmation of the generic characteristics of the larvae is needed.

Acknowledgment

I thank Terry Butler, Pacific Biological Station, Nanaimo, British Columbia, Canada, for identifying the ovigerous females.

Literature Cited

HAYNES, E.
1976. Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory. Fish. Bull., U.S. 74:323-342.

IVANOV, B. G.
1971. The larvae of some eastern shrimps in relation to their taxonomic status. [In Russ., Engl. summ.] Zool. Zh. 50:657-665.

KURATA, H.
1964. Larvae of decapod Crustacea of Hokkaido. 4. Crangonidae and Glyphocrangonidae. [In Jpn., Engl. summ.] Bull. Hokkaido Reg. Fish. Res. Lab. 28:35-50. (Translated by Division of Foreign Fisheries, Natl. Mar. Fish. Serv., NOAA.)

LOVELAND, H. A., JR.
1968. Larval development under laboratory conditions of *Crangon alaskensis* Rathbun, (Crustacea:Decapoda). M.A. Thesis, Walla Walla Coll., Walla Walla, Wash., 22 p.

MAKAROV, R. R.
1967. Larvae of the shrimps and crabs of the west Kamtschatkan shelf and their distribution. (Translated from Russ. by B. Haigh.) Natl. Lending Libr. Sci. Technol., Boston Spa, Yorkshire, 199 p.

NEEDLER, A. B.
1938. The larval development of *Pandalus stenolepis*. J. Fish. Res. Board Can. 4:88-95.
1941. Larval stages of *Crago septemspinosus* Say. Trans. R. Can. Inst. 23:193-199.

PIKE, R. B., AND D. I. WILLIAMSON
1961. The larvae of *Spirontocaris* and related genera (Decapoda, Hippolytidae). Crustaceana 2:187-208.
1964. The larvae of some species of Pandalidae (Decapoda). Crustaceana 6:265-284.

TESMER, C. A., AND A. C. BROAD.
1964. The larval development of *Crangon septemspinosa* (Say) (Crustacea:Decapoda). Ohio J. Sci. 64:239-250.

WILLIAMSON, D. I.
1960. Crustacea, Decapoda: Larvae VII. Caridea, Family Crangonidae, Stenopodidea. Cons. Int. Explor. Mer, Fiches Identification Zooplankton 90, 5 p.

EVAN HAYNES

Northwest and Alaska Fisheries Center Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155
Auke Bay, AK 99821

LENGTH-WEIGHT RELATIONSHIPS OF WESTERN ATLANTIC BLUEFIN TUNA, *THUNNUS THYNNUS*[1]

The Atlantic bluefin tuna, *Thunnus thynnus*, is seasonally distributed over most of the North Atlantic Ocean from Newfoundland to Brazil and from Norway to the Canary Islands (Gibbs and Collette 1967). There has been a great reduction in the Atlantic-wide catch (including Mediterranean) from 38,500 metric tons (t) in 1964 to 12,500 t in 1973 (Miyake et al. 1974). Because of this, a number of studies have been made and are being continued in order to understand the reason for this decline (Parks 1977; Shingu and Hisada 1977).

[1]Contribution Number SEFC 80-01M, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, Fla.

Length-weight, length-to-length, and weight-to-weight relationships are necessary in population analyses for converting one measurement to another. In this paper I present the relationships of the following: round weight-straight fork length, round weight-dressed weight, and straight fork length-curved fork length.

During my review of bluefin tuna literature, I found a lack of information on size relationships. Mather and Schuck (1960) used a length-weight curve based on 778 bluefin tuna from Cape Cod to estimate length. They did not indicate, however, when these fish were collected. They did not give a regression formula for the length-weight relationship, but they did present a straight length-curved length relationship based on 185 measurements fitted by inspection. Rodriguez-Roda (1964, 1971) collected 793 bluefin tuna and then determined the length-weight relationship. Of these, 467 bluefin tuna (prespawning) were entering the Mediterranean during May and June and 326 bluefin tuna (postspawning) were leaving the Mediterranean during July and August 1956, 1958, 1959, and 1961. Butler (1971) determined the length-weight relationship by the standard least squares regression method for 237 giant bluefin tuna caught during July through September 1966 from Conception Bay, Newfoundland. Mather et al. (1974) presented regression equations for converting from weight to length for bluefin tuna from Newfoundland, Libya, and the Bahamas from data supplied by the Fisheries Research Board of Canada, the International Council for the Exploration of the Sea, and the Woods Hole Oceanographic Institution. They also presented an equation for converting dressed weight to round weight. The method of determining the equations, the sample sizes, and time period sampled were not presented. Coan (1976) gave a length, weight, and age conversion table for bluefin tuna of both sexes. He converted length to weight based on a length-weight regression given in Sakagawa and Coan (1974), who had in turn, obtained this regression from Frank J. Mather, Woods Hole Oceanographic Institution. Unfortunately, there was no mention of sample size, location, or date.

Methods

Bluefin tuna length and weight measurements were collected during 1974 through 1977 from various landing points and processing plants along the east coast of the United States from Florida to Maine and from the Bahamas. These fish had been caught by purse seine, rod and reel, handline, and harpoon. Straight fork length (centimeters) was measured by caliper, and curved fork length (centimeters) was measured along the body contour by tape. Round weight (total weight of fish when caught) and dressed weight (head, viscera, and tail removed) were recorded in pounds and later converted to kilograms.

Ricker (1973) showed that the geometric mean (GM) regression can be used for a majority of biological situations as a reasonable and consistent estimate of the functional slope because most of the variability is natural.

The functional (GM) regression was calculated for the logarithmic transformation of the length-weight relationship for 3,578 bluefin tuna taken from May through October. The GM regression was also calculated for the relationship between round weight and dressed weight for 685 bluefin tuna taken from July through September, and for the straight fork length to curved fork length relationship for 606 bluefin tuna taken from July through October.

The general equation for the GM regression as given by Ricker is: $Y = u + vX$, with variables X and Y, and u is the y-axis intercept, where $u = \bar{Y} - v\bar{X}$, v is the slope, and $v = [\Sigma y^2/\Sigma x^2]^{1/2}$, where $y_i = Y_i - \bar{Y}$ and $x_i = X_i - \bar{X}$. The limits on all Σ are $i = 1, \ldots, n$.

The standard error of the slope was computed for each regression equation using the following equation from Ricker (1973): $S_v = [S_{yx}{}^2/\Sigma x^2]^{1/2}$, where S_v is the standard error of the slope and $S_{yx}{}^2$ is the mean square or variance of the observations from the regression line in the vertical direction.

Results and Discussion

Based on the classification system of Rivas and Mather (in press), the fish sampled mainly consisted of two size categories, giant bluefin tuna (>180 cm straight fork length and 130 kg round weight) and small bluefin tuna (< 130 cm straight fork length or < 45 kg round weight). Based on previous growth studies by Mather and Schuck (1960), the giant fish are probably age 9 and older and the small bluefin tuna are most likely age 4 or younger. Very few medium bluefin tuna (130-180 cm straight fork length and 45-130 kg round weight) probably ages 5 through 8 were sampled.

The functional (GM) regressions for straight fork length-round weight (log transformation), round weight-dressed weight, and straight fork length-curved fork length are presented in Table 1. All of these relationships were characterized by high correlation coefficients. The data points are plotted with regression lines in Figures 1-3. The data points show that the GM regression model fits the data reasonably well for the size ranges studied. Extrapolation beyond the size range of observations may yield erroneous predictions. Regression statistics for each relationship are presented in Table 2.

The use of logarithmic transformations may lead to bias in data estimates (Pienaar and Thomson 1969; Beauchamp and Olson 1973; Lenarz 1974). However, since the mean square error for the round weight-straight fork length logarithmic transformation is low (Table 2), the bias in the data estimate was found to be minimal (1%).

Previous publications have not included standard errors or confidence limits or statistics necessary for their estimation. Therefore, comparisons with my data could not be made. To compare results from my study with studies by other authors, I compared estimates of Y using both their regression equations and mine. Whenever possible, I selected X values at each end of their range of values that corresponded with my range of values. I also compared estimates of Y for an X value taken at the middle of their size range.

TABLE 1.—Functional (GM) regression equation and correlation coefficient for the relationships between round weight (Y) and straight fork length (X), round weight (Y) and dressed weight (X), and straight fork length (Y) and curved fork length (X) for western Atlantic bluefin tuna. Weights in kilograms and lengths in centimeters.

Geometric mean regression equation	r
Log_{10} round weight = log_{10} straight fork length $\log_{10} Y = -4.52307 + 2.91920 \log_{10} X$	0.997
Round weight = dressed weight $Y = -7.92240 + 1.29607 X$	0.935
Straight fork length = curved fork length $Y = -2.06971 + 0.963300 X$	0.892

My estimates of round weight from straight fork length using the functional (GM) regression agreed most closely with my estimates obtained using the regression equation of Sakagawa and Coan (1974), with the greatest difference in estimates of only 2% occurring for a 270 cm fork length (FL) bluefin tuna. My calculated functional regression estimates next most closely agreed with estimates obtained using the length-weight relationship of Butler (1971), with the largest difference of 6% occurring at 250 cm FL. My esti-

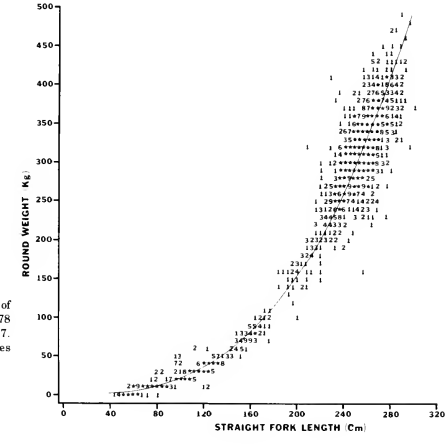


FIGURE 1.—Functional (GM) regression of round weight on straight fork length for 3,578 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

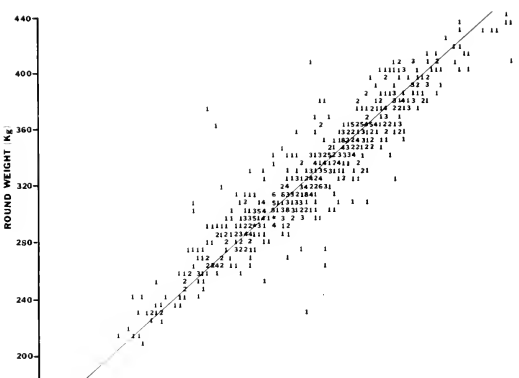


FIGURE 2.—Functional (GM) regression of round weight on dressed weight for 685 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

TABLE 2.—Regression statistics for $\log_{10}$ round weight (Y) – $\log_{10}$ straight fork length (X), round weight (Y) – dressed weight (X), and straight fork length (Y) – curved fork length (X) of western Atlantic bluefin tuna. Weights in kilograms and lengths in centimeters.

n	$\overline{X}$	$\overline{Y}$	$\sum x^2$	$\sum y^2$	$\sum xy$	$S_{yx}{}^2$	S_y
			$\log_{10}$ round weight – $\log_{10}$ straight fork length				
3,578	2.19254	1.87739	222.745	1,898.17	648.054	0.00356051	0.00399809
			Round weight – dressed weight				
685	256.993	325.158	832.635	1,396.650	1,009.090	257.261	0.0175776
			Straight fork length – curved fork length				
606	271.477	259.444	120.979	112.262	103.959	37.9615	0.0177140

mates of weight from length differed most from estimates which I calculated using equations of Rodriguez-Roda (1964, 1971). The largest variation (12%) was found for a prespawning fish measuring 48 cm.

No size range was reported by Mather et al. (1974) for estimating length from weight. However, estimated length corresponding to the extremes and middle of the size range in weight I studied agree closely to values I calculated using their regression equation for Newfoundland, with the greatest difference being only 3% for a 5 kg fish. A greater difference (13%) was noted when comparing estimates from my functional (GM) regression with estimates obtained using their regression equation for the Bahamas for a 5 kg fish. This large difference may have resulted from their not including fish in this size range when calculating their equation because differences at the middle and upper end of my size range were small, 4% or less. There appears to be a typographical error in the equation these authors gave for bluefin tuna from Libya, so no comparison was made.

My functional (GM) regression estimates of round weight from dressed weight agree well with the estimates I obtained using the regression equation of Mather et al. (1974). The largest dif-

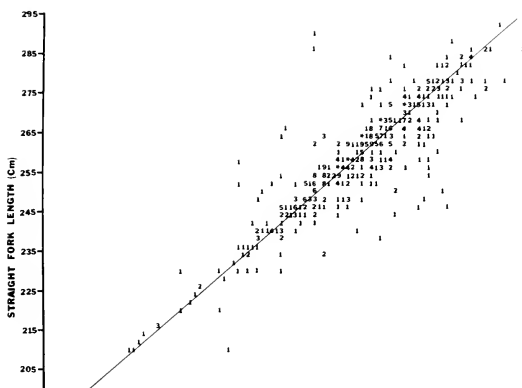


FIGURE 3.—Functional (GM) regression of straight fork length on curved fork length for 606 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

ference I found was 3% for a 130 cm bluefin tuna. Again I used my range of values for dressed weight since the range was not given by these authors.

My functional (GM) regression estimates of straight fork length from curved fork length agree very closely over my entire size range with estimates I obtained using the regression equation given by Mather and Schuck (1960). The largest difference I found, only 1%, occurred at the lower end of my range of curved fork length values of 200 cm.

Acknowledgments

I thank Gary Sakagawa of the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA; Emma Henderson of the Northeast Fisheries Center, NMFS, NOAA; Frederick Berry, Raymon Conser, Mark Farber, Michael Parrack, William Richards, Luis Rivas, James Tyler, and James Zuboy of the Southeast Fisheries Center, NMFS, NOAA; and Arvind Khilnani of Stanford University for their helpful comments on the manuscript. I also thank Tom Chewning of the Southeast Fisheries Center for computer programming assistance.

Literature Cited

BEAUCHAMP, J. J., AND J. S. OLSON
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.

BUTLER, M.
1971. Biological investigation on aspects of the life history of the bluefin tuna 1970-1971. Newfoundland and Labrador Tourist Development Office, St. Johns, 169 p.

COAN, A. L.
1976. Length, weight and age conversion tables for Atlantic tunas. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 5 (SCRS-1975):64-66.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1967. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish Wildl. Serv., Fish. Bull. 66:65-130.

LENARZ, W. H.
1974. Length-weight relations for five eastern tropical Atlantic scombrids. Fish. Bull., U.S. 72:848-851.

MATHER, F. J., III, J. M. MASON, AND A. C. JONES.
1974. Distribution, fisheries and life history data relevant

to identification of Atlantic bluefin tuna stocks. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 2 (SCRS-1973):234-258.

MATHER, F. J., III, AND H. A. SCHUCK.
1960. Growth of bluefin tuna of the western North Atlantic. U.S. Fish Wildl. Serv., Fish. Bull. 61:39-52.

MIYAKE, M. P., A. A. DEBOISSET, AND S. MANNING (compilers).
1974. International Commission for the Conservation of Atlantic Tunas. Stat. Bull. 5, Unnumbered pages.

PARKS, W. W.
1977. Cohort and equilibrium yield-per-recruit analyses for the Atlantic bluefin tuna fisheries system accounting two system configurations and two natural mortality models. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 6 (SCRS-1976):385-401.

PIENAAR, L. V., AND J. A. THOMSON.
1969. Allometric weight-length regression model. J. Fish. Res. Board Can. 26:123-131.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board. Can. 30:409-434.

RIVAS, L. R., AND F. J. MATHER III.
In press. Proposed terminology for size groups of the north Atlantic bluefin tuna *Thunnus thynnus*. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. (SCRS-1978).

RODRIGUEZ-RODA, J.
1964. Biologia del Atún, *Thunnus thynnus* (L.), de la costa sudatlántica de España. Invest. Pesq. 25:33-146.
1971. Investigations of tuna (*Thunnus thynnus*) in Spain. *In* Report for biennial period 1970-71, Part II, p. 110-113. Int. Comm. Conserv. Atl. Tunas.

SAKAGAWA, G. T., AND A. L. COAN.
1974. A review of some aspects of the bluefin tuna *Thunnus thynnus thynnus* fisheries of the Atlantic Ocean. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap. 2 (SCRS-1973):259-313.

SHINGU, C., AND K. HISADA.
1977. A review of the Japanese Atlantic longline fishery for bluefin tuna and the consideration of the present status of the stocks. Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap 6 (SCRS-1976):366-384.

RAYMOND E. BAGLIN, JR.

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Fl 33149
Present address: *National Marine Fisheries Service, NOAA*
c/o Alaska Department of Fish and Game
P.O. Box 686, Kodiak, AK 99615

DEVELOPMENTAL ANATOMY AND INFLATION OF THE GAS BLADDER IN STRIPED BASS, *MORONE SAXATILIS*

In 1974, a percentage of striped bass, *Morone saxatilis*, fingerlings reared at the Cooperative Fishery Research Laboratory, Southern Illinois University, lacked an inflated gas bladder. The purpose of this study was to describe the developmental anatomy of the gas bladder and its associated structures in striped bass so that a better understanding of the inflation mechanism could be obtained.

With regard to gas bladder morphology, bony fishes are classified as physostomes or physoclists. Generally, the more ancient, soft-rayed fishes (Malacopterygii) are physostomous, while the more modern, spiny-rayed fishes (Acanthopterygii) are physoclistic (Lagler et al. 1962). A physotome possesses a hollow connection, the pneumatic duct, between the gut and the gas bladder throughout its entire life. Some physotomes gulp surface air through the pneumatic duct to initiate inflation of the gas bladder (Tait 1960). Fish that are physoclistic do not possess this open connection as adults. Some physoclists, however, do possess a pneumatic duct as larvae, but the duct atrophies prior to adulthood. Günther's (1880) examinations have shown that adult striped bass are physoclistic. Doroshev and Cornacchia (1979) give a partial description of the development of the gas bladder in striped bass.

Several theories have been advanced to explain how the gas bladder is initially inflated in fishes that do not gulp surface air or are physoclistic prior to initial inflation. Some of these theories include: gases produced by the disintegration of organic materials (Powers 1932); production of gasses as a result of digestion (Johnston 1953); vacuolation of the gas bladder epithelia (McEwen 1940); and functioning of a rete mirabile, or gas gland (Schwarz 1971).

Methods

Histomorphological Studies

Striped bass larvae were obtained from the Hudson River, N.Y., and Lake Charles, La. Upon arrival, the 1- to 4-day-old larvae were transferred into 200 l aquaria and maintained at 16°-18° C. Brine shrimp, *Artemia salina*, were fed regularly to the larvae. Eighty-three striped bass larvae 4.3-24 days old (from the time of hatching) were removed from the aquaria and prepared for histological study. The larvae were fixed in either 10% Formalin[1] or Bouin's fluid, dehydrated in a series of graded alcohols, cleared in benzene, and embedded in Carbowax. From a representative

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

series of 34 larvae, we prepared transverse and longitudinal series sections 7 and 10 μm thick (Table 1). The mounted specimens were stained with either Harris's hematoxylin and eosin or a modification of Mallory's connective tissue stain (Martan[2]).

TABLE 1.—Number of striped bass larvae sectioned to determine the internal anatomy of the gas bladder and its associated structures.

Age (days)	With inflated gas bladder	Without inflated gas bladder
4 3	1	2
4 8	2	3
5 5	2	2
6 0	5	1
7 0	2	0
8 0	2	2
14 0	0	3
21 0	0	1
24 0	4	2

Results

During laboratory aquaria experiments, striped bass larvae were observed with inflated gas bladders as early as day 4. A peak period of inflation occurred during day 5, closely corresponding with the absorption of the yolk sac. Doroshev and Cornacchia (1979) found that striped bass inflated their gas bladder from the 5th to the 7th day.

Striped bass larvae with inflated gas bladders were easily distinguished from larvae with uninflated gas bladders. Morphologically, the newly inflated gas bladder has the general appearance of a small air bubble, located dorsal to the gut. Behaviorly, larvae that had inflated gas bladders oriented horizontally within the water column and maintained their position without continual swimming motion. Larvae without inflated gas bladders assumed a vertical swimming position, sinking when swimming movements ceased. This characteristic swimming behavior of larvae with noninflated gas bladders was defined as "swim-up" behavior.

In 4.8-day-old striped bass larvae, the noninflated gas bladder primordium was dorsal and slightly posterior to the junction of the esophagus and the stomach. The stomach was at the right of the dorsomedial gas bladder primordium. The walls of the noninflated gas bladder primordium were much thicker ventrally than either dorsally or laterally. Columnar epithelium comprised the ventral mass of the gas bladder primordium. The noninflated gas bladder possessed a slight, dorsally located lumen. An open pneumatic duct connected the foregut with the right side of the posterior wall of the gas bladder primordium. The duct was composed of a single layer of cuboidal epithelium, surrounded by a layer of connective tissue.

A network of arterioles and venules, a rudimentary rete mirabile, ran parallel and ventral to the noninflated gas bladder primordium. At the posterior end of the gas bladder, the rete arterioles and venules turned dorsoanteriorally and entered a layer of loose connective tissue adjacent to the ventral columnar epithelium of the gas bladder. Within this connective tissue, a network of capillaries connected the arterioles and venules. Since the rete mirabile proceeded directly to the secretory epithelium of the gas bladder, the whole structure may properly be called a gas gland (Steen 1970). A gas gland is formed in striped bass before the initial inflation of the gas bladder.

In older (8 days) striped bass larvae that still had a noninflated gas bladder, the capillary network was more developed and pushed closer to the ventral columnar epithelium of the gas bladder. This gave the epithelium a festooned appearance.

In striped bass larvae that were in the process of inflating their gas bladders, the initial inflation occurred at the anterior end of the gas bladder. The columnar epithelium, which previously had dominated the ventral wall of the gas bladder, became confined to the posterior portion of the gas bladder as inflation progressed. At no time were distinct vacuoles visible within the ventral, columnar epithelium.

In 5.5-day-old striped bass larvae that possessed an inflated gas bladder, the ventral epithelium was reduced to cuboidal epithelium and was restricted to the posteriorventrad portion of the gas bladder where it was in close association with the gas gland. The remaining walls of the inflated gas bladder were composed of stretched epithelium. The rete mirabile still ran parallel and ventral to the newly inflated gas bladder. Capillaries of the rete mirabile made contact with secretory epithelium towards the posterior of the gas bladder.

In all striped bass larvae which were 4.3-5.5 days old and possessed an inflated gas bladder, a

[2]Martan, J. 1968. Laboratory instructions: Histological techniques in zoology. South. Ill. Univ., Carbondale, 98 p.

pneumatic duct with a well-defined lumen still appeared to form a connection between the gut and the gas bladder. However, in the older larvae of this group, the lumen of the pneumatic duct was smaller. In some sections, the openings between the pneumatic duct and the gut and the pneumatic duct and the gas bladder were not plainly visible, indicating that the pneumatic duct was beginning to atrophy.

We examined 14- and 21-day-old striped bass larvae without inflated gas bladders, and 24-day-old larvae with and without inflated gas bladders. In 14-, 21-, and 24-day-old larvae that had noninflated gas bladders, a well-developed rete mirabile still ran ventral and parallel to the gas bladder, turning dorsally to make a medial connection. The retail capillary network was developed, distending the overlaying connective tissue into a villuslike structure which was bordered by the ventral, columnar (secretory) epithelium of the gas bladder. The villuslike projections occupied most of the internal volume of the gas bladder. The pneumatic duct was well defined and continued to connect the gut with the gas bladder.

In 24-day-old striped bass larvae that had inflated gas bladders the pneumatic duct was absent. Unfortunately, we did not collect any striped bass larvae with inflated gas bladders between day 8 and day 24. We were thus unable to accurately describe the atrophication of the pneumatic duct, which seemingly occurs after inflation of the gas bladder. The rete mirabile was connected to a narrow band of cuboidal epithelium at the ventromedial wall of the gas bladder.

Discussion

Striped bass larvae possess an open pneumatic duct. An experiment designed to determine if striped bass have to gulp surface air to initiate gas bladder inflation was inconclusive, as was a similar experiment conducted by Doroshev and Cornacchia (1979). However, allowing striped bass larvae unobstructed access to the surface did not guarantee inflation in either study.

In our study, the pneumatic duct had atrophied in 24-day-old larvae which had inflated their gas bladders, but an open pneumatic duct was still present in 24-day-old larvae which had not inflated their gas bladders. This suggests that inflation of the gas bladder stimulates the atrophication of the pneumatic tube in striped bass. Johnston (1953) observed a similar phenomenon in the largemouth bass, *Micropterus salmoides*.

The rete mirabile, or gas gland, is developed before initial inflation of the gas bladder in larval striped bass. Since the gas gland concentrates gases within the gas bladders of many adult fishes, it is reasonable to assume that the gas gland plays a role in achieving initial inflation of the gas bladder in larval striped bass. The continued presence of a gas gland, and the prolonged retention of an open pneumatic duct in striped bass larvae that had not achieved initial inflation of the gas bladder within 24 days suggests that initial inflation may occur over an extended period of time.

Other workers have indicated that failure to initiate inflation of the gas bladder may lead to slower growth rates (Tait 1960), a higher percentage of morphological abnormalties (Baker[3]), and an increased susceptibility to stress (Lewis et al.[4]). Studies designed to define the stimuli responsible for the initiation of gas bladder inflation in striped bass, an important sport fish species that is often cultured, would be beneficial.

Literature Cited

DOROSHEV, S. I., AND J. W. CORNACCHIA.
1979. Initial swim bladder inflation in the larvae of *Tilapia mossambica* (Peters) and *Morone saxatilis* (Walbaum). Aquaculture 16:57-66.

GUNTHER, A. C. L. G.
1880. An introduction to the study of fishes. Adams and Charles Black, Edinb., 720 p.

JOHNSTON, P. M.
1953. The embryonic development of the swim bladder of the largemouth black bass *Micropterus salmoides salmoides* (Lacepede). J. Morphol. 93:45-67.

LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER.
1962. Ichthyology. Wiley, N.Y., 545 p.

MCEWEN, R. S.
1940. The early development of the swim bladder and certain adjacent parts in *Hemichromis bimaculata*. J. Morphol. 67:1-59.

POWERS, E. B.
1932. The relation of respiration of fishes to environment. Ecol. Monogr. 2:385-473.

SCHWARZ, A.
1971. Swimbladder development and function in the had-

[3]Baker, J. F. 1975. The rearing of Hudson River striped bass at the Edenton National Fish Report prepared for Consolidated Edison Company of New York, Inc., 30 p.

[4]Lewis, W. M., R. C. Heidinger, and B. L. Tetzlaff. 1977. Striped bass rearing experiments 1976. Report prepared for Consolidated Edison Company of New York, Inc., 197 p.

dock, *Melanogrammus aeglefinus* L. Biol. Bull. (Woods Hole) 141:176-188.
STEEN, J. B.
1970. The swimbladder as a hydrostatic organ. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. IV, p. 413-443. Acad. Press, N.Y.
TAIT, J. S.
1960. The first filling of the swim bladder in salmonoids. Can. J. Zool. 38:179-187.

JAMES S. BULAK

Fisheries Research Laboratory and Department of Zoology
Southern Illinois University, Carbondale, Ill.
Present address: *South Carolina Wildlife and*
Marine Resources Department
P.O. Box 170, Bonneau, SC 29431

ROY C. HEIDINGER

Fisheries Research Laboratory and Department of Zoology
Southern Illinois University
Carbondale, IL 62901

FOOD OF AGE 1 AND 2 ATLANTIC TOMCOD, *MICROGADUS TOMCOD*, FROM HAVERSTRAW BAY, HUDSON RIVER, NEW YORK

Atlantic tomcod, *Microgadus tomcod* (Walbaum), are opportunistic feeders (Howe 1971; Grabe 1978) with amphipods *Gammarus* spp. and the decapod *Crangon septemspinosa* identified as primary prey (Howe 1971; Alexander 1971; Scott and Crossman 1973; Grabe 1978; Nittel[1]). Limited data are available on the biology of yearling and older Hudson River tomcod due to their low overall abundance and because they are most abundant during winter when ice cover restricts sampling. This note summarizes feeding data of 339 tomcod, ages 1 and 2, from the Haverstraw Bay area of the Hudson River (37.5-41.5 mi north of the Battery, New York City) on 19 dates, January 1973-June 1976, and supplements food preference data on juveniles (Grabe 1978). All fish were collected as part of an ecological monitoring program conducted by Lawler, Matusky & Skelly Engineers for Orange and Rockland Utilities, Inc.

Methods

Collections (Table 1) were made with a 9.1 m otter trawl (64 mm mesh cod end liner) towed against the tide at 1.5-2.0 m/s during both day and night. The data are likely to be biased towards daytime feeding preferences since almost twice as many tows were taken during daytime as at night. Diel differences in feeding could not be evaluated because day and night collections were often combined for other analyses. Fish were preserved in 10% buffered Formalin.[2] In the laboratory they were measured (±1 mm total length, TL) and weighed (±0.1 g), and the stomachs were removed and preserved in 70% ethanol. Prey were identified and counted, and the contents of 195 stomachs were dried at 103° C. The number of fish per sampling period whose stomach contents were analyzed were limited by contract and were randomly selected from the total catch. Whenever possible, I analyzed additional fish to increase both sample size and temporal coverage. Yearling and older tomcod collected during fall 1973 were separated from young-of-the-year by examination of length-frequency histograms drawn from larger samples (Lawler, Matusky & Skelly Engineers[3]); by this method age 1 and 2 fish were those ⩾160 mm TL. On other sampling dates young-of-the-year were present only as larvae or as juveniles <110 mm TL.

TABLE 1.—Collections of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Season	Sample size	Total length (mm) Mean	95% confidence limits
Winter (Jan.-Feb.)	72	130.5	126.2-134.7
Spring (Apr.-June)	166	158.7	155.8-161.6
Summer (July-Aug.)	10	156.3	142.2-170.3
Fall (Oct.-Dec.)	91	182.6	178.3-186.8

Food preference data were classified seasonally and examined as percentage occurrence (number of fish in which prey item "a" occurred/total number of fish), percentage composition (number of prey item "a"/total number of prey), and as importance, I, the geometric mean of these two measurements (Windell 1971). This approach, however, may overestimate the utilization of smaller prey (e.g., copepods) but should provide a better indication of feeding preference than either percent occurrence or percent composition taken singly. An index of fullness (Windell 1971), I_f, was calculated to evaluate feeding intensity (dry

[1]Nittel, M. 1976. Food habits of Atlantic tomcod (*Microgadus tomcod*) in the Hudson River. *In* Hudson River Ecology. Fourth Symposium on Hudson River Ecology. Bear Mountain, N.Y., March 28-30 1976. Hudson River Environmental Society, Inc.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Lawler, Matusky & Skelly Engineers. 1976. Environmental impact assessment—water quality analysis: Hudson River. Natl. Comm. on Water Quality. NTIS PB-251099.

weight of stomach contents $\times 10^4$ as a percentage of wet weight of fish). Empty stomachs were included in seasonal measurements of feeding intensity. Statistical tests were from Sokal and Rohlf (1969).

Results and Discussion

Gammarus spp. were the most important prey during all seasons (Table 2). Secondary prey included copepods (winter), the oppossum shrimp, *Neomysis americana* (spring and fall) *Monoculodes* sp. (Amphipoda) (spring), *Cyathura polita* (Isopoda) (spring and fall), and sand shrimp, *Crangon septemspinosa* (fall). *Gammarus* spp., *N. americana*, and *Monoculodes* sp. are numerically important tychoplankters in this area of the Hudson River (Ginn 1977; Lauer et al.[4]). Abundant infaunal species in the Haverstraw Bay area include the polychaete *Scolecolepides viridis* the amphipod *Leptocheirus plumulosus*, and *Cyathura polita* (Ristich et al. 1977). Tychoplankton appears to be more important as prey of Hudson River tomcod than infauna. In other estuaries, however, infauna may be more important; e.g., Alexander (1971) found that polychaetes, even though

[4]Lauer, G. J., W. T. Waller, D. W. Bath, W. Meeks, R. Heffner, T. Ginn, L. Zubarik, P. Bibko, and P. C. Storm. 1974. Entrainment studies on Hudson River organisms. *In* L. D. Jensen (editor), Entrainment and intake screening. Proceedings on the second entrainment and intake screening workshop, p. 37-82. Johns Hopkins Univ. Edison Electric Inst. Rep. 15.

TABLE 2.—Seasonal prey of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

	Percent occurrence[1]				Percent composition[2]				Importance[3]			
Taxon	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Nematoda		0 6		2 2		0 1		0 1		0 1		0 5
Polychaeta												
Scolecolepides viridis		2 4		2 2		0 1		0 1		0 5		0 5
Oligochaeta				1 1				0 4				0 7
Hirudinea		1 2		2 2		0 1		0 2		0 3		0 7
Glossiphoniidae	6 9			0 3					1 4			
Helobdella sp		0 6				0 1				0 1		
Theromyzon sp		2 4				0 2				0 7		
Piscicola milneri		0 6				0 1				0 1		
Mollusca												
Amnicola sp		1 2		1 1		0 1		0 1		0 2		0 3
Crustacea												
Ostracoda		0 6				0 1				0 1		
Copepoda	45 8	4 8		2 2	47 7	1 3		0 3	46 7	2 5		0 8
Mysidacea												
Neomysis americana	13 9	18 1	10 0	40 7	2 9	3 5	12 5	9 6	6 3	8 0	11 2	19 8
Isopoda												
Chirridotea almyra		6 6				0 3				1 4		
Cyathura polita	2 8	18 7		14 3	0 1	0 9		2 3	0 5	4 1		5 7
Edotea triloba	1 4			5 5	0 1			0 5	0 4			1 7
Amphipoda												
Corophium lacustre	1 4	1 8		2 2	0 1	0 1		0 1	0 4	0 4		0 5
Gammarus spp	81 9	87 3	60 0	64 8	43 5	88 6	62 5	70 2	59 7	87 9	61 2	67 4
Leptocheirus plumulosus		6 6		1 1		0 3		0 1		1 4		0 3
Melita nitida				1 1				0 1				0 3
Monoculodes sp	12 5	13 3		14 3	2 0	4 0		3 0	5 0	7 3		6 5
Decapoda												
Callinectes sapidus				5 5				0 6				1 8
Crangon septemspinosa	1 4		30 0	49 1	0 1		18 8	7 2	0 4		23 7	18 8
Rhithropanopeus harrisii		1 2		20 9		0 1		2 3		0 3		5 7
Insecta												
Odonata												
Enallagma spp		0 6				0 1				0 1		
Trichoptera larvae		0 6		1 1		0 1		0 1		0 1		0 3
Diptera												
Chaoborus punctipennis larvae		1 8	10 0	1 1		0 1	6 2	0 1		0 4	7 9	0 3
Chironomidae larvae	2 8	4 8		4 4	0 1	0 2		0 7	0 5	1 0		1 8
Unidentified pupae		1 8				0 1				0 4		
Pisces												
Alosa spp				5 5				0 6				1 8
A. aestivalis				*								
A. pseudoharengus				*								
Anchoa mitchilli				2 2				0 1				0 5
Anguilla rostrata		0 6				0 1				0 1		
Microgadus tomcod eggs	4 2				3 3				3 7			
M. tomcod larvae		1 2				0 1				0 3		
M. tomcod juveniles		1 8				0 1				0 4		
Unidentified	1 4	3 6		14 3	0 1	0 1		1 1	0 4	0 6		4 0

[1]Number of occurrences/total number of fish
[2]Number of prey item i/total number of prey
[3]Geometric mean of (percent occurrence · percent composition)

underestimated, ranked second to *Crangon septemspinosa* in the percent volume of stomach contents of tomcod from Montsweag Bay, Maine.

Feeding intensity showed significant differences between seasons by analysis of variance using arc-sine transformed I_f values ($F_{3,190} = 11.9$; $P < 0.001$). A Student Newman-Keulls test showed that I_f was greatest during fall, and spring values were greater than winter and summer, which were similar ($P < 0.05$) (Table 3). Percentage of empty stomachs was highest during winter, least during fall and spring. Feeding intensity, then, was greatest both prior to and subsequent to spawning, when, presumably, energy requirements were greatest. A similar seasonal cycle was described for juveniles (Grabe 1978).

A shift in importance of primary prey, from *C. septemspinosa* to copepods, occurred from fall to winter. A similar shift from the larger prey to smaller prey was noted for juveniles (Grabe 1978), and it was suggested that constriction of the alimentary canal by maturing gonads (Schaner and Sherman 1960) was a factor. To clarify this shift, predation on the primary species (*Gammarus* spp.) and large (*C. septemspinosa*) and small (copepods) secondary prey were examined for the period November 1974 through February 1975 (November and December fish were young-of-the-year; data summarized in Grabe 1978). *Gammarus* spp. were important throughout this period, especially on 4 December (Table 4). *Crangon septemspinosa* was important only during November and copepods were important during January and February. Since gonad production was generally greatest November through December and coefficient of maturity peaks during November for males and January for females (Orange and Rockland Utilities, Inc.[5]), the observed shift in prey selection corresponded well with gonad maturation. Causation has yet to be determined and small sample sizes may not depict the situation accurately.

Tomcod are occasionally piscivorous (Alexander 1971; Scott and Crossman 1973; Nittel see footnote 1). Five fish species, including eggs, larvae, and juvenile tomcod were identified as prey and were most important during the fall (Table 2). Cannibalism occurred at low levels during winter and spring. Cannibalism has been reported in other fishes, e.g., *Alosa pseudoharengus* (Rhodes et al. 1974) and *Stizostedion v. vitreum* (Chevalier 1973) and may be a factor affecting recruitment.

TABLE 3.—Index of fullness[1] (for subsamples) and percentage of empty stomachs of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Season	Sample size	Index of fullness: Mean	Index of fullness: 95% confidence limits	Percent empty[2]
Winter	70	6 21	4 19- 8 23	12 5
Spring	68	10 24	7 94-12 53	4 2
Summer	5	0 32	0 09- 0 55	10 0
Fall	52	20 62	12 08-29 12	3 3

[1]Dry weight of stomach contents × 10^4 as a percentage of wet weight of fish
[2]Based on total number of fish analyzed; see Table 1

Acknowledgments

Appreciation is extended to Orange and Rockland Utilities, Inc. for permission to analyze the fish, to Lawler, Matusky & Skelly Engineers for laboratory facilities, and to R. E. Schmidt for reviewing an earlier draft of the manuscript.

Literature Cited

ALEXANDER, L. C.
1971. Feeding chronology and food habits of the tomcod (*Microgadus tomcod* Walbaum) and winter flounder (*Pseudopleuronectes americanus* Walbaum) in Montsweag Bay (Sheepscot River) Maine. M.S. Thesis. Univ. Maine, Orono, 36 p.

[5]Orange and Rockland Utilities, Inc. 1977. Bowline Point Generating Station: Near-field effects of once-through cooling system operation on Hudson River biota.

TABLE 4.—Changes in the importance of *Crangon septemspinosa* (CS), copepods (Cop), and *Gammarus* spp. (Gamm) in the diet of Atlantic tomcod from Haverstraw Bay, Hudson River during the period November 1974 through February 1975

Date	Sample size	Percent occurrence[1] CS	Cop	Gamm	Percent composition[2] CS	Cop	Gamm	Importance[3] CS	Cop	Gamm	Mean number/stomach CS	Cop	Gamm
5 Nov	14	57 1	0 0	85 7	14 8	0 0	77 4	29 1	0 0	81 4	1 2	0 0	6 4
13 Nov	13	69 2	0 0	46 2	41 2	0 0	23 5	53 4	0 0	33 0	2 2	0 0	1 2
4 Dec	28	0 0	7 1	100 0	0 0	0 2	95 4	0 0	1 2	97 7	0 0	0 1	48 9
25 Jan	15	6 7	73 3	66 7	0 1	68 1	18 7	0 9	70 7	35 3	0 1	39 1	10 7
19 Feb	4	0 0	75 0	75 0	0 0	26 3	61 1	0 0	44 4	6 7	0 0	11 5	26 8

[1]Number of occurrences/total number of fish
[2]Number of prey item a /total number of prey
[3]Geometric mean of (percent occurrence × percent composition)

CHEVALIER, J. R.
1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Trans. Am. Fish. Soc. 102:739-744

GINN, T. C.
1977. An ecological investigation of Hudson River macrozooplankton in the vicinity of a nuclear power plant. Ph.D. Thesis. New York Univ., N.Y., 292 p

GRABE, S. A.
1978. Food and feeding habits of juvenile Atlantic tomcod, *Microgadus tomcod*, from Haverstraw Bay, Hudson River. Fish. Bull., U.S. 76:89-94.

HOWE, A. B.
1971. Biological investigations of Atlantic tomcod, *Microgadus tomcod* (Walbaum), in the Weweantic River estuary, Massachusetts, 1967. M.S. Thesis. Univ. Massachusetts, Amherst, 82 p.

RHODES, R. J., D. A. WEBB, AND T. S. MCCOMISH.
1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. Proc. 17th Conf. Great Lakes Res., p. 593-595.

RISTICH, S. S., M. CRANDALL, AND J. FORTIER.
1977. Benthic and epibenthic macroinvertabrates of the Hudson River. I. Distribution, natural history and community structure. Estuarine Coastal Mar. Sci. 5:255-266.

SCHANER, E. AND K. SHERMAN.
1960. Observations on the fecundity of the tomcod, *Microgadus tomcod* (Walbaum). Copeia 1960:347-348.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish Res. Board Can., Bull. 184, 966 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

WINDELL, J. T.
1971. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 215-226. IBP (Int. Biol. Programme) Handb. 3.

STEPHEN A. GRABE

Normandeau Associates, Inc.
15 Pickering Avenue
Portsmouth, NH 03801

INDEX

Fishery Bulletin Vol. 77, No. 1-4

ERRATUM

Fishery Bulletin, Vol. 77, No. 3

Lancraft, Thomas M., and Bruce H. Robison, "Evidence of postcapture ingestion by midwater fishes in trawl nets," p. 713-715.

1) Page 713, right column, line 13, correct line to read:
Data from haul 8 are biased toward larger indi-

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including Zip code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to $5^{1}/_{4}$ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor, if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations.* (*Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, °C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Jay C. Quast, Scientific Editor
Fishery Bulletin
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Notes

☆GPO 696-364