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(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

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CONTENTS

Vol. 76, No. 1 January 1978

(Continued on next page)

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DISEASES, PARASITES, AND TOXIC RESPONSES OF COMMERCIAL PENAEID SHRIMPS OF THE GULF OF MEXICO AND SOUTH ATLANTIC COASTS OF NORTH AMERICA[1]

JOHN A. COUCH[2]

ABSTRACT

A reference work and review of both infectious and noninfectious diseases of commercial penaeid shrimps of the Gulf and South Atlantic region of the United States is presented. Disease is second only to predation and periodic physical catastrophes in limiting numbers of penaeid shrimps in nature and second only to nutritional and reproductive requirements in limiting aquacultural successes with penaeid shrimps.

Infectious agents causing disease in penaeid shrimps are a virus, bacteria, fungi, protozoa, helminthes, and nematodes. A well-described *Baculovirus* infects larval and adult shrimp and is associated with mortality, particularly in larval shrimp. Bacteria of the genera *Vibrio, Beneckea,* and *Leucothrix* are associated with disease in penaeid shrimps, but bacterial roles in mortality are unclear. The same is largely true for fungi with members of the genera *Lagenidium* and *Fusarium* causing pathogenesis in cultured shrimp. *Lagenidium* causes severe destruction of larval shrimp tissues. Of the many protozoan groups represented in and on penaeid shrimps as tissue parasites and commensals, the Microsporida of the genera *Nosema, Thelohania,* and *Pleistophora* are the most destructive. The ciliate protozoa *Zoothamnium* sp., *Lagenophrys* sp., and *Parauronema* sp. may cause dysfunction in shrimp. An undescribed apostome ciliate is associated with black gill disease. A suctorian, *Ephelota* sp., is an ectocommensal of larval shrimp, attaching to the cuticle. The six species of gregarines reported cause little or no pathogenesis, and a single reported flagellate species role in shrimp health is uncertain.

Flatworms found in penaeid shrimps are metacercariae of a species of *Microphallus* in muscles and viscera, metacercariae of *Opecoeloides fimbriatus* in viscera, plerocercoid larvae of *Prochristianella hispida* in the hepatopancreas and hemocoel, and four other cestode developmental stages. Nematodes found are *Thynnascaris* sp., *Spirocamallanus pereirai, Leptolaimus* sp., and *Croconema* sp.

Noninfectious disease agents in penaeid shrimps are chemical pollutants, heavy metals, and environmental stresses. Organochlorine, organophosphate, and carbamate pesticides all have adverse effects in penaeids. Fractions of petroleum, particularly the naphthalenes, are very toxic to shrimp. Little other work has been done on the effects of petroleum on penaeid shrimps. Cadmium causes black gills in shrimp by killing gill cells. Mercury is accumulated by penaeids and may interfere with their osmoregulatory abilities. Many chemotheropeutic chemicals used routinely in treatment of fish diseases are toxic to shrimp at certain determined concentrations.

Spontaneous pathoses found are a benign tumor, muscle necrosis, and gas bubble disease. "Shell disease" is discussed from points of view of possible causes. A syndrome of "broken backs" is reported in penaeid shrimps for the first time. An overview is presented for general needs in penaeid shrimp health research.

Recent attempts to culture penaeid shrimps in large quantities have stimulated renewed interest in the pathobiology of crustacean species. Pathogens and disease, in general, have been indicted as causes for many failures in maintaining various life-cycle stages of Crustacea. Therefore, considerable amounts of new information and data on known and recently discovered diseases of penaeid shrimps have been published or reported in the last decade. This recent information, along with an older but equally valuable series of publications, presents a substantial body of knowledge which describes and defines problems of disease encountered in the biology, management, and massive culture of penaeid shrimps.

Major contributions to the study of shrimp diseases in North America have been made by sev-

[1]Contribution No. 283 from the Gulf Breeze Environmental Research Laboratory.

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eral individuals. Sprague (1954, 1970, footnote 3), Kruse (1959, 1966), Hutton et al. (1959), Iversen and Manning (1959), Hutton (1964), and Iversen and Van Meter (1964) were early explorers in penaeid shrimp infectious diseases. More recently the works of Overstreet (1973), Lightner (1974, 1975), Lightner and Fontaine (1973), Johnson (1974), Feigenbaum (1973, 1975), Couch (1974a, b, 1976) and Sindermann[4] have contributed to the general fund of data. Overstreet's 1973 paper is particularly valuable because it gives prevalence data for many of the parasites of penaeid shrimps of the northern Gulf. Many other authors of single, significant works on penaeid diseases will be cited in specific sections later in this paper.

The scientific reports and reviews mentioned above, along with much unpublished experience, present a consensus which impresses me with the high significance of disease to the overall ecology and biology of penaeid shrimps. In its broadest sense, disease is probably second only to predation and periodic physical catastrophes (e.g., freshets, temperature fluctuations) as a continuous environmental factor limiting numbers of penaeid shrimps in nature. In attempts at massive culture of penaeid shrimps, infectious disease may rank below only reproductive and nutritional requirements as a limiting factor. Toxicants, in the form of pollutants, are threats to the well being of estuarine species, particularly in certain chronically polluted regions. Toxic responses in penaeid shrimps have been studied experimentally recently, and, therefore, some data are available on this subject.

This paper is concerned with the present status of diseases, parasites, and toxic responses of four commercial species of penaeid shrimps from the Gulf and South Atlantic region of North America. These are the pink shrimp, *Penaeus duorarum*; the brown shrimp, *P. aztecus*; and the white shrimp, *P. setiferus*. Occasional reference will be made to parasites of *P. braziliensis* which occupies a marginal portion of the U.S. range of the three other species. The subjects will be treated in the following order: Infectious diseases and parasites; noninfectious diseases and toxic responses; and overview and future research.

[3]Sprague, V. 1950. Notes on three microsporidian parasites of Decapod crustacea from Louisiana waters. Occas. Pap. Mar. Lab., La. State Univ. 5:1-8.

[4]Sindermann, C. J. 1974. Diagnosis and control of mariculture diseases in the United States. Tech. Ser. Rep. No. 2, Natl. Mar. Fish. Serv., NOAA, Highlands, N.J., 306 p.

INFECTIOUS DISEASES AND PARASITES

Viruses

To date, only a single virus disease has been described for shrimps. Couch (1974a, b) and Couch et al. (1975) have described a rod-shaped virus (Figures 1-3) which has many characteristics of the baculoviruses (nuclear polyhedrosis viruses) previously described only from insects or mites. The virus has been named *Baculovirus penaei* (Couch 1974b).

This virus commonly has been found to infect the hepatopancreas of juvenile and adult stages of pink and brown shrimp in nature. Laboratory-reared larval brown shrimp (protozoea and mysis stages) have been found with virus-infected midgut and hepatopancreas.

Infected hepatopancreatic cells in pink shrimp display striking cytopathological changes when compared with normal, noninfected cells. Nuclear hypertrophy (Figure 3), chromatin diminution (Figure 3), nucleolar degeneration (Figure 3), and polyhedral inclusion body (PIB, Figure 2) production are characteristic of patent virus infections observable with bright field or phase contrast microscopy.

Electron microscopy (EM) reveals the rod-shaped virions (269 nm × 50 nm) in infected, hypertrophied nuclei prior to, during, and after the PIB is formed. Various stages of the virus replicative cycle are observable with EM of thin sections of moderately to heavily infected hepatopancreas. The ultimate cytopathological effect of the virus is destruction of the host cell through rupture or lysis. This is accomplished usually by the growth of the PIB to a size too large for the host cell to accommodate (Figure 4), concomitant with virus-induced nuclear hypertrophy and probable stressing of nuclear membranes.

The PIB's produced during infections are patently diagnostic for the baculovirus of penaeid shrimp (Figures 4, 5). To find a single characteristic PIB in tissue squashes of shrimp hepatopancreas or midgut is to diagnose infection. Quantitation of patent infections (PIB's present) can be made on a relative basis by hemocytometer counts of PIB's in aliquots of fresh tissue. Degree of latent infections, however, may be estimated only with great difficulty through laborious EM examinations. Over 2,000 PIB's/mm^3 of hepatopancreatic tissue are considered a heavy infection as determined by hemocytometer counts. Heavy patent

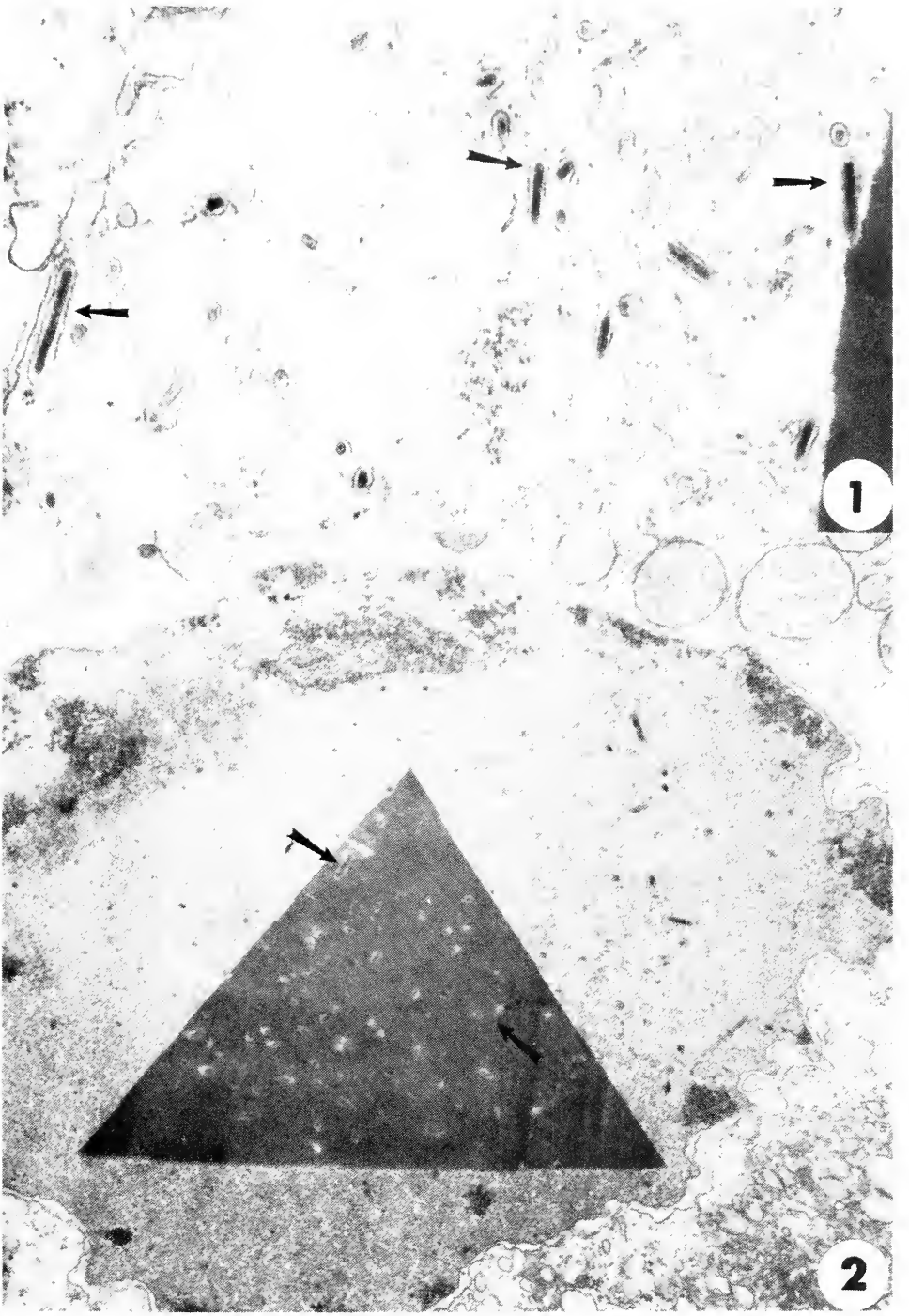


FIGURE 1.—*Baculovirus* virions in nucleus of hepatopancreatic cell of pink shrimp; note rod form (arrows) and outer envelope surrounding nucleocapsid (electron micrograph). ×70,000.

FIGURE 2.—Polyhedral inclusion body (PIB) in virus-infected nucleus; note characteristic triangular form, and rod-shaped virions in PIB (arrows); also note heterochromatin diminution and granular nucleoplasm. ×22,260.

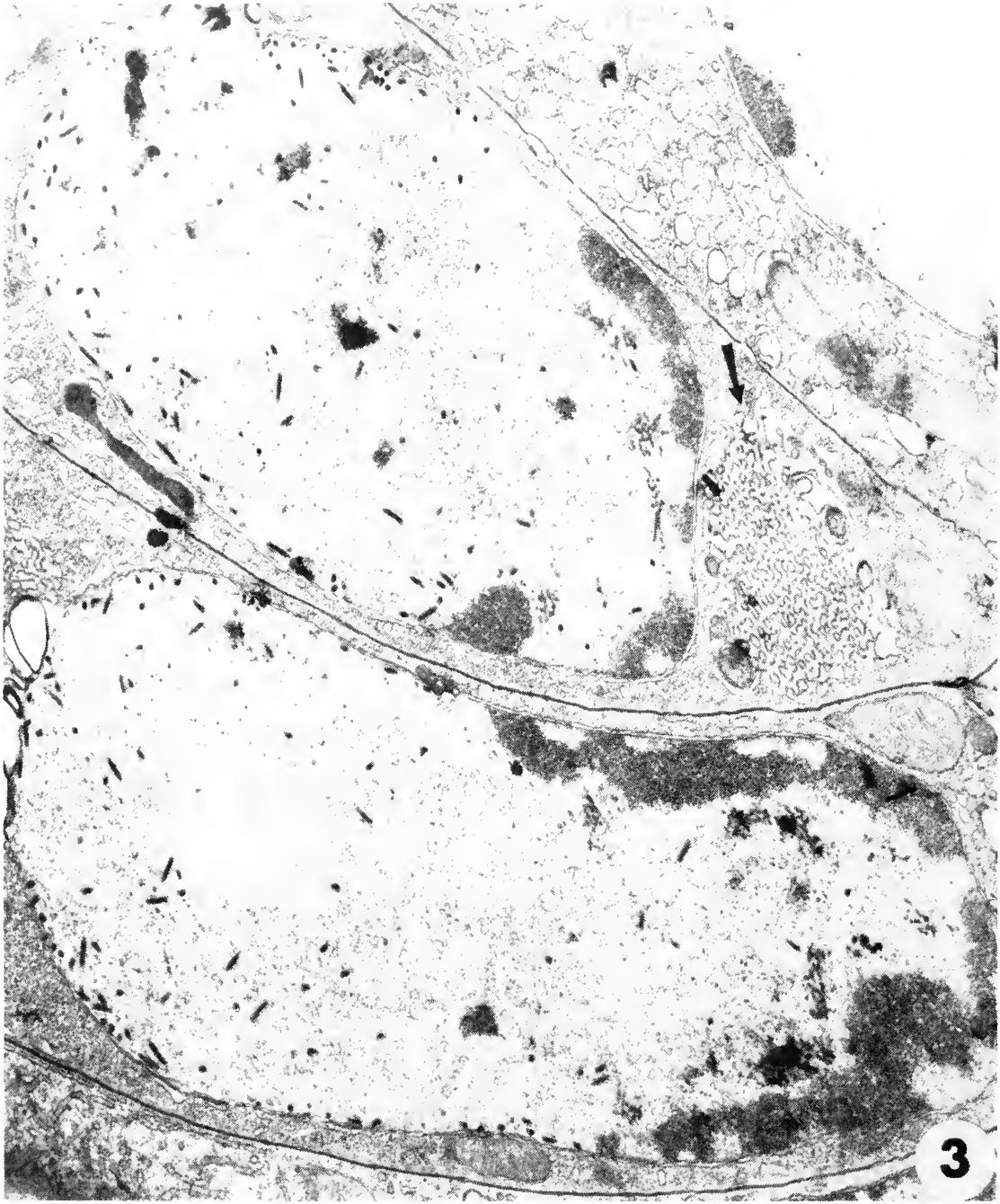
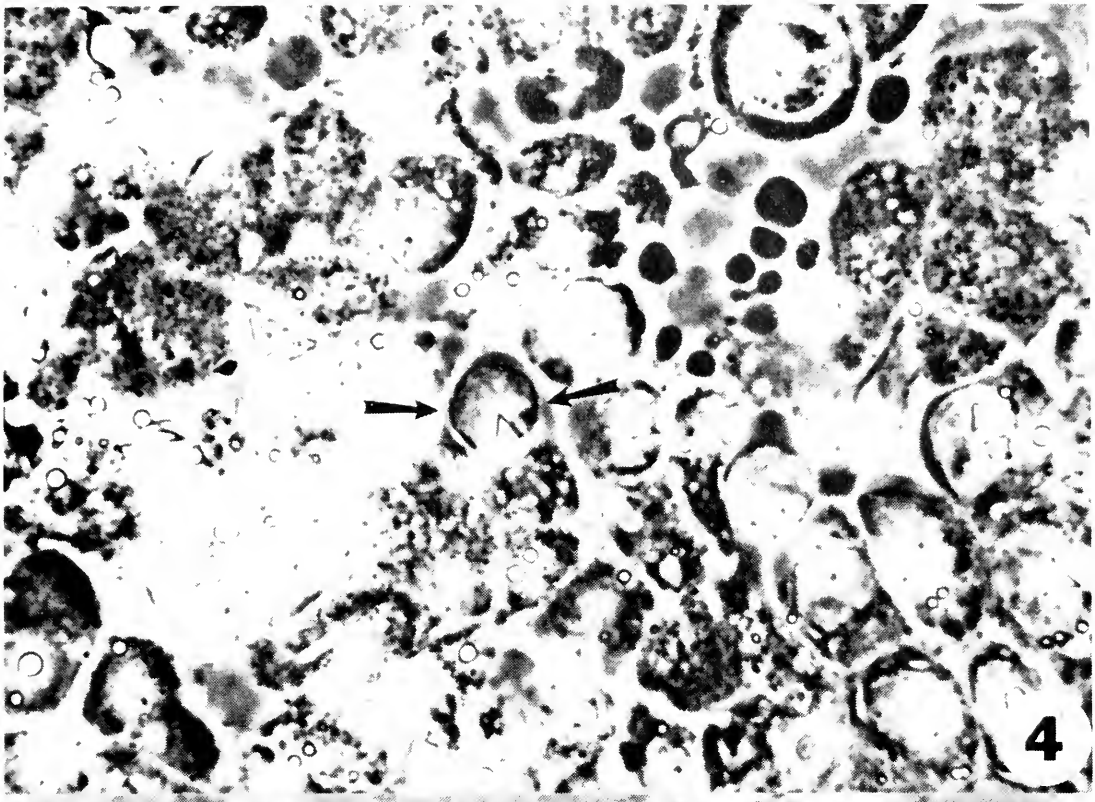


FIGURE 3.—Two hepatopancreatic cells with *Baculovirus*-infected nuclei; note nuclear membrane proliferation (arrow) and nuclear hypertrophy. ×14,400.



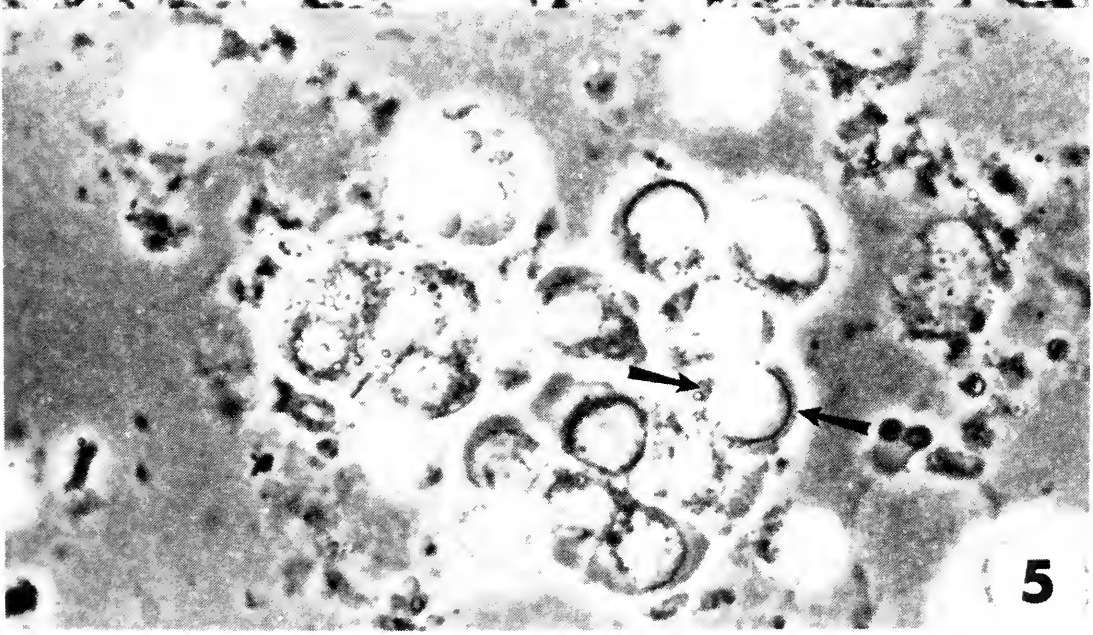


FIGURE 4.—Phase contrast micrograph of fresh squash preparation of heavily, patent, virus-infected hepatopancreas from pink shrimp, note hypertrophied nuclei (arrows) and characteristic refringent PIB's. ×1,000.

FIGURE 5.—Phase contrast micrograph of fresh squash showing PIB's (arrows) of varying sizes, some free of nuclei following nuclear rupture. ·1,000.

infections are obvious in fresh squash preparations because PIB's fill every microscopic field.

Prevalence of virus in feral pink shrimp from several locations on the northern gulf coast of Florida has varied among samples collected. There appears to be no seasonal intensification of prevalence that is statistically significant; however, fall samples have been best for recovering heavy infections. To date, of 4,676 shrimp examined, 808 have been patently infected. In the laboratory, virus prevalence and intensity have increased repetitively in 20- to 30-day periods in different lots or samples of feral shrimp held under crowded, sublethally stressful conditions (Couch 1974b). This increase in prevalence associated with crowding provides indirect evidence for the infectious nature of the shrimp baculovirus. There is also increasing evidence, from our research, that exposures to low levels of certain chemicals, such as polychlorinated biphenyl (PCB), enhance spread of virus through captive populations (Couch and Courtney 1977). We have induced a 50% increase in prevalence in captive shrimp by exposing shrimp to sublethal levels of PCB's (Aroclor 1254).[5] Transmission in nature probably is achieved via cannibalism of infected shrimp by noninfected shrimp. Laboratory transmission has been minimally successful when hatchery-reared or nonpatently infected juvenile or adult shrimp were fed heavily infected hepatopancreas. Only about 20% of fed shrimp show patent infections 20 to 30 days after initial feeding. Degree of infection in adult shrimp is not useful in predicting mortality of shrimp.

Recently the shrimp baculovirus was associated with massive mortality of larval and postlarval brown shrimp in a commercial aquaculture attempt. Brown shrimp, hatched and reared to protozoal and mysid stages in laboratory tanks, suffered a mass mortality in a 48-h period (95% of several million larvae). Water quality was not found to be at fault and there were no toxicants known to be in the water. Upon careful histological examination of a sample of surviving and dead larvae, I discovered that 19.4% (n = 139) had patent virus infections, mostly heavy, in midgut and hepatopancreatic cells (Table 1). Subsequent electron microscopical study confirmed that 60 to 90% of hepatopancreatic cell profiles in larvae had infections, many with prepatent stages of the virus. Present in higher prevalences in these dying shrimp were a flagellate protozoon and a ciliate protozoon. The relative roles of the three pathogens in the shrimp mortality will be discussed in later sections of this paper (Tables 1, 2).

TABLE 1.—Relative prevalence of pathogens in 139 larval (late protozeal and mysid stages) brown shrimp, *Penaeus aztecus*,[1] in April 1974.

Condition	Number of larvae affected	Percent of total examined
Not infected	41	29.5
Flagellate	89	64.0
Ciliate	40	28.8
Virus	27	19.4

[1]Whole mount slides with Protargol stain (Bodian-activated protein silver).

TABLE 2.—Prevalence and concurrent infections of pathogens in 139 larval brown shrimp examined in April 1974. [Concurrent vs. single infections.]

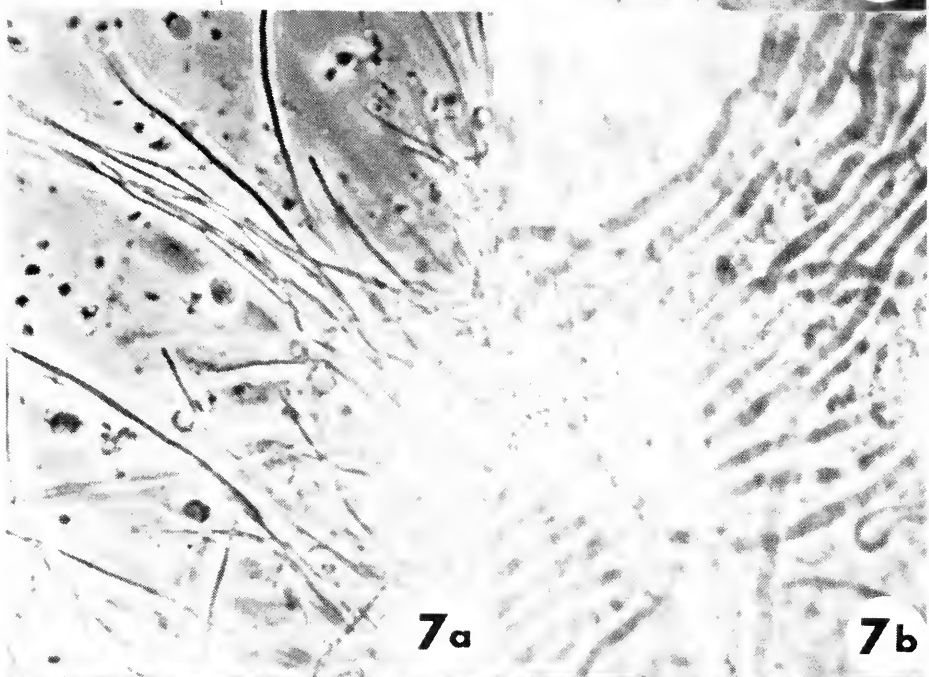
Types of pathogens	Number of larvae affected	Percent of total examined
None	41	29.5
Flagellate only	38	27.3
Ciliate only	1	0.7
Virus only	8	5.8
Flagellate and ciliate	32	23.0
Flagellate and virus	12	8.6
Ciliate and virus	0	0.0
Flagellate, virus, and ciliate	7	5.0

Bacteria

The role of bacteria in diseases of penaeid shrimps is presently being investigated seriously for the first time. A few scattered reports deal with bacteria as pathogens, contaminants, or ectocommensals in shrimps.

Cook and Lofton (1973) reported isolation of three genera of bacteria, *Beneckea, Vibrio,* and *Pseudomonas,* from penaeid shrimp suffering from "shell disease," also known as black spot disease. This disease (Figure 6) is characterized by brown to black spots on the external carapace or cuticle of shrimp and has been observed in brown, pink, and white shrimps. In advanced cases of the disease, considerable erosion and destruction of the cuticle occurs. This disease has been reported from many other decapod Crustacea (Rosen 1970). Chitinoclastic bacteria such as *Beneckea* sp. have been thought to be the causative agents of black spot disease, although attempts to experimentally produce the disease in shrimp by innoculating *Beneckea* have had uncertain results (see section on "shell disease" under Noninfectious Diseases). Mechanical injury to shrimp that results in breakage in the normal cuticle probably plays an

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



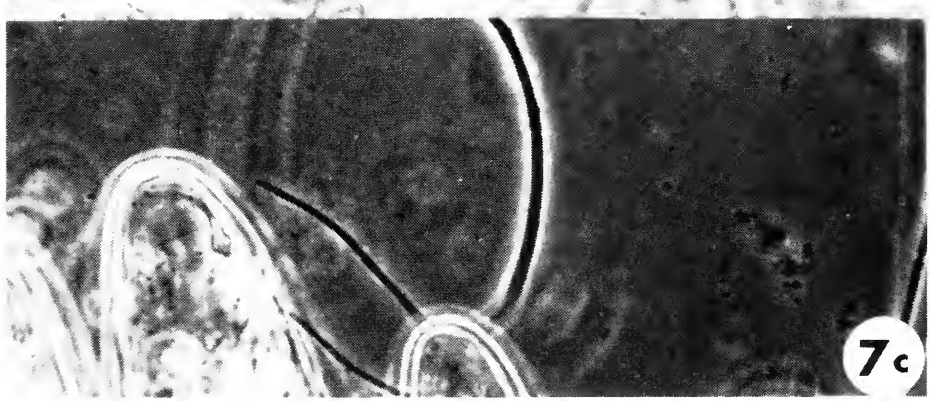


FIGURE 6.—"Shell disease" in pink shrimp; note black spots of varying sizes (arrows); none of these have penetrated cuticle of shrimp at this stage.

FIGURE 7.—a. Filaments of *Leucothrix mucor* (bacteria) in heavy infestation on gills of pink shrimp. ×400. b. Wet mount preparation of *L. mucor* from heavy gill infestation; note granules in some filaments. ×900. c. Single filaments of *L. mucor* showing attachment to end of gill filament; note few bacterial filaments in light infestation shown here. ×900.

initiating role in the genesis of black spot disease (Cook and Lofton 1973).

The effects of black spot disease on individual shrimp is apparently a breakdown of cuticular protection, thus permitting loss of hemolymph and invasion by internally destructive pathogens. Black spot disease in penaeids is fairly common, at least in early manifestation. However, the disease probably plays a minor role in mortalities of feral shrimp because shrimp probably tolerate the initial lesions well.

Vanderzant et al. (1970) isolated *Vibrio parahemolyticus* from white shrimp from the Gulf of Mexico. This bacterium is one etiological agent for human gastroenteritis in Japan and possibly in the United States (Krantz et al. 1969). The pathogenicity of *V. parahemolyticus* for Crustacea, including shrimp, has not been conclusively established. One should remember that natural seawaters, particularly from inshore regions, may be considered "gram negative bacterial soups." Therefore, the presence of *Vibrio* sp. and other gram negative rods on marine organisms living in the "soup" should be expected. The role that *Vibrio* plays in the health of shrimps is uncertain. Ulitizur (1974) has pointed out that certain strains of *Vibrio parahemolyticus* isolated from seawater have very short generation times (12-14 min) at higher temperatures (39°C). In subtropical areas where temperatures might soar in hot seasons, particularly in ponds, the role of *Vibrio* sp. as pathogens of shrimp might be enhanced. Lightner (1975) discussed at length the suspect role of *Vibrio* spp. in penaeid shrimp health.

Ectocommensal bacteria may play a significant role in the well being of penaeids, particularly those held in crowded volumes of water where rich organic substrate and optimum temperatures prevail. Pertinent among this group is the filamentous bacterium *Leucothrix mucor* (Oersted), a widespread epiphyte of marine animals and plants (Johnson et al. 1971). *Leucothrix* has been found in high numbers attached to the gill filaments of brown, white, and pink shrimp (Figure 7 a, b). The filaments are nonbranching, attached singly to the cuticle of the gills (Figure 7c), have a modal diameter of 2 μm, and consist of septate chains of almost square-shaped bacteria. Each bacterium has several mesosomes along its cytoplasmic membrane (Figure 8).

A study was conducted with EM to determine the mode of attachment of *Leucothrix* to shrimp gill cuticle. Figure 9a, b shows cross sections of a basal portion of a filament at its point of adhesion to gill cuticle. The bacterium does not possess a differentiated holdfast. There is no penetration of the epicuticle, and apparently the filament is secured to the gill epicuticle by an electron-opaque mucouslike substance. I presume that this substance is secreted by the bacterium.

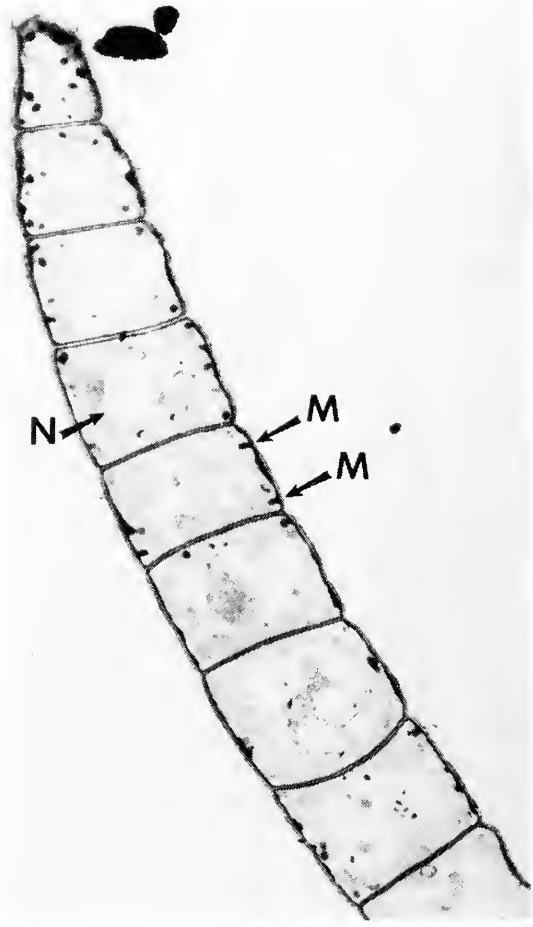


FIGURE 8.—Electron micrograph of single filament of *Leucothrix mucor* showing nearly square cell profiles; note nucleoids (N) and mesosomes (M) (arrows) of bacterial cells plus septa separating each cell in filament ×25,900.

Leucothrix grows best on penaeid shrimps when the shrimps are crowded and when there is a rich organic seawater medium. Salinities of 20-35‰ and temperatures of 20°-25°C have been adequate for overgrowths of *Leucothrix* on gills of shrimp. Terminal gonidia were not searched for or observed in the fresh natural infestations on shrimp that I have studied with phase contrast, bright field, and electron microscopy.

The major adverse effect of *Leucothrix* infestations on shrimp is probably interference with gas diffusion across gill cuticle, particularly in massive infestations (Figure 7a, b). In experiments at my laboratory, I found that pink shrimp when exposed to various levels of an ethylene glycol-containing waste in bioassay systems had heavy growths of *L. mucor* on their gills, whereas nonexposed, control shrimp had little or no growth on their gills. Mortality of the exposed shrimp was proportionate to the extent of growth of *Leucothrix* on their gills. Indications from EM studies are that the mucoid substance with which *L. mucor* attached to gills may cover gills (Figure 9a, b) in

FIGURE 9.—a. Relationship of *Leucothrix mucor* filaments to gill cuticle of pink shrimp; note electron-opaque mucoid substance (arrow) at point of attachment and adjacent to base of bacterium; no penetration of cuticle occurs, demonstrating that the bacterium is not invasive. ×14,400. b. Higher magnification of *L. mucor* at point of attachment to gill; note distribution of electron-dense mucoid substance probably secreted by bacterium (arrow); shrimp cuticle is intact. ×28,500.

heavy infestations. Massive amounts of this substance overlying gill cuticle could block normal gas diffusion across gill surfaces.

Fungi

Our knowledge of fungal diseases of penaeid shrimps is in a state similar to that of our knowledge of bacterial diseases. The only clear-cut case of a fungal pathogen affecting large numbers of penaeid shrimps in the United States was reported by Cook (1971) and by Lightner and Fontaine (1973). These authors described infections of white shrimp larvae by a phycomycete, *Lagenidium* sp., an estuarine fungus. The fungus infects the second protozoal stage of white shrimp, and disappears by the time the first mysis stage is reached. Figure 10a shows a heavily infected protozoea. According to Lightner and Fontaine (1973), the major pathogenic effect is almost complete tissue destruction and replacement by invasive fungal mycelia (Figure 10a). Hyphae of the fungus are branched, septate, with thin walls, and range from 8.0 to 11 μm in diameter. Under bright field microscopy the hyphae were yellow-green and contained round oil droplets (Lightner and Fontaine 1973).

The lifecycle of *Lagenidium* sp. in penaeid shrimps involves a sporulation phase. This begins when a hyphal extension penetrates the cuticle of the shrimp from within (Figure 10b). Following formation of a vesicle in the apical region of the extension, planonts (flagellated zoospores) are formed in the vesicle. The whole extension becomes a discharge tube, releasing motile planonts (8.7-12 μm) which presumably infect other shrimp.

Lightner and Fontaine (1973) were able to infect larval brown shrimp (protozoea I) with planonts and hyphae on a large scale (2,000 larvae). Resulting mortality in the experimentally infected shrimp was 20%. Approximately 60 h were required for infections to become patent. The role of this fungus in natural shrimp populations is not known. In aquaculture the fungus could be a definite limiting factor in the survival of shrimp larvae. Brown shrimp larvae in commercial hatcheries have been found to die of this disease (Cook 1971).

The only other report of natural fungal infection in penaeid shrimps in the United States was that of Johnson.[6] He briefly described a *Fusarium* species which infected the gills and antennal scales of *Penaeus duorarum*. Less than 5% of shrimp studied were infected and the spread of the fungal mycelium in the body of affected shrimp was slow.

Solangi and Lightner (1976) have described the cellular inflammatory response of *Penaeus aztecus* and *P. setiferus* to experimental infections of *Fusarium* sp. According to these authors, both species of shrimps showed "complete resistance to infection by the fungal spores when normal or wounded shrimp were held in seawater containing the spores or when spores were injected directly into the shrimp in low concentrations." Cellular "melanization" and encapsulation of the micro- and macroconidia occurred in gill tissues of penaeid shrimp. Only massive doses of 3.2×10^6 spores injected into brown shrimp resulted in death of shrimp; this lethality was a result of mechanical blockage, by spores, of the blood sinuses of the shrimp's gills. Gills of affected shrimp sometimes were blackened.

Protozoa

More than any other phylum, the Protozoa as pathogens and parasites have had significant, known effects on shellfish populations. Representatives of every class of Protozoa are found as symbionts, commensals, parasites, or pathogens in penaeid shrimps. Certain groups such as the Microsporida have a long history as pathogens of not only penaeid shrimps, but arthropods in general. Only recently, however, species of such groups as the Ciliophora and the Sarcomastigophora have been indicted as serious pathogens of decapod Crustacea, including penaeid shrimps.

Herein Protozoa associated with shrimps will be classified according to the scheme of the Honigberg Committee in "A Revised Classification of the Phylum Protozoa" (Honigberg et al. 1964). Sprague and Couch (1971) published an annotated list of protozoan parasites, hyperparasites, and commensals of decapod Crustacea. This list includes most of the known species of Protozoa associated with penaeid shrimps. However, since its publication, several undescribed species have been found and will be included herein.

Subphylum Sporozoa Leuckart 1879

This subphylum includes the gregarines and

[6]Johnson, S. K. 1974. *Fusarium* sp. in laboratory-held pink shrimp. Texas A&M Univ., Fish Disease Diagnostic Lab. Note FDDL-51, 1 p.

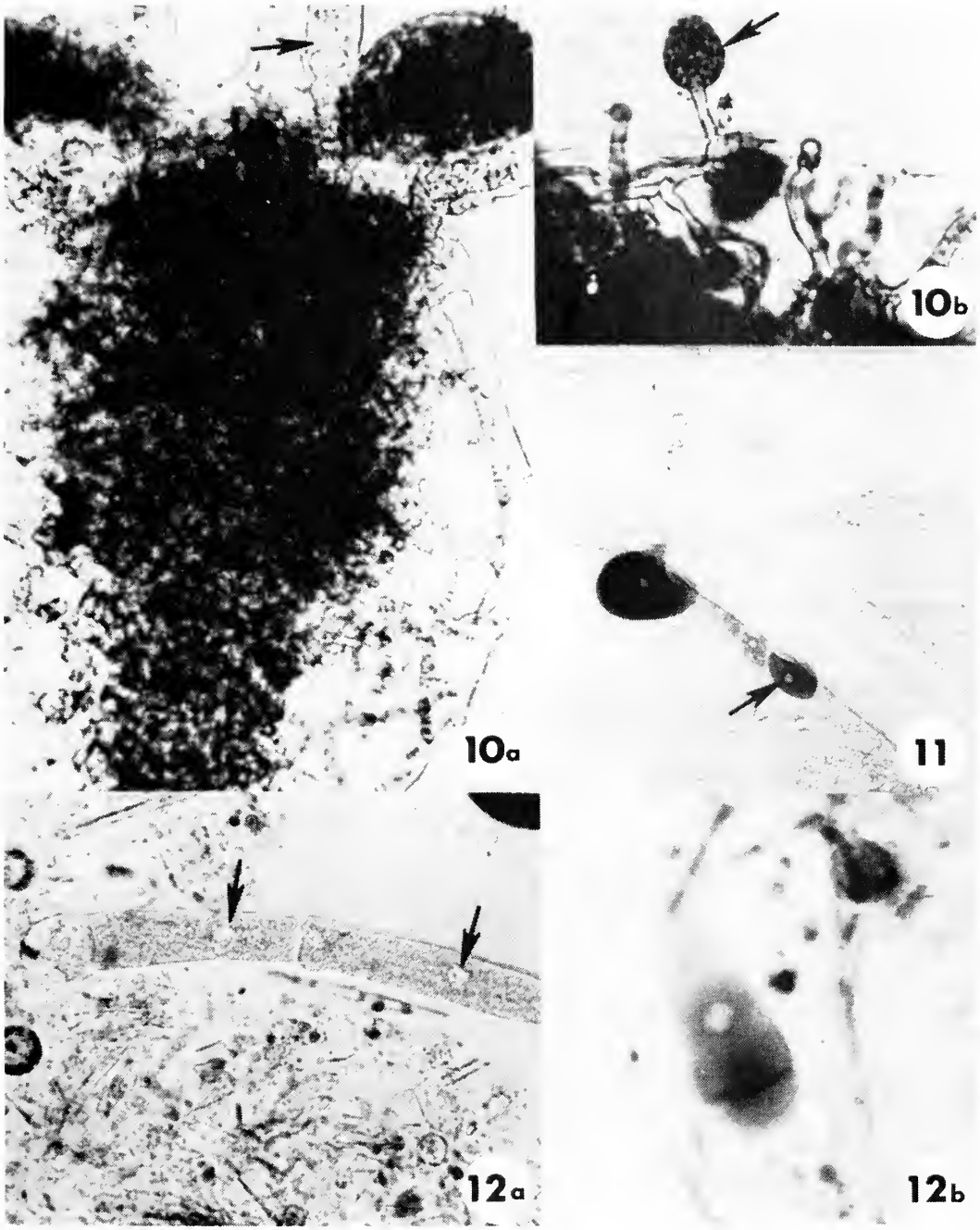


FIGURE 10.—a. *Lagenidium* sp. hyphae throughout body of larval penaeid shrimp; note fungus has invaded antenna near eye (arrow). ×300. b. *Lagenidium* sp. sporulation stage; note sporulation vesicle, filled with planonts, on end of hyphal extension (arrow) that has penetrated larval shrimp cuticle. ×400.

FIGURE 11.—*Cephalolobus penaeus*, gregarine trophonts attached to lappet of gastric mill from pink shrimp; note nucleus (arrow) and mode of attachment. ×150.

FIGURE 12.—a. *Nematopsis* sp. trophonts in syzygy, from midgut of pink shrimp; arrows point to nuclei of trophonts. ×900. b. Single, young trophont of *Nematopsis* sp. from gut of pink shrimp; note protomerite and septum separating it from rest of primite. ×1,000.

coccidians. The only group considered here are the gregarines of penaeids. Gregarines, in general, are not highly pathogenic to their hosts. Therefore, information presented here is brief and the reader is referred to referenced works for details.

Class Telosporea Schaudinn 1900
Subclass Gregarinia Defour 1828
Order Eugregarinida Leger 1900
Family Cephaloidophoridae Kamm 1922
Cephalolobus penaeus Kruse 1959

This species attaches to chitinous walls and terminal lappets of the stomach filter in *Penaeus aztecus* and *P. duorarum* (Figure 11). Usually the attached stage is a trophozoite consisting of a primite with an anterior protomerite division that is modified into a holdfast organ. The single nucleus is in the center of the primite (Figure 11). The primite, including the protomerite, is from 100 to 200 μm long. Often attached to the primite posteriorly will be 1 or 2 satellites (young trophozoites). Spores, sporozites, and cysts have not been observed. Overstreet (1973) reported this species in *P. setiferus* from Louisiana, extending its range from Florida as previously reported. I have observed this species in pink shrimp occasionally from Pensacola, Fla. This gregarine apparently has no harmful effect on the shrimp host. It may be possible that large numbers attached to the filter apparatus of the host could interfere with filtration of particles bound for the hepatopancreatic ducts or passing through the stomach.

Cephalolobus sp. Feigenbaum 1975

This form, reported from *Penaeus brasiliensis,* utilizes the stomach filter as position of attachment within host. Trophozoites consist of protomerite and deutomerite separated by a septum. As in *C. penaeus,* the anterior end is modified into a holdfast organelle. This species has been reported in shrimp only from Biscayne Bay, Fla., and differs from *C. penaeus* in that the trophozoites occur solitarily and are smaller (43-100 μm long) than those of *C. penaeus.*

Family Porosporidae Labbe 1899
Nematopsis penaeus Sprague 1954

This species has been reported from brown, pink, and white shrimps. It is found in the intestinal tract. Figure 12a, b show specimens of *Nematopsis* from the gut of a pink shrimp. These may be *N. penaeus* or *N. duorari* (see below). Works by Sprague (1954, see footnote 3), Sprague and Orr (1955), Kruse (1959, 1966), Hutton et al. (1959), and Hutton (1964) give information on hosts including the intermediate molluscan hosts, for *N. penaeus.* Overstreet (1973) discussed the prevalence and morphology of *N. penaeus* and pointed out that syzygy is multiple with up to seven trophozoites in line attached to one another reaching a length of over 0.5 mm. Characters for distinguishing *N. penaeus* and *N. duorari* are size of gymnospore and number of different molluscan intermediate hosts. No pathogenesis is associated with this form.

Nematopsis duorari Kruse 1966

This gregarine is restricted to the gut of pink shrimp. Kruse (1966) attempted to transmit it to brown and white shrimp, but could not. Figure 12a shows an immature association of a trophozoite of *Nematopsis* sp. in syzygy. Since two of the known *Nematopsis* species of penaeids appear identical in their trophozoite stages, no attempt will be made here to identify the specimens in Figure 12 to species.

Nematopsis sp. Kruse 1966

Kruse (1966) described, but did not name, this species from concurrent infections with *N. duorari* in pink shrimp in Florida. This form had smaller gymnospores than did *N. duorari.*

Nematopsis brasiliensis Feigenbaum 1975

This is a recently described species of *Nematopsis* in a penaeid shrimp. Found in the intestine of *Penaeus brasiliensis,* this species consists of both individual trophozoites and syzygies of biassociations (two trophs). It has been described from Biscayne Bay only. Hutton (1964) reported *N. penaeus* from *P. brasiliensis.* However, Feigenbaum (1973) believes that the species Hutton reported as *N. penaeus* may have been *N. brasiliensis.*

Subphylum Cnidospora Doflein 1901
Class Microsporea Corliss and Levine 1963
Order Microsporida Balbiani 1882

Microsporida are highly pathogenic to shrimps

and are probably one of the most destructive groups of pathogens to penaeid hosts. Rarely, however, have epizootics been recorded in which large numbers of penaeids have been lost to microsporidan infections. Infection prevalences in samples of penaeids from nature and aquaculture rarely exceed 10%. Due to their highly pathogenic nature, however, emphasis is placed on the importance of these protozoa to the health of penaeids. Table 3 summarizes salient characteristics of species of Microsporida discussed below. Kelley (1975) described histopathological changes in pink shrimp infected with Microsporida.

Family Nosematidae Labbe 1899
Nosema nelsoni Sprague 1950

This species is widespread, found in *Penaeus duorarum*, *P. aztecus*, and *P. setiferus* along the South Atlantic and Gulf coasts of the United States. The spores are found singly (one spore per sporont) in masses in infected tail muscle (Figure 13). As with certain other Microsporida, *N. nelsoni* causes white discoloration of muscle or viscera giving infected shrimp a cotton or paper-white color (Figure 14). Fishermen call these shrimp "milk" or "cotton" shrimp. The spores of *N. nelsoni* are 1.7 to 2.5 μm long by 1.0 to 1.5 μm wide. Their polar filaments are 20 to 25 μm long. This parasite kills shrimp, and massive single infections with whole musculatures affected are found (Figure 15a, b).

Thelohania penaei Sprague 1950

Members of this genus have eight spores in each sporocyst (Figure 16a, b). Found originally in the reproductive organs of *Penaeus setiferus* in Louisiana, this species has been reported from Mississippi, Texas, and Georgia. It infects muscle, gonads, and is seen grossly along the middorsal region of the abdomen and in appendages as white spots or clusters (Figures 17, 18). Spores are pyriform and occur in two size classes (2.0 to 5.0 μm long and 5.0 to 8.2 μm long). The polar filament is unusual in that it has a thin distal half and a thick proximal half. Sprague (1970) reported that this is probably the microsporidan that Viosca (1943) observed in the reproductive organs of about 90% of *P. setiferus* along the Louisiana coast in 1919. This epizootic is one of the few reported in which penaeids have suffered en masse from a microsporidan. Viosca reported that the reproductive organs of the white shrimp were destroyed by the parasite.

Iversen and Kelly (1976) reported the first successful experimental transmission of a microsporidan (*T. penaei*) in shrimp. Postlarval pink shrimp fed *T. penaei* spores, conditioned by passing through seatrout, showed tissue infections.

Overstreet (1973) reported that pink and brown shrimps reared together in ponds showed only gill infections of *T. penaei*.

Thelohania duorara Iversen and Manning 1959

This organism was first reported from *Penaeus duorarum* from the Dry Tortugas. A similar species has been reported from brown and white shrimps (Kruse 1959) in Florida. Overstreet (1973) reported that this species occurs in pink shrimp in the Mississippi Sound, and Iversen and Van Meter (1964) found it in *P. brasiliensis* in south Florida. Spores are 5.4 μm × 3.6 μm. This microsporidan parasitizes the muscle of shrimp causing white or "cotton" shrimp. The extent of impact it has on wild populations of penaeids is not understood. According to Sprague and Couch

TABLE 3.—Characteristics of Microsporida in penaeid shrimps.

Species	Spores/sporont (averages)	Spore size (μm)	Tissues	Host(s)	Locales
Nosema nelsoni Sprague 1950	1	2.0 × 1.2	Muscle	*P. aztecus* *P. duorarum* *P. setiferus*	Gulf coast Georgia coast
Theolohania penaei Sprague 1950	8	2.0 × 5.0 5.0 × 8.2	Gonads Muscle	*P. setiferus*	Gulf coast Georgia coast
Theolohania duoara Iversen and Manning 1959	8	5.4 × 3.6	Muscle	*P. aztecus* *P. duorarum* *P. setiferus*	Gulf coast Florida east coast
Pleistophora sp. Baxter et al. 1970 Constransitch 1970 Kruse (in Sprague 1970) Iversen and Kelly 1976	16 to 40+	2.6 × 2.1	Muscle Heart Gills Hepatopancreas	*P. aztecus* *P. setiferus* *P. duorarum*	Gulf coast Southeast Florida

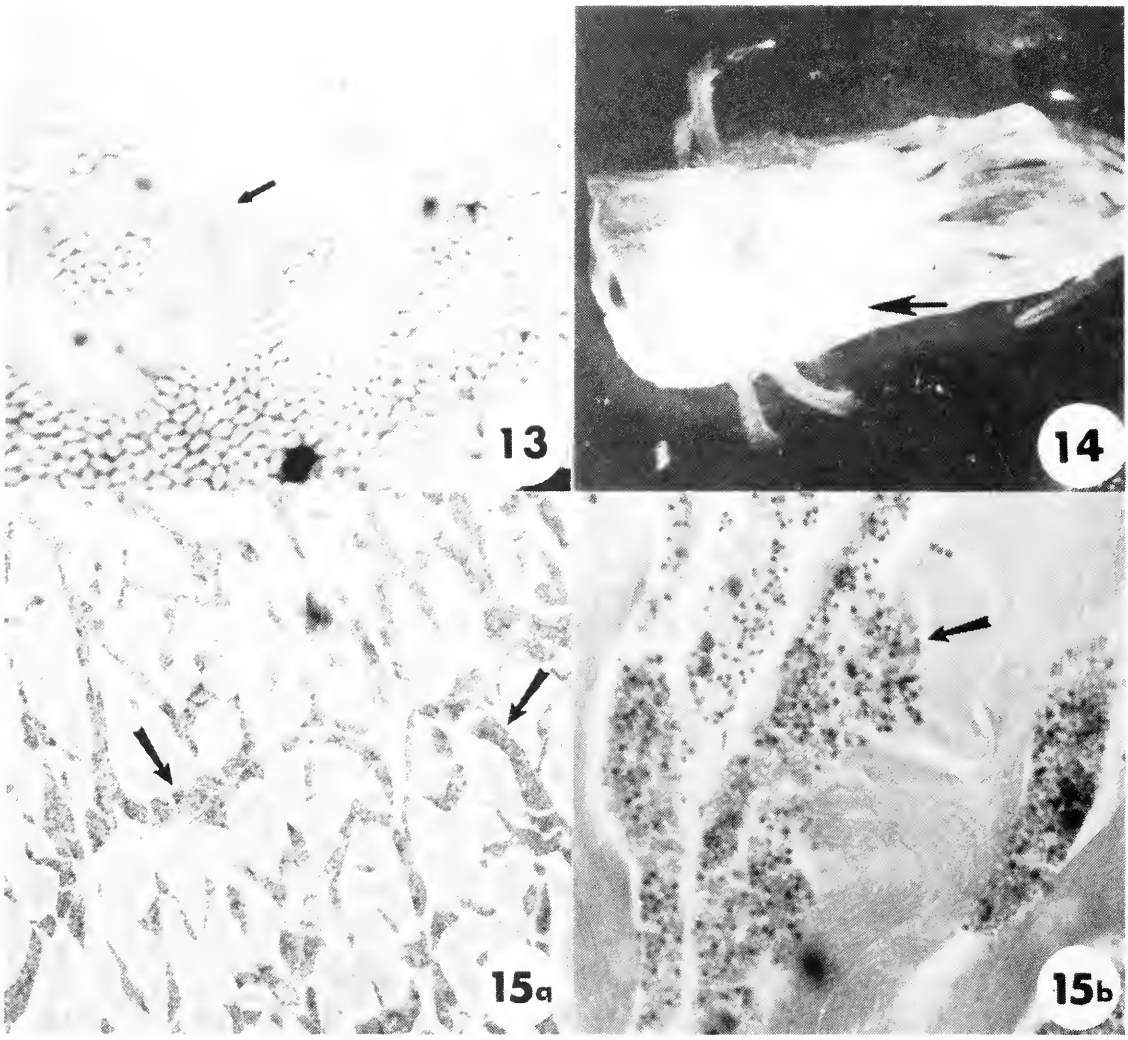


FIGURE 13.—*Nosema nelsoni* spores in fresh squash preparation of muscle from pink shrimp. ×1,500.

FIGURE 14.—White or cotton appearance of organs and muscle of penaeid shrimp infected with *Nosema nelsoni*, and *Thelohania penaei;* note opaque white appearance of gonads (arrow).

FIGURE 15.—a. Abdominal musculature heavily infected with *Nosema nelsoni;* note long spore masses between and around every muscle bundle (arrows). ×100. b. Higher magnification of spore masses of *Nosema* in histological section of muscle. ×500.

(1971), *Thelohania hunterae* (a nomen nudum) was probably *T. duorara.*

Roth and Iversen (1971) reported attempts to transmit *T. duorara* to uninfected pink shrimp in the laboratory. They were unable to do this with their method of feeding heavily infected tissue. These authors did supply some clues as to the possible modes of transmission in nature. They observed that spores of *T. duorara* found between old cuticle and new cuticle at time of molting could infect shrimp that feed on cast cuticles. Therefore, transmission could depend only on molting of the exoskeleton and not on death of the infected host.

Iversen and Kelly (1976) have reported concurrent infections of *T. duorara* and *T. penaei* in single specimens of pink shrimp.

Pleistophora (= Plistophora) penaei
Constransitch 1970

Members of this genus are characterized by sporocysts that contain 16 or more spores. Kruse

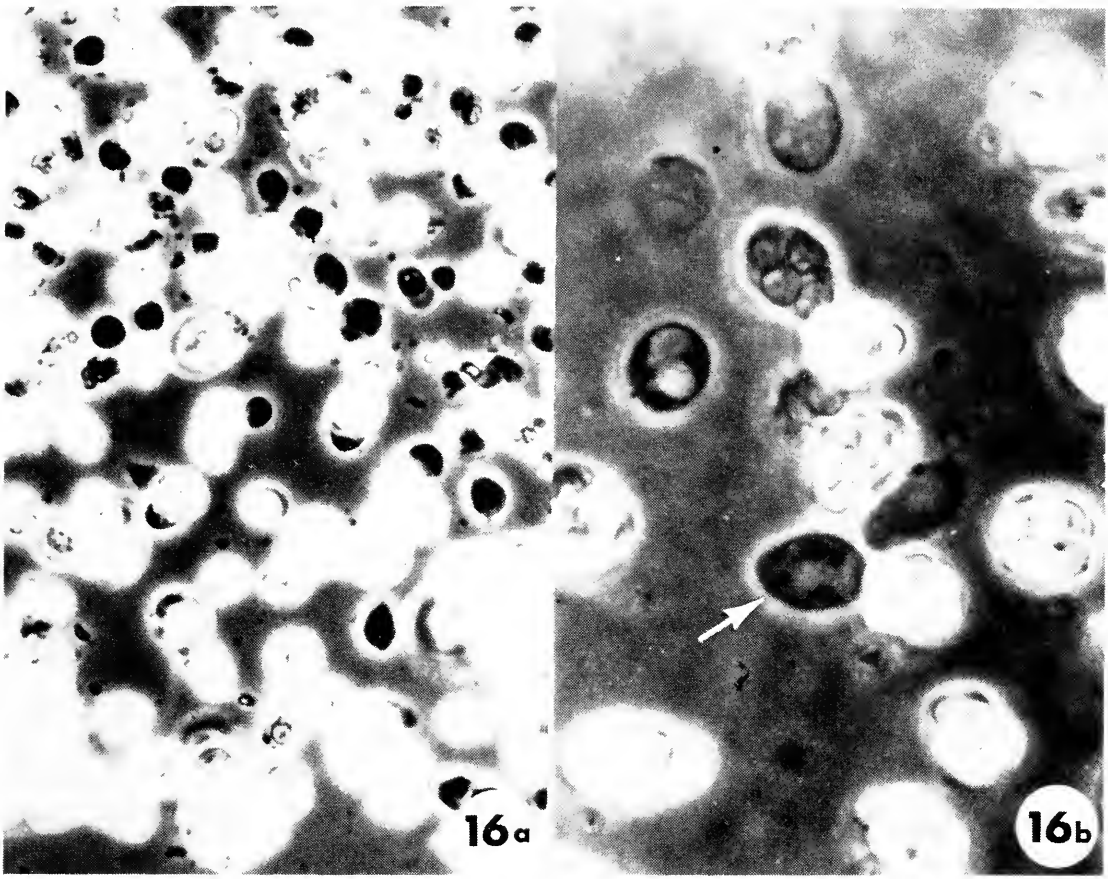


FIGURE 16.—a. *Thelohania penaei* sporocysts and spores; note approximate size of sporocysts with eight spores each; dark bodies are trophozoites or early sporonts. ×1,000. b. *Thelohania penaei* sporocysts, higher magnification; note that each sporocyst contains about eight spores; dark body (arrow) is probably an early sporont or trophozoite of this species. ×1,500.

(in Sprague 1970) first reported the genus *Pleistophora* in penaeid shrimps (*Penaeus aztecus* and *P. setiferus* from Louisiana). Constransitch (1970) named the species from Louisiana *Pleistophora penaei*. Tissues infected were tail muscle, cardiac muscle, hepatopancreas, and intestinal and stomach walls. Baxter et al. (1970) then reported a similar species from the same hosts from Texas. The Texas *Pleistophora* consisted of sporocysts that contained 40 or more spores.

Recently, Iversen and Kelly (1976) reported a *Pleistophora* sp. from the pink shrimp for the first time.

Therapeutic Measures for Microsporidosis

Very little work has been done on attempting to control or treat microsporidan infection in reared shrimp. Quick removal of "cotton" or obviously infected shrimp from tanks or ponds should aid in preventing spread of infections. Overstreet (1975) has reported some success in treating blue crabs with the drug Buquinolate to prevent infection by *Nosema michaelis*, a common microsporidan in blue crabs. He fed the drug to crabs in food contaminated with *N. michaelis* spores. He also fed the drug in food without spores 48 h preceding or following spore feeding. Control crabs were fed spores, but no drug. Drug and spore-fed blue crabs had significantly fewer infections develop than did crabs fed spores only. Whether Buquinolate or other drugs would be helpful in preventing microsporidosis in shrimp remains to be determined. Even if a drug is useful in therapy of a disease in

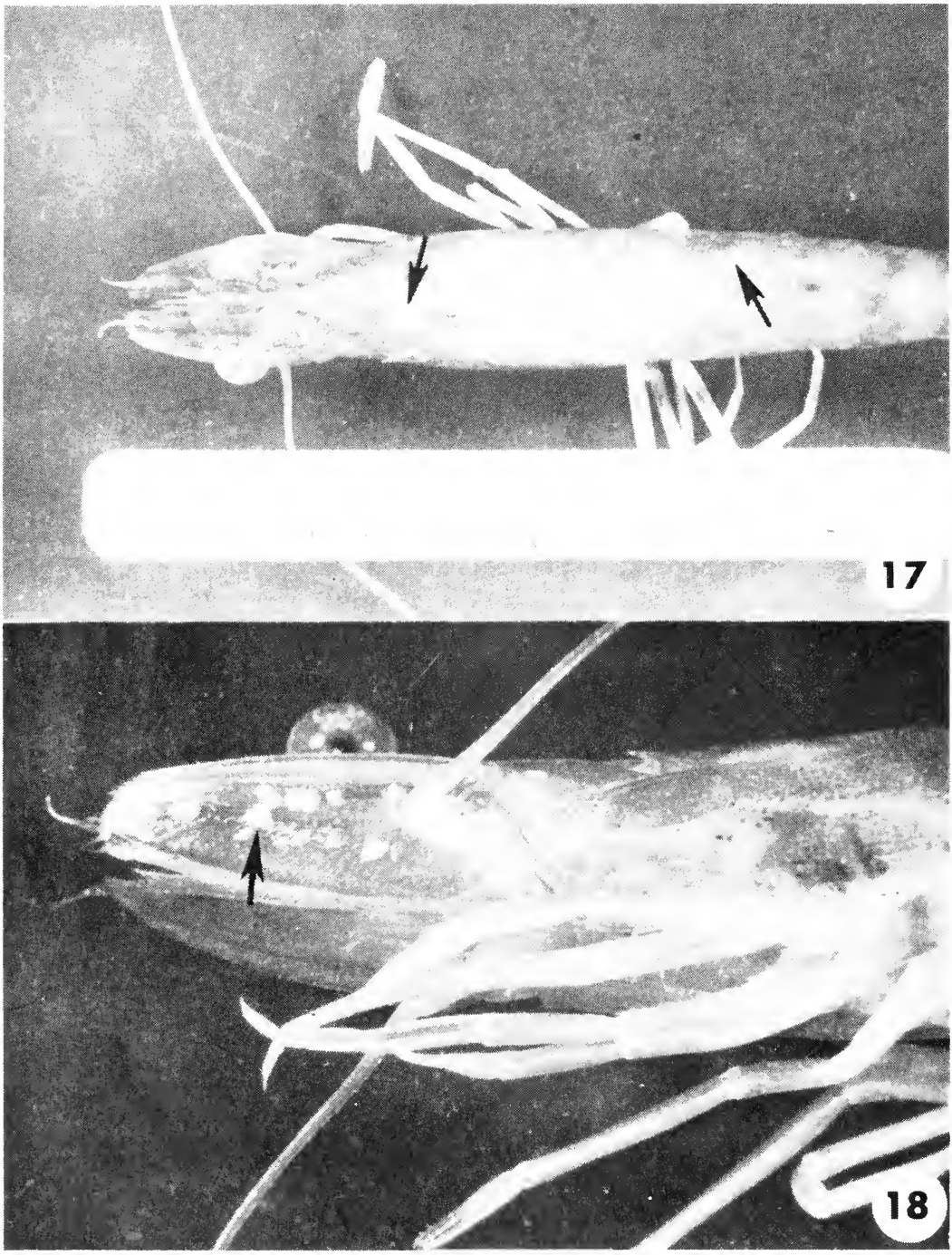


FIGURE 17.—Whole shrimp showing dorsal areas of white that indicate microsporidan infection (arrows), in this case, *Thelohania penaei*.

FIGURE 18.—White clusters of *Thelohania penaei* sporocysts in antennal scale of pink shrimp (arrow).

cultured shrimp, the problem remains for depuration of the drug from tissues prior to human consumption of the shrimp.

Subphylum Ciliophora Doflein 1901[7]

Ciliate Protozoa are very common associates of penaeids. As commensals, parasites, and pathogens, they are among the Protozoa more often encountered in or attached to penaeid shrimp. Their role, however, in the health of penaeids has not been conclusively demonstrated in most ciliate-penaeid relationships. Sprague and Couch (1971) presented a list of ciliates (and other Protozoa) found on or in decapod Crustacea. Since that report, several new finds of ciliates in penaeid shrimps have been made.

Ciliates discussed herein will be presented in order of their frequency of occurrence in penaeid shrimps (common to rare).

Class Ciliatea Perty 1852
Order Peritrichida Stein 1859
Suborder Sessilina Kahl 1933
Family Vorticellidae Ehrenberg 1838
Genus *Zoothamnium* Bory 1826
Zoothamnium sp.

An heretofore undescribed species of peritrichous ciliate, of the genus *Zoothamnium,* has been reported on penaeid shrimps along the coast of the southeastern United States Villella et al. (1970), Overstreet (1973), Johnson (1974), D. V. Lightner (pers. commun.), and I have found the colonial, stalked peritrich to be very common and frequently abundant on the gills of three commercially valuable species of penaeid shrimps.

Stalked peritrichs of the genera *Vorticella, Zoothamnium, Epistylis, Carchesium, Rhabdostyla,* and *Opisthostyla* are found attached to many hard substrates in the marine environment. The vast majority of species in these genera have not been studied, described, and named. Therefore, with this background in mind, I propose to describe, but not to formally name, the common species of *Zoothamnium* on gills and body of adults, juveniles, protozoea, and mysis of *Penaeus aztecus, P. setiferus,* and *P. duorarum.* This species will be named after further study and comparison with other species in the genus *Zoothamnium.*

[7]Most ciliatologists and many protozoologists now consider the Ciliophora as a phylum, but herein the Honigberg et al. (1964) classification scheme is followed.

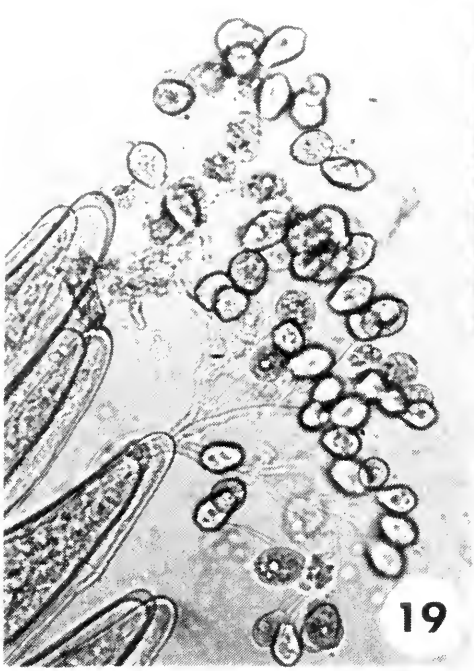
Description. Vorticellid; colonial, rarely observed as individuals; 3 to 30 trophonts per colony (Figure 19); usually attached to the tips of gill filaments of hosts listed above; trophonts variable in form but usually resemble an inverted bell (45.2 μm $\times$ 33.9 μm—means of measurement of 30 individuals); with long, branching stalks (8.1 μm in diameter); phase contrast and silver-stained (protargol) specimens show that myonemes in stalks are continuous and joined, and the diameter of myonemes averages 2.0 μm (Figure 20a, b). Silver-stained specimens (Figure 20c) also reveal adoral kineties consisting of a three-component polykinety (peniculus) and a haplokinety; telotroch (Figure 21) produced by division of stalked trophont, slightly smaller than stalked trophont; lifecycle direct, that is, the telotroch may swim free of mother colony and attach to surface of gill or body of shrimp, secrete a stalk, and become progenitor of a colony; sexual reproductive cycle not observed for this species, but probably is a conjugative process as in other peritrichs having microconjugants and macroconjugants. I have observed only pairs and small colonies (3, 4 trophonts) of *Zoothamnium* sp. attached to body surfaces of larval (mysis and protozoea) brown shrimp.

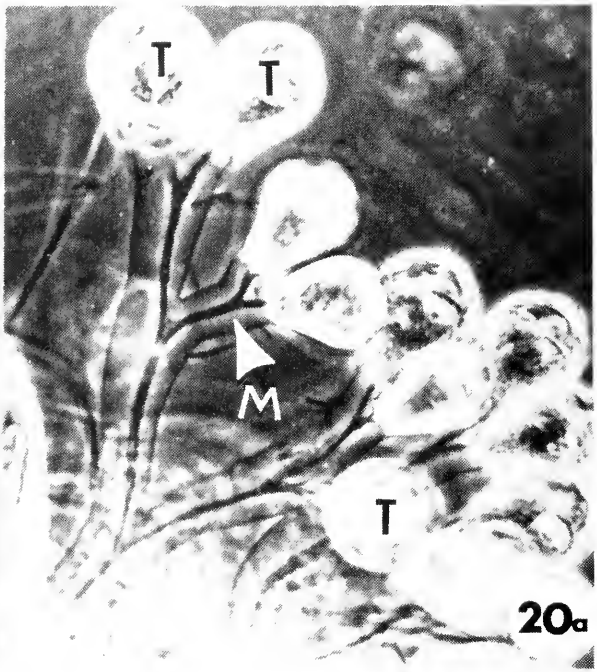
Overstreet (1973) gave extensive data on the frequency of occurrence of *Zoothamnium* on penaeid shrimps. He found that an increase in density of hosts held in captivity was paralleled by an increase in density of peritrichs on gills. This is similar to what Couch (1971) observed for blue crabs infested with *Lagenophrys callinectes* Couch (1967), a gill peritrich. Overstreet (1973) also was able to correlate, positively in one test, increased mortality in shrimp with heavy infestations by *Zoothamnium* on their gills. However, he was not convinced that the correlation was valid. More extensive work on this relationship is needed.

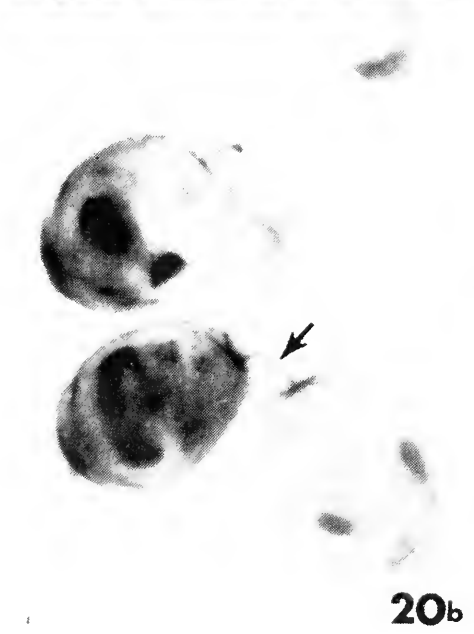
The mechanism of injury to penaeids infested with peritrichous ciliates would probably be oxygen starvation or asphyxiation due to blockage of gas exchange at the gill surface. The attachment stalk of *Zoothamnium* sp. does not penetrate the cuticle of shrimp.

Family Lagenophryidae Kahl 1935
Genus *Lagenophrys* Stein 1852
Lagenophry lunatus Imamura 1940

A species of *Lagenophrys* was reported from the cuticle of *Penaeus setiferus* by Johnson (1974) and







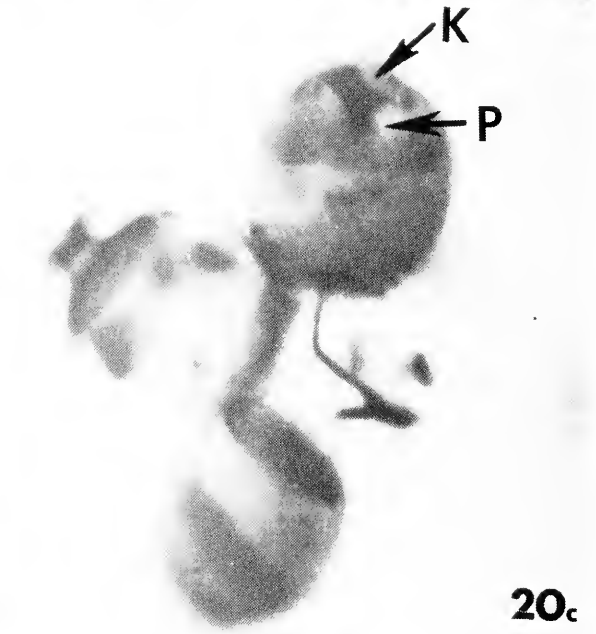


FIGURE 19.—Colonies of *Zoothamnium* sp. attached to end of gill filaments in pink shrimp; this represents a light infestation; heavy infections would cover all filaments. ×200.

FIGURE 20.—a. Phase contrast photomicrograph of *Zoothamnium* colony showing stalk myonemes (M) that are continuous with one another, the major distinguishing characteristic of the genus; note inverted bell shape of contracted trophonts (T) and thickness of stalk sheath that surround myonemes (arrow). ×500. b. Protargol treated specimens of *Zoothamnium;* note beltlike, horseshoe-shaped macronucleus and Protargol-positive myonemes of stalk (arrow). ×1,200. c. Protargol-treated *Zoothamnium;* trophont (in focus) shows peniculus (P) in infundibulum (arrow); note pattern of kineties (K) making up peniculus. ×1,200.

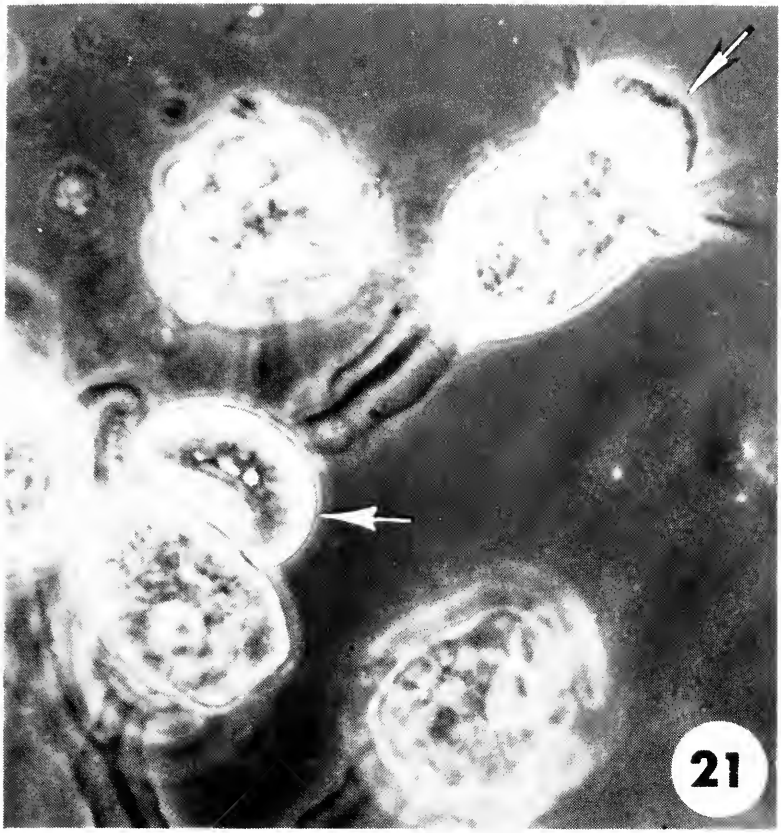


FIGURE 21.—Telotroch stage (arrow) of *Zoothamnium* produced from division of trophont (phase contrast); this is the dispersal stage for the species; the telotroch is motile and possesses a ventral girdle of cilia. Note the trophont at upper right with extended adoral ciliature (arrow). ×500.

by Lightner (1975) in Texas. From a photomicrograph kindly loaned to me by Johnson, I have tentatively identified this loricate peritrich as *Lagenophrys lunatus*. This species is commonly found on the cuticle of paleomonid shrimps along the east coast and gulf coast of the United States, but Johnson's report, if accurate, is the first for a penaeid. It is possible that the species of shrimp examined by Johnson was a grass shrimp, *Paleomonetes* sp. Species of *Lagenophrys* are usually host specific, and though I have examined many penaeid shrimps, I have not observed *Lagenophrys* sp. on any. Couch (1971) gave a detailed discussion of the possible effects of *Lagenophrys* spp. on the cuticles and gills of decapod Crustacea with particular reference to *L. callinectes* on the gills of the blue crab, *Callinectes sapidus*. Erosion of cuticle surface and interference with gas exchange at the gill surface in heavy infestations are possible effects of *Lagenophrys*.

Order Apostomatida Chatton and Lwoff 1928
Family Foettingeriidae Chatton 1911
Genus Uncertain

The encysted form (phoront) of an undescribed apostome ciliate has been observed on the gills of *Penaeus duorarum* (Figures 22, 23) in northwest Florida. The cysts are decumbent, ellipsoidal bodies that are 41 μm wide by 60 μm long (range: 20.7-41.4 μm by 27.6-60.0 μm). The cyst wall is from 1 to 3 μm thick and is semitransparent.

Heavy infestations of this ciliate occur on gills of pink shrimp during periods of warm to moderately cool weather when shrimp are held under crowded conditions (Figure 22). The cysts are most often attached to the gills at the point of branching of the distal processes variously termed lamellae, filaments, or tertiary structures (Figure 22). The lifecycle of this ciliate has not been elucidated, and it cannot be assigned to a genus until silver-

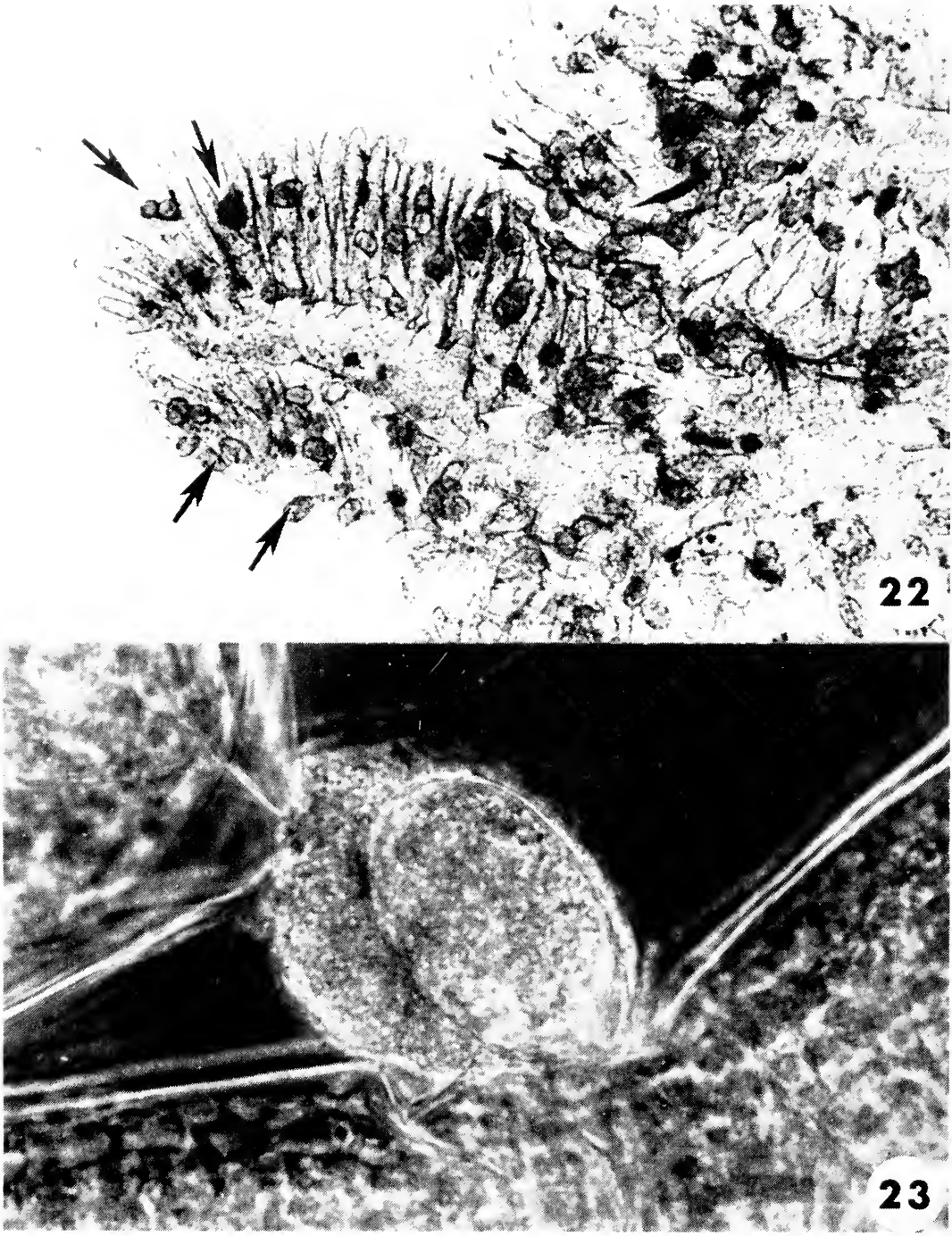


FIGURE 22.—Cysts (phoront) of apostome ciliate (arrows) on gills of pink shrimp; this is a moderately heavy infestation. ×150.
FIGURE 23.—Single cyst (phoront) of unidentified apostome attached near base of gill filament; note ellipsoid form. ×1,000.

staining studies and lifecycle studies are more complete.

Reports by Chatton (1911), Chatton and Lwoff (1935), Debaisieux (1960), and Bradbury (1966, 1973) have demonstrated the common occurrence of apostomes on Crustacea that occupy ecological niches near that of the pink shrimp. The present species has not been found associated with mortality in shrimp, although severe infestations may cover much gill surface and blackened areas of infested gills are found. Species of two known apostome genera, *Synophyra* and *Terebrospira*, cause considerable damage by penetrating the cuticle of their crustacean hosts (Chatton and Lwoff 1926; Bradbury 1974).

R. M. Overstreet (pers. commun.) has found similar cysts on gills of brown and white shrimp, and Feigenbaum (1973) reported cysts similar to those described above on gills of *Penaeus brasiliensis* from Biscayne Bay. The cysts of apostomes could be confused with the loricae of species of *Lagenophrys*, Care should be taken to distinguish them. Loricae of *Lagenophrys* spp. have apertures surrounded by liplike structures (Couch 1973).

Order Scuticociliatida Small 1967
Genus *Parauronema* Thompson 1967
Parauronema sp.

An undescribed species of ciliate was observed in the hemocoel of protozoeal, mysid, and juvenile stages of living, moribund, and dead brown shrimp from a mass mortality which occurred at a commercial shrimp hatchery[8] during April 1974. In a sample of 139 larvae examined, 28.8% were infected by the ciliate (Tables 1, 2). The ciliate is ovoid to pyriform in shape, ranging in length from 23.6 to 31.6 μm, and in width from 9.2 to 12.2 μm (Figures 24, 25). It has a uniform body ciliature originating from longitudinal kineties (Figure 25) as revealed by Protargol silver staining.

The ciliate was observed swimming about in hemolymph of infected shrimp larvae and juveniles. Often the affected shrimp were still alive and active, but several that were dead or quite moribund contained ciliates. John Corliss (University of Maryland) tentatively identified the ciliate as a species of *Parauronema*. More studies are required in order to name this ciliate.

[8]Mortality was that reported on preceding pages (under virus section). Several microorganisms were associated with this mortality.

Apparently the ciliate causes mechanical injury in infected shrimp by replacing and dislodging tissues. I have been unable to determine from limited observations whether or not the ciliate is histophagous. In some shrimp the ciliates were numerous enough to fill the entire hemocoel and abdomen. The fact that living shrimp larvae were infected by the ciliates strongly suggests that the ciliate probably contributes to pathogenesis and mortality and that it is an opportunistic invader following initial breaks in the host's defense mechanisms due, possibly, to the presence of other pathogenic microorganisms (the *Baculovirus* and a flagellate to be described next). Tables 1 and 2 show the relationship of prevalence of ciliate with virus and flagellate in a sample of young brown shrimp from a stock suffering mortality.

Subclass Suctoria Haeckel 1866
Order Suctorida Claparede and Lachmann 1858
Family Ephelotidae Kent 1881
Genus *Ephelota* Wright 1858
Ephelota sp.

Protozoeal and mysid stages of brown shrimp were found infested on a single occasion with an undescribed species of *Ephelota*. The larval shrimp were examined in March. Each larva had from one to seven individual *Ephelota* sp. attached to their cuticles usually on the pleural plates or on the telson. The suctorian possesses a characteristically striated attachment stalk and a trophont with both suctorial and prehensile tentacles. These Protozoa were not abundant enough to cause embarrassment to the larval shrimp.

Subphylum Sarcomastigophora
Honigberg and Balamuth 1963
Class Zoomastigophorea Calkins 1909
Order Kinetoplastida Honigberg 1963
Suborder Trypanosomatina Kent 1880
Family Trypanosomatidae Doflein 1901
Genus *Leptomonas* Kent 1880
Leptomonas sp.

An undescribed species of flagellate was associated with the mass mortality of brown shrimp larvae (see *Baculovirus* and *Parauronema* sections) (Figure 26). This form is tentatively assigned to the genus *Leptomonas* based on subsequently described characteristics. The flagellate was studied alive (bright field and phase contrast), fixed, and stained with Harris' hematoxylin and

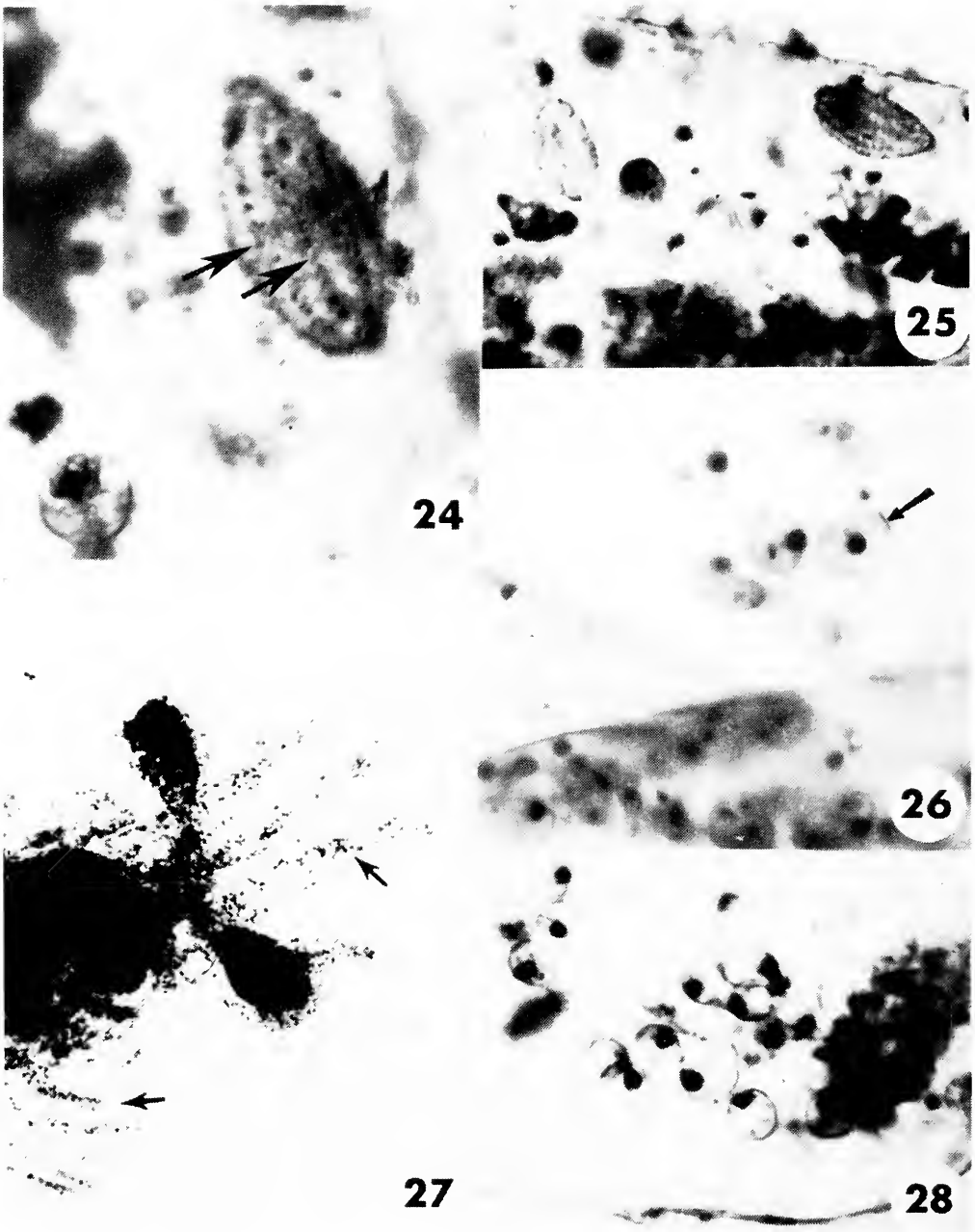


FIGURE 24.—Trophont of ciliate, *Parauronema* sp., in hemocoel of brown shrimp larva; note body form and longitudinal rows of kinetosomes on body surface (arrows) (Protargol). ×1,300.

FIGURE 25.—Two trophs of *Parauronema* sp. in body of brown shrimp larva; in living shrimp these ciliates swim about in hemolymph. ×900.

FIGURE 26.—Cells of *Leptomonas* sp., a flagellate, from hemolymph space in appendage of larval brown shrimp; note flagellar base as revealed by Protargol stain (arrow); compact nucleus is also visible. ×1,000.

FIGURE 27.—Head and anterior appendages of larval brown shrimp heavily infected with *Leptomonas* sp.; note antennae, antennules, and thoracic legs filled with flagellate (arrows).

FIGURE 28.—Cystlike stages of *Leptomonas* in hemocoel of larval brown shrimp (Protargol). ×1,000.

Protargol silver protein. It is the first flagellate reported to be associated with shrimp mortalities. The flagellate occurred in the hemocoel, abdomen, and all appendages of protozoel and mysid stages of brown shrimp during April 1974 (Figure 27). The flagellate was found in 64% of larvae examined from the mortality; living, moribund, and dead larvae were infected (Tables 1, 2).

The flagellates were variable in form ranging from 7.8 to 11.7 μm with an average diameter of 9.4 μm. A compact nucleus (2 or 3 μm) containing a large endosome was situated medianly. The cytoplasm ranged from clear to opaque and often contained various inclusions. In life, the flagellate was slightly pyriform with a terminal, single flagellum (Figure 29). Specimens stained with protargol clearly demonstrated a flagellar base, parabasal body, or blepharoplast (karyomastigont) (Figures 26, 29). A possible cyst stage (7-9 μm) was observed in advanced or heavy infections in the hemocoel (Figures 28, 29f). Dividing stages, observed occasionally, contained nuclei undergoing division without loss of nuclear membranes (Figures 29e).

The role, if any, that *Leptomonas* sp. plays in the mortality of shrimp larvae is unknown. Other than mechanical damage, there appears to be little evidence of a pathogenic mechanism for the flagellate. It is possible that the flagellate is a secondary invader of a weakened host, possibly from encysted forms which may exist in the hindgut of the host.

Platyhelminthes

Flatworms have been described as parasites of all commercial species of penaeid shrimps in the United States. These include digenetic trematodes

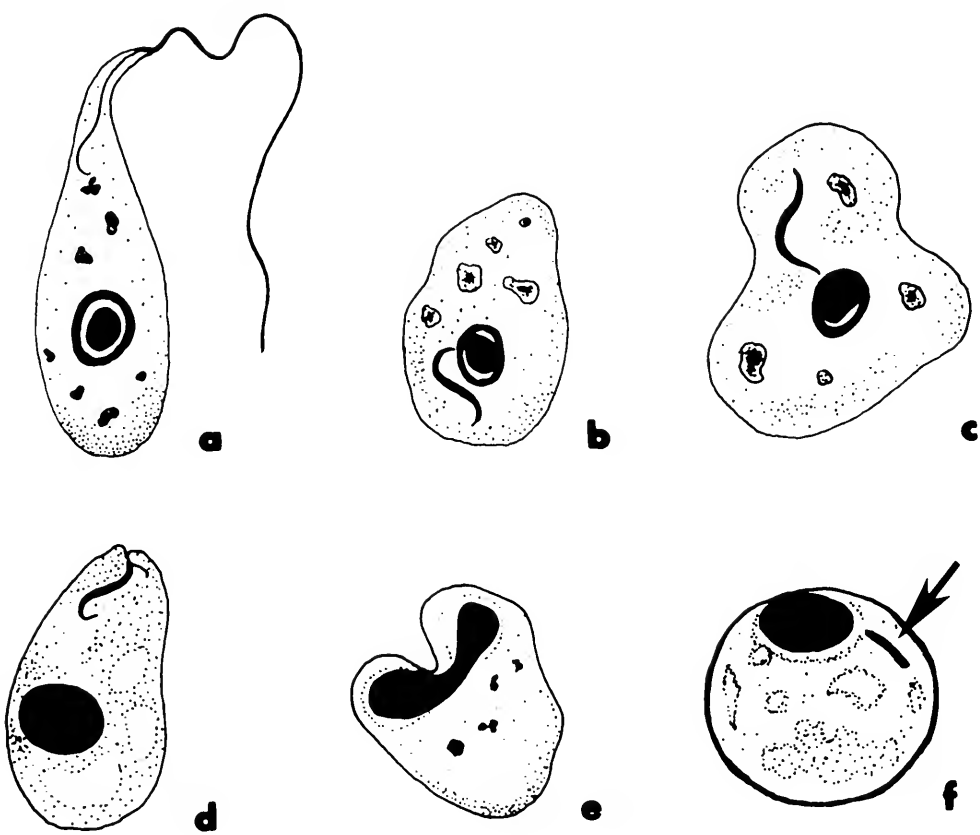


FIGURE 29.—a. *Leptomonas* sp. drawn from life with flagellum. b, c, d. Forms of the flagellate (possibly amastigote stages) as they appear in Protargol-stained body (hemolymph) of brown shrimp. e. Cell division in flagellate showing karyokinesis and longitudinal cytoplasmic fission. f. Possible cyst stage *Leptomonas* from hemocoel of larval shrimp. Note Protargol-positive kinetoplast near nucleus (arrow points to kinetoplast). (All figures ×2,900.)

and cestodes. The role of these worms as agents of disease in shrimps is uncertain. Most of the species reported, to date, appear to have little effect on individual shrimp infested, and probably little significant effect on populations of penaeids. However, flatworms in penaeid shrimps are often conspicuous and, thus, attract considerable attention. Penaeid shrimp usually play the role of intermediate host for most, if not all, flatworms they harbor; therefore, shrimps play a significant role in the ecology of parasites that may be transmitted through the food web to higher vertebrate hosts.

Class Trematoda Rudolphi 1808
Subclass Digenea Carus 1863
Famly Microphallidae (Travassos 1920)
Genus *Microphallus* Ward 1901
Microphallus sp.

Hutton et al. (1959) reported an undescribed species of microphallid trematode metacercariae from pink shrimp. They found that from two to three metacercarial cysts up to hundreds (from 1.2 to 1.5 mm in diameter) were encysted in muscle tissue surrounding internal organs, particularly the cephalothoracic and abdominal musculature. No effect on the shrimp host was reported.

Overstreet (1973) also reported an unidentified microphallid metacercaria from abdominal muscles of white shrimp from Barataria Bay, La. The cysts were 93-95 μm to 77-83 μm, much smaller than those reported from pink shrimp from west Florida by Hutton et al. (1959).

Family Opecoelidae Ozaki 1925
Genus *Opecoeloides* (Odhner 1928)
Opecoeloides fimbriatus (Linton 1934)
Sogandares-Bernal and Hutton 1959

Metacercariae of this trematode (Figure 30) encyst in hepatopancreas, other internal organs, and beneath the exoskeleton of *Penaeus duorarum, P. setiferus,* and *P. aztecus.* This is a very common parasite of penaeids, occurring in up to 90% of some samples of pink shrimp taken during the summer from Apalachee Bay, Fla. No extreme pathogenesis in shrimp has been reported associated with *O. fimbriatus.* The worm is approximately 1.5 to 2.0 mm long when excysted and is quickly identified by its possession of an extremely pedunculate acetabulum (Figure 30). The sexually mature worm (adult) is found mostly in fishes of the family Sciaenidae which feed on shrimps. The metacercaria is found in penaeids from the Gulf and Georgia coasts.

Class Cestoidea Rudolphi 1809
Order Trypanorhyncha Diesing 1863
Family Eutetrarhynchidae Guiart 1927
Genus *Prochristianella* Dolfus 1946
Prochristianella hispida (Linton 1890)
Campbell and Carvajal 1975
Synonyms: *Rhynchobothrium hispidum*
Linton 1890; *P. penaei* Kruse 1959

Plerocercoid larvae of this tapeworm are very common in *Penaeus setiferus, P. duorarum,* and *P. aztecus.* I have found up to 95% of large samples of *P. duorarum* from northwest Florida to harbor the cestode. This cestode is found mainly in the hepatopancreas of the host (Figure 31), and most often fails to elicit any strong pathologic response from the shrimp. Sparks and Fontaine (1973) and Feigenbaum and Carnuccio (1976) reported a strong host reponse to the plerocercoid when it encysted in hepatopancreas. I have not observed this in several hundred hosts examined, but host destruction of trypanorhynchan plerocerci may occur rarely in shrimp. Most evidence suggests a long and relatively tolerant relationship between shrimp and cestode. Often a single shrimp will have one to two dozen encysted larvae in its hepatopancreas.

According to my measurements, the worm (Figure 32a, b) has the following mean dimensions: length = 1.12 mm; bladder or blastocyst = 0.58 mm long by 0.37 mm wide; and scolex (below bothridia) = 0.11 mm wide by 0.35 mm long. These measurements are close to those of Kruse's (1959) description. Though no lifecycle has been experimentally completed for a trypanorhynchan, the hosts for adult worms of this group are probably sharks and rays. From nature, cestodes of this order have been found in the spiral valves of elasmobranchii (Kruse 1959). Aldrich (1965) and Ragan and Aldrich (1972) gave host-parasite data on this species.

Parachristianella monomegacantha Kruse 1959
P. dimegacantha Kruse 1959

Kruse (1959) described two other trypanorhynchan plerocercoid larvae from *Penaeus duorarum.* These species were found in the hepatopancreas of shrimp from the northern gulf coast and are distinct from one another "in hook arrangement and

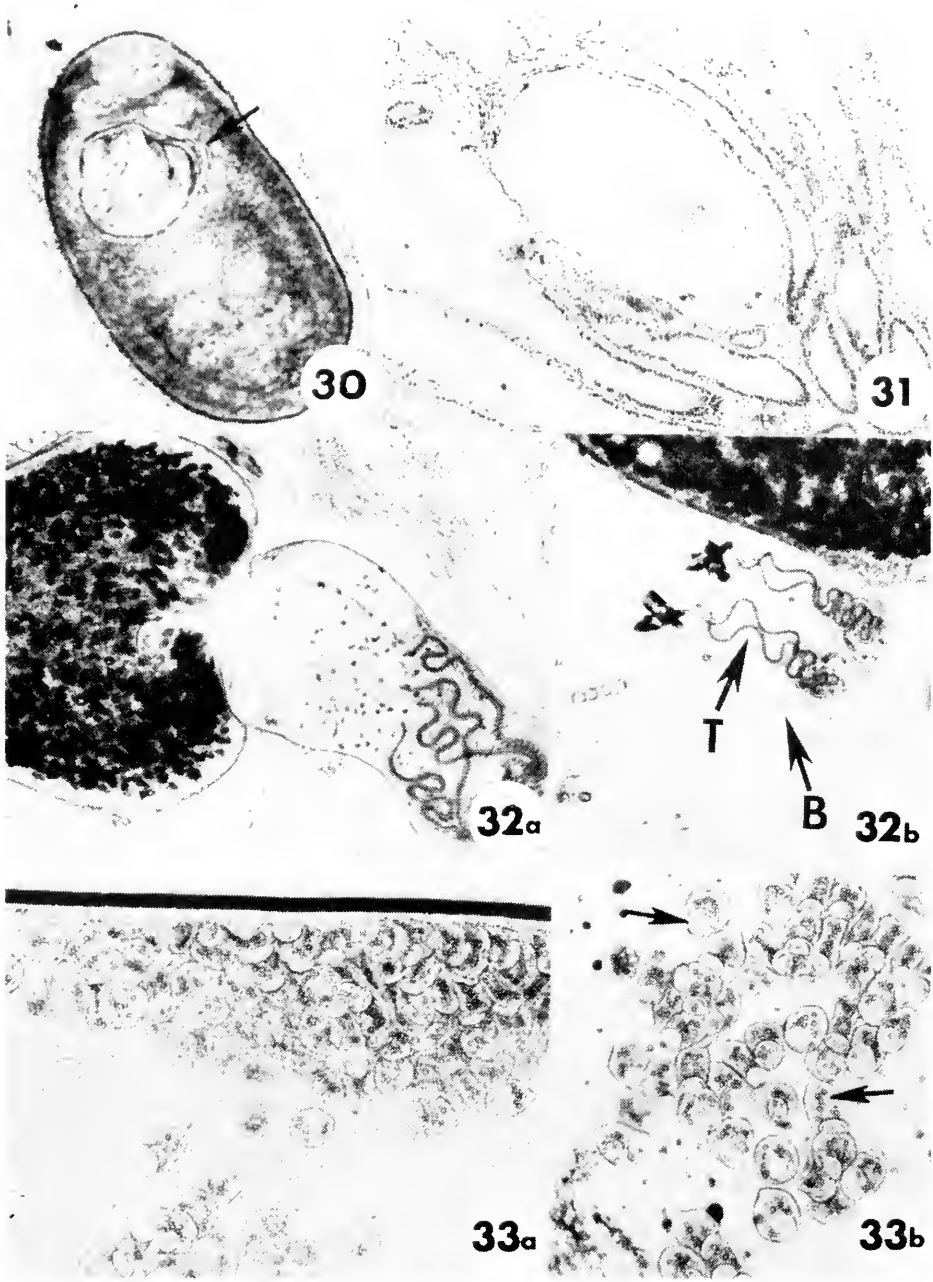


FIGURE 30.—Metacercaria of *Opecoeloides fimbriatus*, digenetic trematode, from hepatopancreas or hemocoel of adult pink shrimp. This species is quickly identified by its large, pedunculate acetabulum (arrow). ×70.

FIGURE 31.—Section of plerocercoid larva of *Prochristianella hispida* encysted in hepatopancreas of pink shrimp; note cyst wall and lack of host cellular response (Feulgen picro-methyl blue stain). ×50.

FIGURE 32.—a. Fresh wet mount of plerocercus of *P. hispida;* note scolex and blastocyst. ×50. b. Scolex of *P. hispida;* note tentacles (T) and bothria (B) (arrows). ×50.

FIGURE 33.—a. Larvae of an unidentified cestode commonly found in hemocoel of penaeid shrimps; this figure shows a mass of larvae against the midgut lining (dark line). ×25. b. Unidentified cestode larvae showing calcareous corpuscles and large sucker (arrows). ×25.

in the relative sizes of their bothridia, bulbs, and post-bulbosal regions."

The genus differs from *Prochristianella* in the morphology of the blastocyst; species of the latter genus having a division between anterior and posterior portions, with large granules contained in the anterior division of the blastocyst. These worms apparently do not harm their hosts significantly.

Parachristianella heteromegacanthus Feigenbaum 1975

The most recent species to be described is from *Penaeus brasiliensis* from Biscayne Bay. Twenty percent of this shrimp were infected with fewer than 1.5 worms occurring in each infected shrimp. Corkern (1970) found an average of 2.3 specimens of *P. dimegacantha* per infected brown shrimp from Galveston Bay, Tex. Prevalence data from Corkern's work shows 23% brown shrimp infected, a figure close to that of Feigenbaum's (1975) 20% for *P. heteromegacanthus*. Tentacle hook arrangements in *P. heteromegacantha* differed from those in *P. monomegacantha* and *P. dimegacantha*.

Family Renibulbidae Feigenbaum 1975
Genus *Renibulbus* Feigenbaum 1975
Renibulbus penaeus Feigenbaum 1975

To date, this species was found in 14.3% of *Penaeus brasiliensis* examined from Biscayne Bay. The short kidney-shaped bulbs in the scolex of this cestode set it apart from other trypanorhynchan cestodes in penaeid hosts. No organ site of infection was given by Feigenbaum (1975) for this worm, and no pathogenesis was indicated.

Unknown Cestode Larva

Hutton et al. (1959), Kruse (1959), Overstreet (1973), Feigenbaum (1975), and I have found a small pyriform cestode larval stage (Figure 33a, b) commonly in the intestine of penaeid shrimps from the Gulf and Atlantic coasts of Florida. This worm also is found in large numbers in several tissues of infected shrimp, namely, the muscles and hemocoel. The worm possesses a large anterior sucker and many refringent calcareous corpuscles in its body, and is approximately 0.61 to 0.81 mm long by 0.12 to 0.22 mm wide. Large numbers of this worm may occlude the intestinal lumen or cause perforation of the intestinal wall. Several hundred larvae have been counted in a single shrimp. Hosts, to date, include *Penaeus duorarum, P. aztecus, P. setiferus,* and *P. brasiliensis.*

Nematodes

Phylum Aschelminthes Grobben 1910
Class Nematoda (Rudolphi 1809) Cobb 1919
Superfamily Ascaridoidea (Railliet and Henry 1915)
Genus *Thynnascaris* Dolfus 1933
Thynnascaris sp.

Overstreet (1973) reported that the nematode larvae identified by Kruse (1959), Hutton et al. (1959), and Corkern (1970) as *Contracaecum* sp. in penaeid shrimps should be considered species of *Thynnascaris*. Norris and Overstreet (1976) have found that at least two species occur in penaeid shrimps in North America. Characteristics of this genus are short intestinal caecum and longer ventricular appendix combined with the position of the excretory pore near the nerve ring. Figures 34 and 35 are photomicrographs of *Thynnascaris* sp. recovered from hepatopancreas and cephalothorax of *Penaeus duorarum* near Pensacola. I have not found it commonly in shrimp from west Florida, but Overstreet (1973) reported that Donald Norris of his laboratory found up to 31% of white and brown shrimp from Mississippi Sound and adjacent waters infected during summer months. *Thynnascaris* sp. juveniles measure 1.02 to 2.40 mm long by 0.06 to 0.10 mm wide.

Overstreet (1973) reported two specimens of *Spirocamallanus pereirai* Olsen 1952, in the intestine of *Penaeus setiferus* from near Biloxi, Miss. These were third stage larval nematodes which measured 1.00 mm long by 0.03 mm wide. Overstreet suggested that the shrimp may serve as a paratenic host and that copepods may serve as a more common source or vector for this nematode which normally matures in fishes.

Several species of free-living nematodes, commonly found in shrimp habitat, have been reported as facultative commensals or inquilines of penaeids. Shrimp may take these worms in larval stages when they feed on detritus or bottom organisms in nature or in artificial ponds. Specimens of *Leptolaimus* sp. and *Croconema* sp. have been found by Overstreet (1973) in brown and white shrimps from Mississippi. Other than phys-

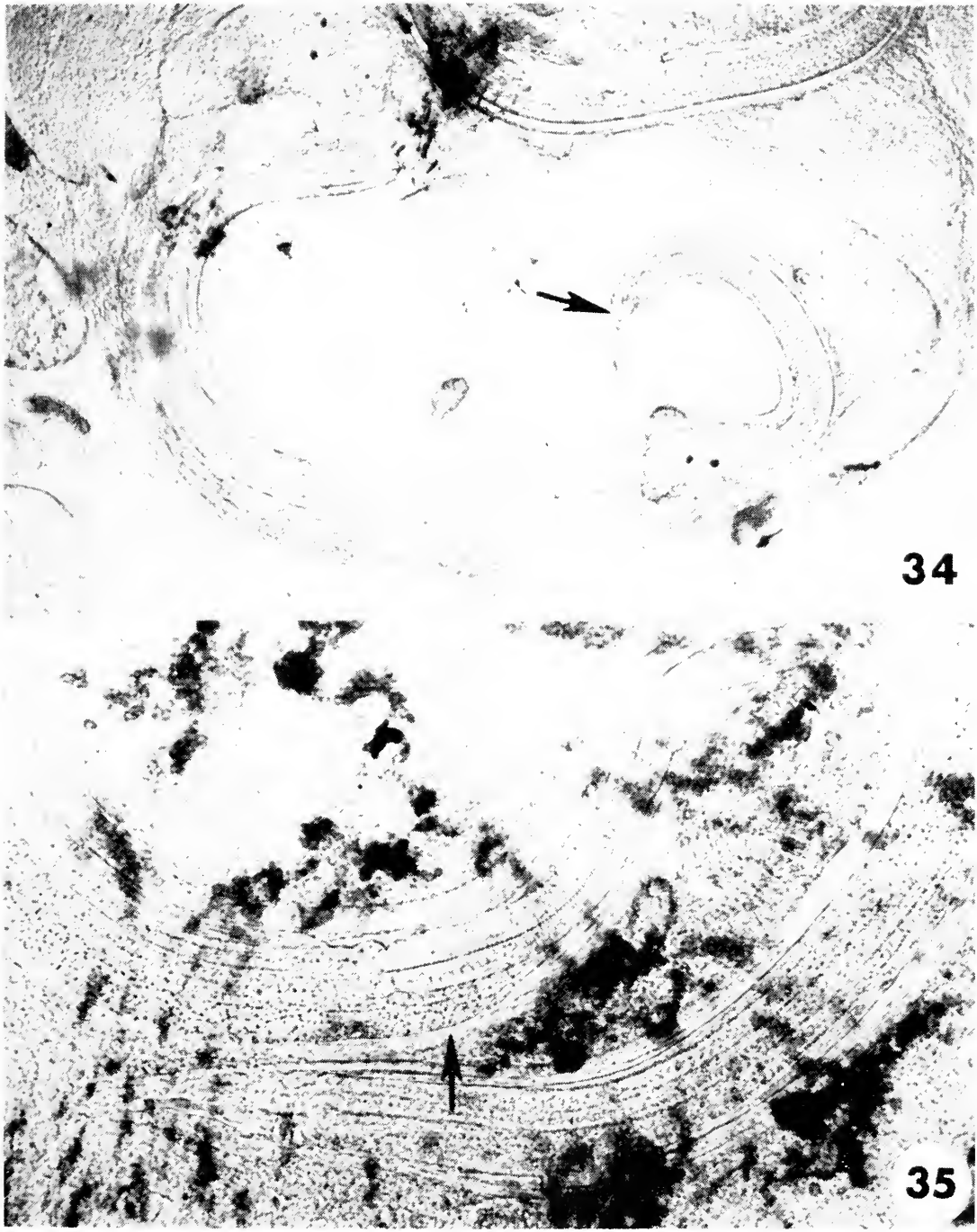


FIGURE 34.—*Thynnascaris* sp. larvae in tissue squash from pink shrimp. Whole worm larva in view; note cellular arrangement at posterior of worm (arrow). ×50.

FIGURE 35.—Higher magnification of *Thynnascaris* sp.; note the intestinal caecum that turns anterior from the intestine (arrow). ×100.

ical disruption of tissues, no mechanism of pathogenesis is apparent for nematodes in shrimp.

NONINFECTIOUS DISEASES

Toxic Responses

In the last decade, because of interest in aquatic pollution, some research has been done on toxic responses of penaeid shrimps to a variety of chemicals and heavy metals. Most of this work has been done in pollution-oriented laboratories; however, few attempts have been made to apply results to interprétation of field conditions. Results obtained have been reported mostly as toxicity of specific chemical agents in terms of short-term lethality or longer-term mortality. Unfortunately, little indicative cellular or tissue changes caused by toxicants has been described for penaeid shrimps. I shall divide this section into categories of toxicants that have been tested or studied in penaeids. The following categories will be covered: organochlorines, organophosphates, carbamates, oil or petroleum products, heavy metals, and chemotherapeutic chemicals.

Organochlorines

Since World War II many kinds of pesticides and industrial chemicals containing or consisting of chlorinated hydrocarbons have been inadvertently or intentionally released into the environment. Aquatic life is exposed to these compounds because the aquatic portion of the biosphere often behaves as a "sink" or receptacle for these compounds due to runoff or fallout. Some of these compounds or their metabolites are refractory to breakdown, and thus tend to accumulate in various compartments of the aquatic environment. Experimental shrimp have been found to accumulate certain chlorinated compounds in the laboratory and feral shrimp have possessed detectable levels when taken directly from contaminated or apparently "clean" waters. Jack Lowe of the USEPA Laboratory, Gulf Breeze, has found, over several years of testing, that penaeid shrimps generally are far more sensitive to toxic effects of most insecticides than are fishes or mollusks (Table 4). The effects of some of the better known compounds will be reviewed here.

TABLE 4.—Comparative toxicity of pesticides to three estuarine taxa—most sensitive (1) to least sensitive (3).[1]

Pesticide	Penaeid shrimp	Fish	Oysters
Chlordane	1	2	3
DDT	1	2	3
Dieldrin	1	3	2
Endrin	1	2	3
Heptachlor	1	3	2
Toxaphene	2	1	3
Guthion	1	2	3
Malathion	1	2	3
Parathion	1	2	3
Carbaryl	1	2	3
Carbofuran	1	2	3
2,4-D (BEE)	3	2	3
Atrazine	1	2	3
Du-ter	3	2	1
Difolatan	3	2	1

[1] This table was prepared by Jack I. Lowe who graciously granted permission for its use here. The table has not been published previously.

DDT

White shrimp, which died as a result of DDT exposure, accumulated up to 40.40 ppm DDT and DDE in hepatopancreas after 18 days exposure to 0.20 ppb in flowing seawater (Nimmo et al. 1970). Exposure to DDT concentrations greater than 0.10 ppb was lethal to pink shrimp in 28 days. A physiological effect of DDT exposure in pink and brown shrimps was loss of certain cations in the hepatopancreas (Nimmo and Blackman 1972). Sodium and potassium concentrations in shrimp exposed to 0.05 ppb DDT for 20 days were lower than in those not exposed. Magnesium, however, was not significantly lowered. The significance of reduced cations in the hepatopancreas of shrimp for the pathophysiological behavior of shrimp is not known. Blood protein levels also have been found to drop in shrimp exposed to DDT. There are no reports of histopathological changes in penaeids following exposure to DDT. In acute, high-concentration exposures, shrimp showed tremors, hyperkinetic behavior, and paralysis, classic signs of DDT poisoning in arthropods. After extended exposure to low concentrations of DDT, shrimp did not become paralyzed, but sank into lethargy, refused food, and then died.

Dieldrin

Pink shrimp were more sensitive to dieldrin than were grass shrimp in test exposures. However, both species died when exposed to concentrations of dieldrin in the low parts-per-billion range. Pink shrimp had a 96-h LC_{50} of 0.9 ppb dieldrin (Parrish et al. 1973). No histopathological effects of dieldrin in penaeid shrimps have been reported.

Mirex

Juvenile pink and brown shrimps died after exposure to low concentrations of mirex. Twenty-five percent of a sample of pink shrimp died during 7 days exposure to 1.0 ppb mirex. However, all survivors from this test died after 4 days in mirex-free seawater, demonstrating a delayed toxic effect of mirex (Lowe et al. 1971).

I have examined both shrimp and blue crabs exposed to low concentrations of mirex for long periods (30 days or more) for histopathological effects. No pathologic effects at the tissue level were found in the animals which I examined. Organs studied were muscle, hepatopancreas, and gonads.

PCB's (Polychlorinated Biphenyls)

These industrial chemicals have been at large in the aquatic environment for many years due to leakage from water and waste effluents, disposal of dielectric fluids, and other industrial sources (Broadhurst 1972). It is a well-established fact that certain fresh and marine bodies of water are contaminated with various compounds of PCB (Sodergren et al. 1972; Nimmo, Blackman, Wilson, and Forester 1971; Nimmo, Wilson, Blackman, and Wilson 1971; Nimmo et al. 1975). As recently as 1970, Duke et al. reported PCB, Aroclor 1254, in water, sediments, and tissue of animals (including penaeid shrimps) from Escambia Bay, near Pensacola.

At the U.S. Environmental Protection Agency Laboratory (Gulf Breeze, Fla.), much research has been done on the effects of PCB's on estuarine species with emphasis on pink and brown shrimps. These two penaeids were killed in 2-wk exposures to 0.9, 1.4, and 4.0 ppb Aroclor 1254 in flowing seawater. The minimum level causing mortality was 0.9 ppb. Penaeid shrimps appeared to suffer greatest mortality when exposed during premolt (just before molting) and during molt. Most exposed shrimp became lethargic, stopped feeding, and did not dig into the substrate (digging is a normal activity for penaeids). Subtle to dramatic chromatophore changes in the cuticle of exposed shrimp were more frequent and obvious than in control shrimp.

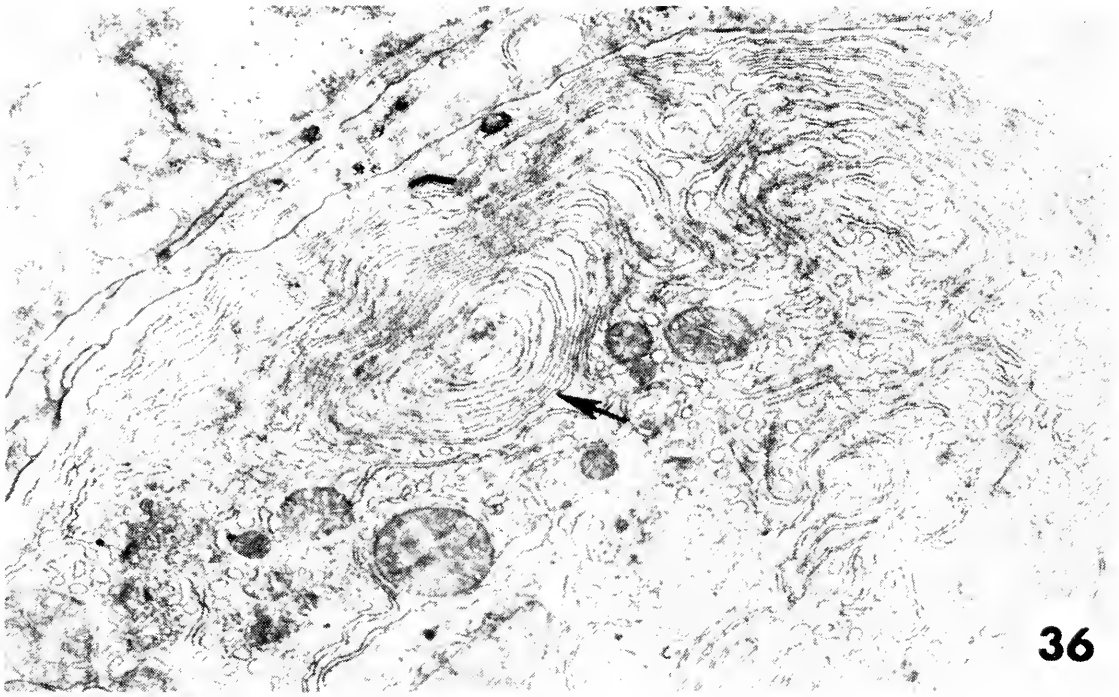
On the light microscopical level, no lesions were consistently found that were indicative of PCB exposure in shrimp (Couch and Nimmo 1974a). However, several interesting cytopathic changes were noted in exposed shrimp studied with EM.

Pink shrimp were exposed to 3 ppb Aroclor 1254 in flowing seawater for 30 to 52 days. During these exposures, up to 50% of the animals died. Living and dead shrimp were analyzed by gas chromatography and from 33 ppm to 40 ppm Aroclor 1254 was found in their hepatopancreatic tissues. Aroclor uptake in hepatopancreas was linear with time (Couch and Nimmo 1974b). Hepatopancreas was fixed and processed for EM. Hepatopancreatic absorptive cells from exposed shrimp revealed the following departures from those of controls: 1) 30 to 50% of cells had increased or proliferated rough endoplasmic reticulum (Figure 36); 2) production of membrane whorls with enclosed lipid droplets (Figure 37); and 3) nuclear degeneration characterized by the occurrence of vesicles in the nucleoplasm (20-50 nm and 100-700 nm in diameter) (Figure 38a, b).

The proliferation of smooth endoplasmic reticulum in hepatocytes of higher animals has been described as indicative of toxic responses to drugs or chemicals such as phenobarbitol, dilantin, dieldrin, and carbon tetrachloride. This proliferation has been related to detoxification of poisons and may, in shrimp, represent an attempt, on the part of hepatopancreatic cells, to metabolize PCB absorbed from the lumen of hepatopancreatic ducts. If this is the case, cellular alterations at the ultrastructural level may be valuable as early indicators of sublethal effects of certain pollutants in penaeid shrimps.

Another PCB, Aroclor 1016, has been more recently introduced for limited use in the United States. This compound has been tested for toxicity in brown shrimp. Aroclor 1016 was found to have nearly the same toxicity for penaeid shrimp as Aroclor 1254: 0.9 ppb Aroclor 1016 in flowing seawater killed 8% of test shrimp in 96 h; 10 ppb Aroclor 1016 killed 43% of test shrimp in 96 h (Hansen, Parrish, and Forester 1974).

It is apparent from research results now published that PCB's as pollutants pose a threat to penaeid shrimps which show a high level of sensitivity to these compounds. In this regard, Nimmo, Blackman, Wilson, and Forester (1971) and Nimmo, Wilson, Blackman, and Wilson (1971) demonstrated that pink shrimp could absorb a PCB (Aroclor 1254) from sediments taken from a PCB-polluted estuary—Escambia Bay, Fla. Hansen, Schimmel, and Matthews (1974) found that some estuarine species could avoid waters contaminated with Aroclor 1254, but pink shrimp showed no avoidance reaction when given



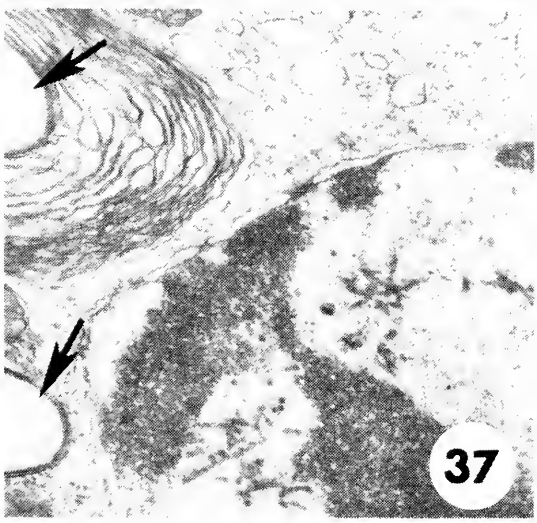


FIGURE 36.—Electron micrograph of profile of hepatopancreatic cell from pink shrimp exposed to 3 ppb Aroclor 1254 (PCB) for 52 days; note endoplasmic reticulum proliferation and beginning formation of cytoplasmic whorls (arrow). ×14,400.

FIGURE 37.—Membrane whorls (myeloid bodies) surrounding lipid in hepatopancreatic cells of shrimp exposed to 3 ppb Aroclor 1254 (arrows). Control nonexposed shrimp did not produce profiles with these configurations. ×28,500.

choices of clean or PCB-contaminated water. These and other data suggest that PCB's, as pollutants, could have influence on relative survival and abundance of penaeid shrimps in natural waters.

Organophosphates and Carbamates

Few organophosphate compounds have been tested in species of crustaceans. However, those tested have shown approximately 1,000 times greater toxicity to shrimps than most other pesticides tested (Butler 1966), and penaeid shrimps have shown greater sensitivity than fishes or mollusks (Table 4).

Baytex (Bayer 29,493) was very toxic to penaeid shrimp (Butler and Springer 1963) in the laboratory. Naled (1,2 dibromo-2,2-dichloroethyl-dimethyl phosphate) had little effect in field tests on shrimp. Fast dilution and instability without persistence of compounds may be reasons for lack of mortality of shrimps in field tests of organophosphates. In the laboratory, Dibrom is lethal to postlarval brown shrimp at 2.0 ppb, and at 5.5 ppb it is lethal to adult pink shrimp (5.5 ppb = LC_{50} for 48 h exposure).

Malathion, at 14 ppb, caused hyperactivity, paralysis, and death in penaeids, and parathion

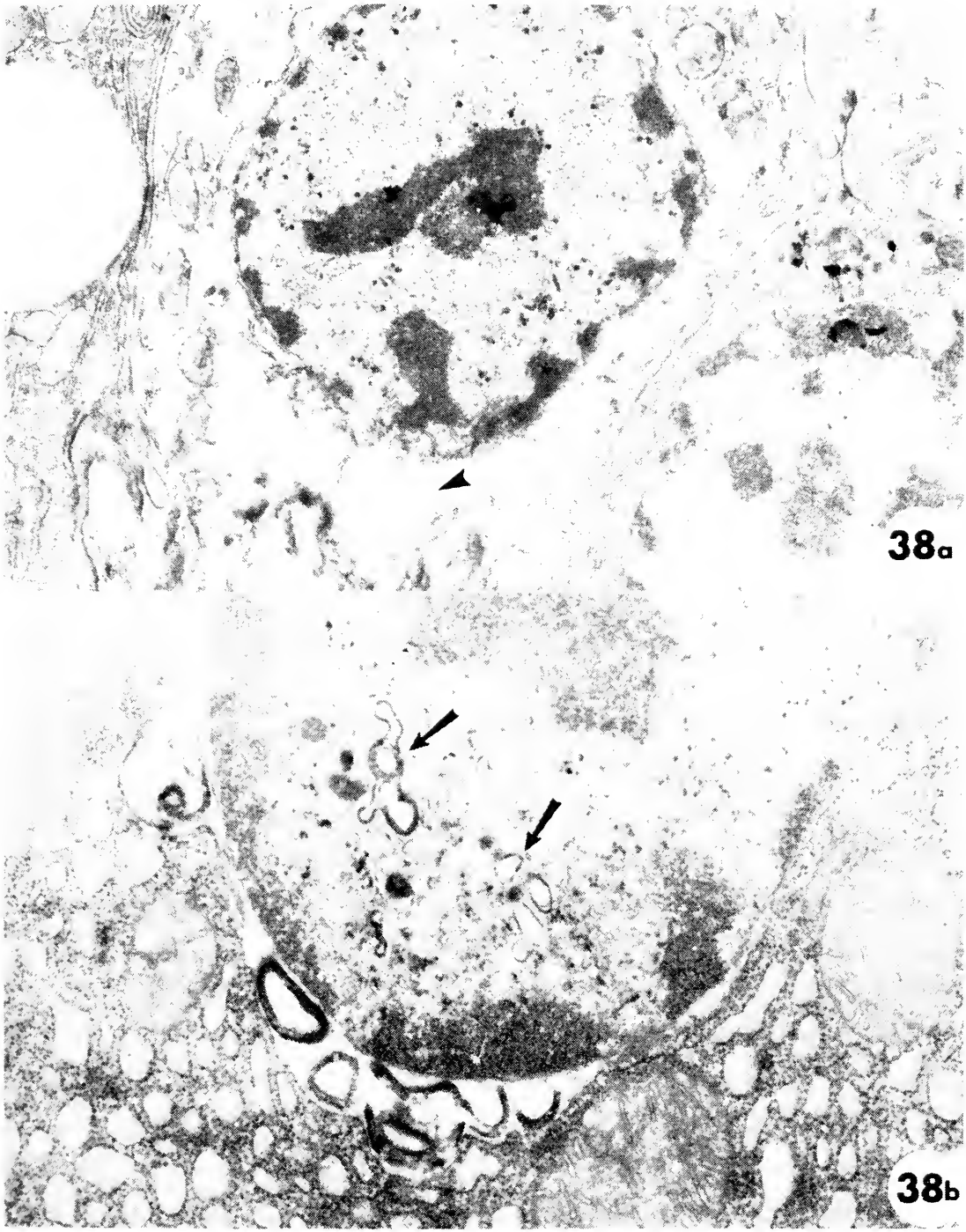


FIGURE 38.—a. Hepatopancreatic cell profiles revealing nuclei with small vesicles (20-50 nm) (white arrows) in nucleoplasm from shrimp exposed to 3 ppb Aroclor 1254; also note cytoplasmic degeneration (black arrow); compare with more normal cell in lower right corner. ×14,400. b. Hepatopancreatic cell profile showing nucleus with major large vesicles (100-700 nm) (arrows) in nucleoplasm; note also dense bodies in nuclear envelope from PCB-exposed shrimp. ×28,500.

lethal concentration for 48 h in pink shrimp was 0.2 ppb (D. Coppage, pers. commun.). No histopathogenesis has been reported for penaeids exposed to organophosphates.

Conte and Parker (1975) found Malathion aerially applied to flooded marshes in Texas caused from 14 to 80% mortality in brown and white shrimps held in cages. They recommended that Malathion not be applied to flooded marshes that maintained shrimp.

Both organophosphates and carbamates are potent acetycholinesterase (AChe) inhibitors. Little evidence of early, presyndromic inhibition of AChe activity in the ventral nerve cord of pink shrimp was found, but inhibition as high as 75% was found in moribund shrimp exposed to Malathion (Coppage and Matthews 1974).

Carbamate pesticides have not been tested much in regard to penaeid shrimps, but it is known that Sevin is lethal to other shrimps and crustaceans when applied to field sites in the marine environment (Haven et al. 1966). J. Lowe (pers. commun.) has found carbaryl (Sevin) to be quite toxic to penaeids (Table 4) in laboratory tests.

Petroleum

Very little information exists on the effects of petroleum or oil products on penaeid shrimps. This is surprising because many offshore oil producing areas are also penaeid shrimp producing regions.

Anderson et al. (1974) and Cox[9] reported results of studies on the toxicity of No. 2 fuel oil on the brown shrimp. The 24-h median tolerance limits of juvenile brown shrimp exposed to components of No. 2 fuel oil (naphthalenes, methylnaphthalenes, and dimethyl napthalenes) ranged from 0.77 to 2.51 ppm. The naphthalenes were the most toxic components of fuel oil. Refined oils, No. 2 fuel oil, and Venezuelan bunker C oil were more toxic to brown shrimp than was Louisiana crude oil. Cox reported that the higher content of toxic aromatics in the refined oils above accounted for their higher toxicity to penaeids.

Yarbrough and Minchew[10] reported several histological lesions in penaeids exposed to 2.0 ppm sonified crude oil. Nonspecific lesions were described in the cuticular chitin, the lining of the gastric mill, and the mouth region of shrimps. The proliferation of cells and necrosis in the basal portion of gill filaments was reported as a more specific lesion associated with exposure. These effects should be examined carefully in relation to "shell" disease resulting from natural conditions.

Heavy Metals

Cadmium

Unusually high levels of cadmium have been reported from certain estuarine areas in which penaeid shrimps commonly occur (i.e., Laguna Madre, Corpus Christi, Tex.). This metal is also a pollutant component from several industrial effluents that are emptied into aquatic systems.

In experiments at Gulf Breeze, Nimmo et al. (1977) observed that in pink shrimp exposed to approximately 760 ppb cadmium (as $CdCl_2$) for 9 days or longer an unusual darkening of gills occurred which eventually led to complete blackening of gills of a significant number of exposed shrimp. Control shrimp did not develop black gills. In other tests, it was found that the LC_{50} of cadmium in 30 days was 718 ppb, and during these tests many exposed shrimp developed the black gill syndrome prior to death (Figure 39).

I have completed light and electron microscopic studies of gill tissues from exposed blackened gills and control gills of surviving pink shrimp which Nimmo supplied from his tests (Couch 1977). My findings indicate that the gross blackening of gills results from necrosis of subcuticular tissues (gill epithelial tissue) (Figure 40a, b). This necrosis stems from the death of cells in the distal gill filaments (smallest unit in gill of shrimp). Actual cell death occurs prior to gross blackening in tiny foci, followed by gradual involvement of the whole filament. Electron microscopy reveals polymorphic black deposits in the cytoplasm of moribund or necrotic cells (early around mitochondria, later throughout). A complete loss of structural and, probably, functional integrity of the gill soft tissue (Figures 41, 42a, b) leads to organ necrosis. However, the cuticle and epicuticle remain intact at the ultrastructural level and hold the moribund or necrotic soft tissue within their boundaries. Grossly, apparent melanization of injured gill filaments account for the blackening syndrome. However, EM (Figure 42a, b) does not present

[9]Cox, B. A. 1975. The toxicity of no. 2 fuel oil on the brown shrimp *Penaeus aztecus*. *In* Program of the first workshop on the pathology and toxicology of penaeid shrimps. U.S. EPA, Gulf Breeze, Fla., 12 p.

[10]Yarbrough, J. D., and D. Minchew. 1975. Histological changes in the shrimp related to chronic exposure to crude oil. *In* Program of the first workshop on the pathology and toxicology of penaeid shrimps. U.S. EPA, Gulf Breeze, Fla., 12 p.

FIGURE 39.—Pink shrimp with black gill syndrome (above) associated with exposure to cadmium chloride. Control, nonexposed shrimp shown below (scale in inches).

evidence for the presence of melanosomes, melanocytes, or melanophores. An alternative possibility, that cell death and necrosis lead to the deposition of metal sulfides or other black deposits in necrotic tissues in the living animal, could account for the blackened gill syndrome. At any rate, the interesting concept of cell and tissue death preceding organismic death is represented in the pink shrimp's response to cadmium exposure. Death of cells (in the gills) concerned with osmoregulation and respiration would lead to dysfunction and eventual death of shrimp.

Bahner[11] has studied the uptake of cadmium in the tissue of pink shrimp. He found that between 1 and 10 ppb Cd in water elicited uptake by hepatopancreas, gills, and exoskeleton. Below concentrations of 1 ppb Cd in water, there was no accumulation of the metal in shrimp tissue. Little is known concerning cadmium effects on feral shrimp in nature.

Mercury

Mercury as a metal has not been suspect in toxic effects on organisms. Mercuric salts and methylated mercury, however, are extremely toxic with both short-term and long-term chronic effects. Mercuric chloride is used in a variety of histological fixative fluids because of its protein-precipitating effects in tissues of invertebrates (Sparks

[11] Bahner, L. H. 1975. Mobilization of cadmium in the tissues of pink shrimp, *Penaeus duorarum*. *In* Program of the first workshop on the pathology and toxicology of penaeid shrimps. U.S. EPA, Gulf Breeze, Fla., 8 p.

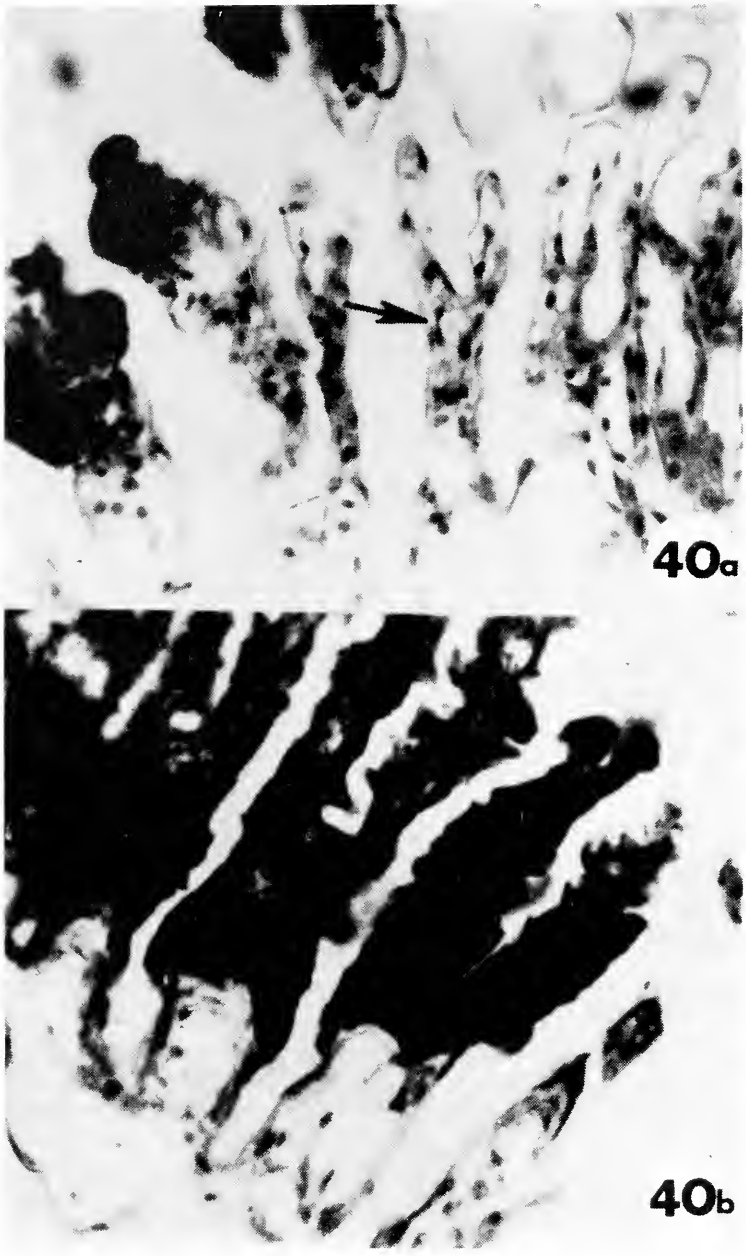


FIGURE 40.—a. Histological appearance of early black gill lesion; note that blackening occurs first near tips of gill filaments; normal gill filament (arrow) is to right of blackened filaments. ×580. b. Histological appearance of advanced black gill in cadmium-exposed pink shrimp; note complete necrosis of gill filaments, but clear line of separation from more normal tissue below. ×580.

1972). Few studies have been reported concerning effects of mercury compounds on penaeid shrimps.

Petrocelli et al.[12] studied the uptake and gross distribution of mercuric chloride in brown shrimp. These authors also examined the effects of mercuric chloride exposure on ability of brown shrimp to adjust to salinity changes. They found that after 2 h exposure to 0.5 ppb mercuric chloride in seawater, residue level of mercury in shrimp was 285 ppb with only 9% of the mercury in the meat (muscle) and 91% in the shell. This suggested a surface adsorptive process for mercury in brown shrimp

[12]Petrocelli, S. R., G. Roseijadi, J. W. Anderson, B . J. Presley, and R. Sims. 1975. Brown shrimp exposed to inorganic mercury in the field. *In* Program of the first workshop on the pathology and toxicology of penaeid shrimps. U.S. EPA, Gulf Breeze, Fla., 1 p.

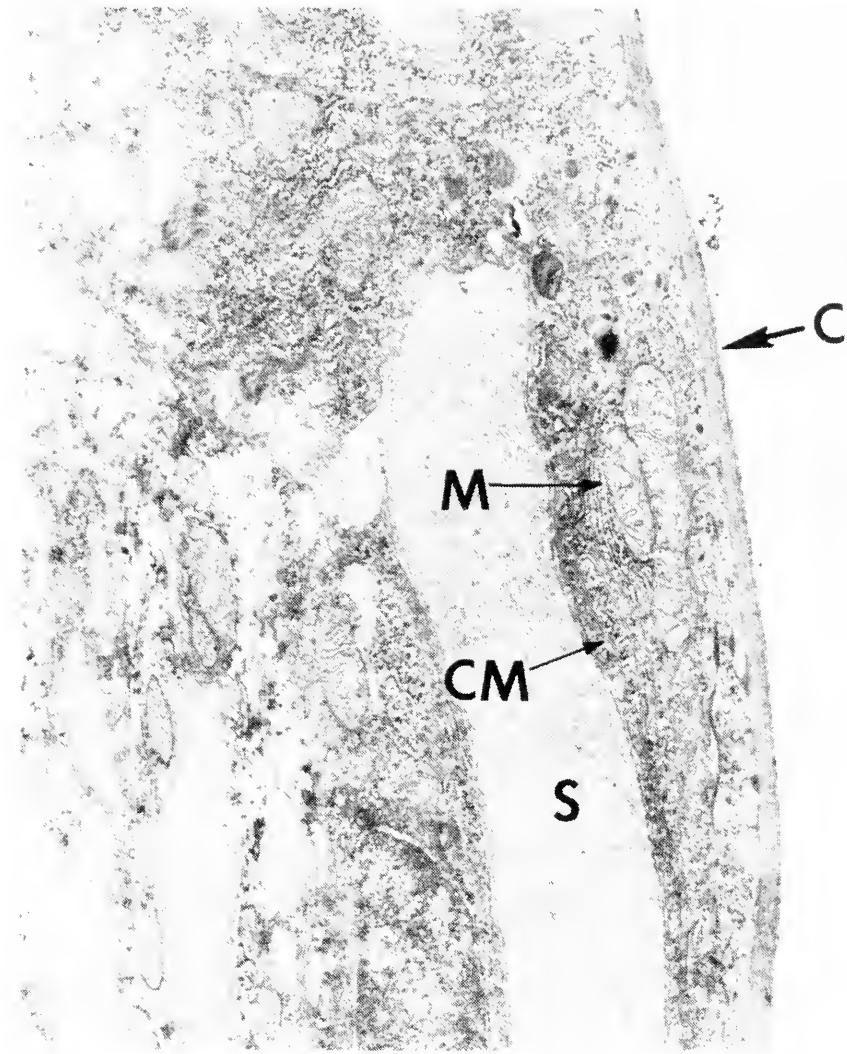


FIGURE 41.—Electron micrograph of normal gill cuticle (arrow) and underlying osmoregulatory and respiratory epithelium; note mitochondria (M), cell membranes (CM), hemolymph sinus (S), and cuticle (C). ×14,400.

exposed for brief periods. These authors also reported that shrimp obtained from off Louisiana's Southwest Pass had natural levels of only 4.6 ppb mercury distributed as 64% in the muscle and 36% in the cuticle.

Brown shrimp are active regulators of blood chloride levels (ion regulators). Petrocelli et al. (see footnote 12) found that exposure of brown shrimp to mercury and to salinity changes resulted in interference with the shrimp's ability to adjust their internal ion levels to external salinity changes. Therefore, mercury could prove to be detrimental to penaeid shrimps if it were present in form and amount enough to prevent their adjustment to freshets or high saline conditions that result from rapid changes in estuaries or tidelands.

Chemotherapeutic Chemicals

Certain inorganic and organic chemicals have been tested for toxic effects in penaeid shrimps because they are used routinely as chemotherapeutic agents in aquatic animal disease control.

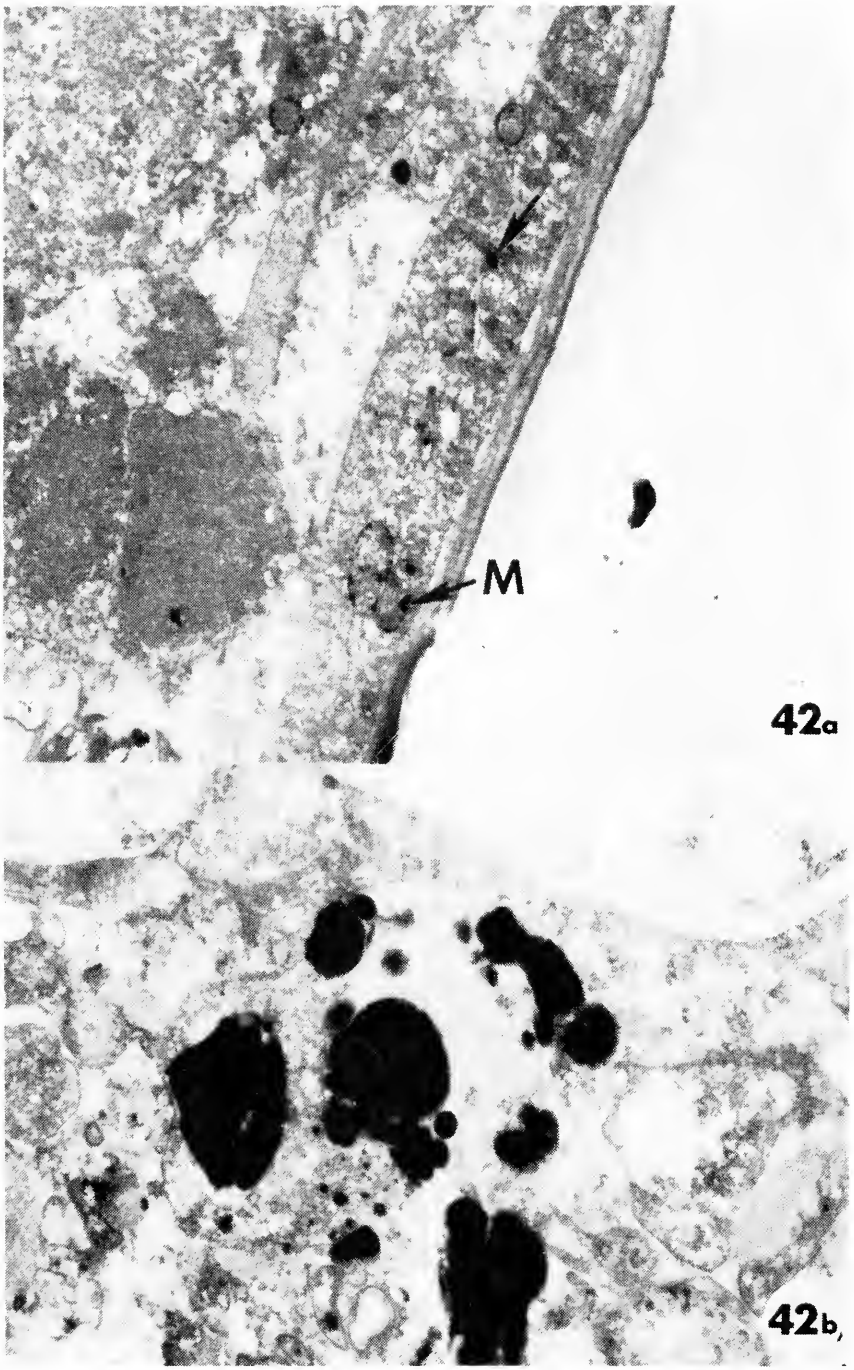


FIGURE 42.—a. Electron micrograph of comparable gill region (to Figure 40) in cadmium-exposed shrimp with black gill syndrome; note cell necrosis, black deposits around mitochondria (arrows); note loss of membrane integrity. ×14,400. b. Higher magnification of black cytoplasmic deposits in gill epithelial cells of cadmium-exposed shrimp; note polymorphic nature of deposits. ×28,500.

Johnson (1975, footnotes 13, 14) has determined toxic concentrations in penaeid shrimps for the following chemicals: Formalin, potassium permanganate, potassium dichromate, copper sulfate, acriflavine, malachite green, and methylene blue. His results are reported below.

Essentially, Johnson found that for Formalin the 96-h LC_{50} at 28°C for pink shrimp was 235 to 270 ppm in seawater. He reported that 25 ppm Formalin applications for killing of external protozoa on penaeid shrimps would be safe for indefinite periods.

Potassium permanganate LC_{50} at 96 h for pink shrimp was 6 ppm. At this concentration a precipitate was formed on the gills of shrimp and death may have resulted from asphyxiation.

Potassium dichromate, which may be of some use as an antibacterial agent, was found to be nontoxic for shrimps below concentrations of 5 ppm for short term exposures.

Copper sulfate has been of use as a herbicide and protozoan control agent in fisheries research. It was found that copper sulfate at low concentrations (0.5-1.0 ppm) was reasonably safe for penaeids.

Acriflavine, an antibacterial agent, had a 96-h LC_{50} for pink shrimp of 1.0 ppm in seawater. This compound was probably not safe for shrimps at effective bacteriostatic concentrations.

Malachite green, a parasiticide for freshwater fishes, has a toxic effect in shrimp associated with molting. Johnson (see footnote 14) reported that newly molted shrimps are much more sensitive to malachite green than intermolt shrimps. From 2.5 to 20 ppm of the compound in seawater resulted in death of all exposed newly molted shrimps. Adult, nonmolting, penaeid shrimps seemed to tolerate higher concentrations of malachite green (20 ppm). Johnson believed that malachite green holds promise as a fungistat for use in penaeid shrimp culture.

Methylene blue should be usable below concentrations of 1.0 ppm for prophylaxis of fungi and protozoa in penaeids.

Quinaldine (product of Eastman Kodak Company) was used by Johnson (see footnote 13) as an anesthetic for white shrimp. He found that shrimp become anesthetized when exposed to all concentrations of quinaldine, but after 48 h, 10%, 20%, and 20% losses occurred respectively in 25-, 30-, and 35-ppm treatment groups. A 25-ppm concentration was set as the minimum effective anesthetic level with white shrimps. This concentration, however, results in death of some shrimp as indicated above. Johnson also reported that spontaneous muscle necrosis occurred in abdominal musculature of some shrimp that became hyperkinetic at concentrations of 25 ppm and above.

[13]Johnson, S. K. 1974. Use of Quinaldine with penaeid shrimp. Texas A&M Univ., Fish Disease Diagnostic Lab. Note FDDL-S4, 2 p.

[14]Johnson, S. K. 1974. Toxicity of several management chemicals to penaeid shrimp. Texas A&M Univ., Fish Disease Diagnostic Lab. Note FDDL-S13, 10 p.

SPONTANEOUS PATHOSES

Under this heading are included diseases of penaeid shrimps for which etiologic agents are not known, or are uncertain.

Tumors

There have been no invasive neoplasms reported for decapod crustaceans. Tumorlike growths have been reported in lobsters (Herrick 1895, 1909; Prince 1897), in a crab (Fischer 1928), and in a paleomonid shrimp (Savant and Kewalramani 1964).

To date, the only published report of a tumorlike growth in a penaeid shrimp is that of Sparks and Lightner (1973). They reported a papilliform, tumorlike growth on the right ventrolateral aspect of the sixth abdominal segment of a specimen of *Penaeus aztecus*. This shrimp had been taken from an experimental rearing pond at Palacios, Tex. The growth was tentatively diagnosed as a benign neoplasm, consisting of hypertrophied and normal tissue.

Robin Overstreet (Gulf Coast Research Laboratory) recently presented me with two larval penaeid shrimp each of which had one small growth on an abdominal segment. Light microscopy and EM revealed that these enlargements contained only striated muscle and sacroplasmic reticulum (Figure 43). There was no evidence that the growths were neoplastic or that parasites (including viruses) were involved. Overstreet is presently completing a detailed study of this condition and is describing the growths as hamartomas, possibly related to polluted water conditions from which the affected shrimp were collected.

Spontaneous Muscle Necrosis

Penaeid shrimps often respond to handling, temperature, and chemical stress by developing a

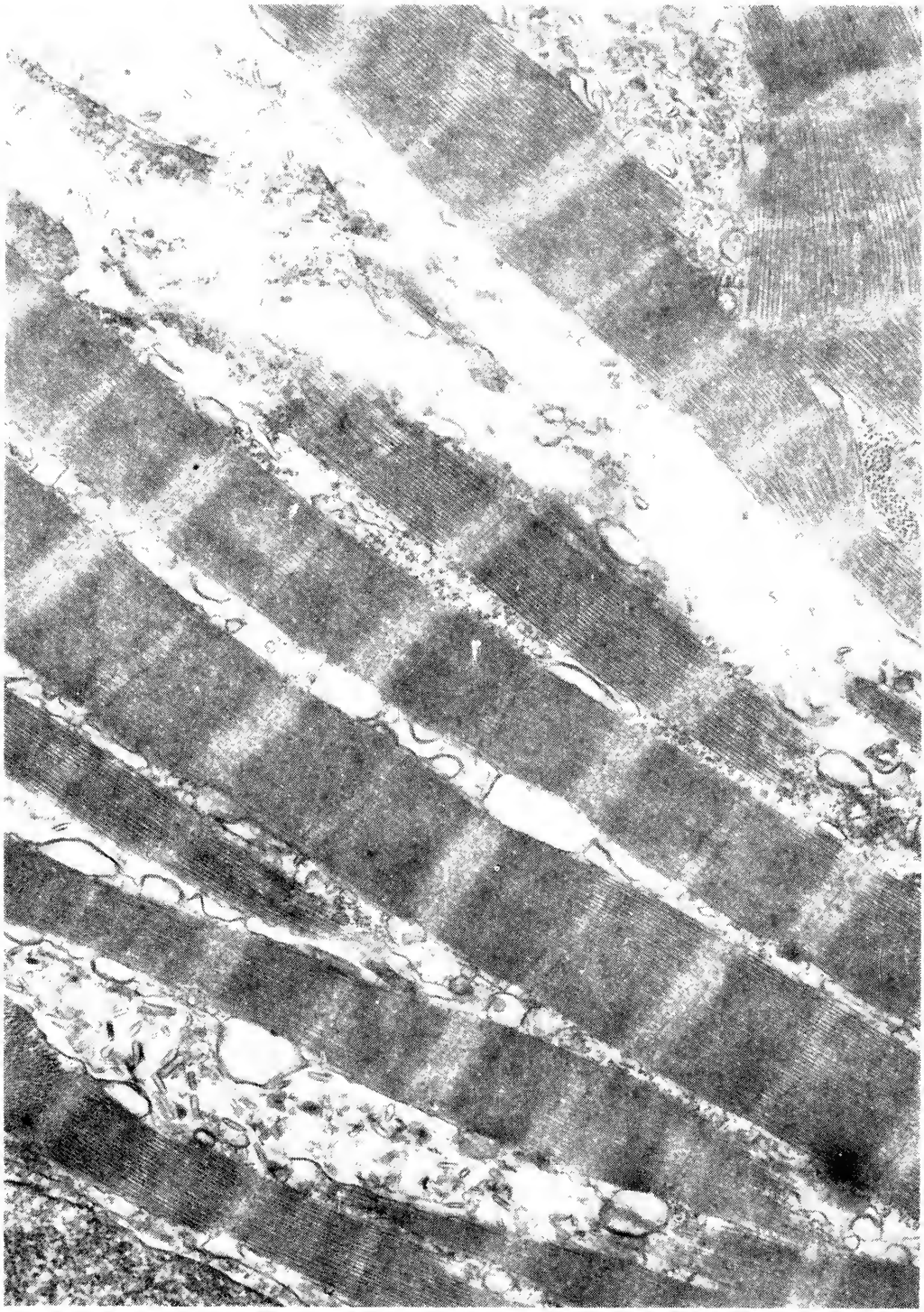


FIGURE 43.—Electron micrograph of striated muscle and sarcoplasmic reticulum from abnormal growth on abdominal appendage of penaeid shrimp. ×14,400.

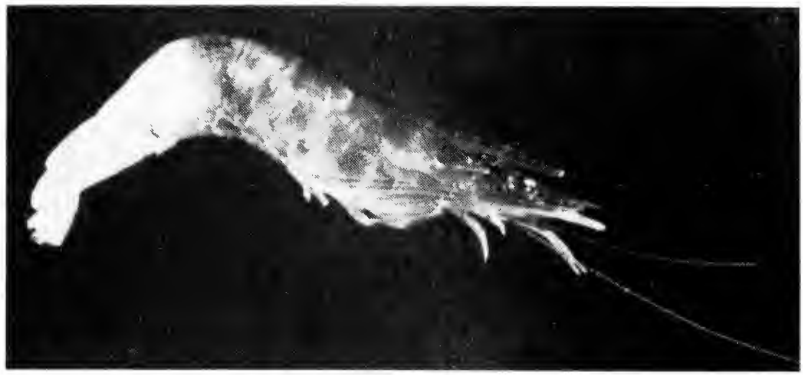


FIGURE 44.—Spontaneous necrosis in pink shrimp exposed to low temperatures (10°C); muscle affected is in whitened area in tail; note uropod and tail degeneration associated with necrotic condition. Shrimp was alive at time photograph was taken.

white or opaque abdominal musculature (Figure 44). Rigdon and Baxter (1970) first reported this disease as spontaneous muscle necrosis and described the histological condition as "degenerated foci of striated muscle" in brown shrimp. Shrimp with this condition are debilitated and usually die unless stress ceases and extent of necrosis is small and limited. Shrimp will recover in many cases, however, if stress ceases. The muscle fibers affected appear lysed microscopically, and their structural integrity is lost. This syndrome may be related to oxygen starvation of muscle tissue when the shrimp is pressed to its physiological tolerance limits for high or low temperatures or hyperkinetic muscular activity. The white appearance of the shrimp abdomen caused by spontaneous muscle necrosis should not be confused with "cotton" shrimp which are infected by microsporidan parasites (diffential diagnosis depends on finding spores of Microsporida in whitened tissue).

Gas Bubble Disease

Lightner et al. (1974) reported that juvenile brown shrimp developed a disease characterized by the presence of many small and large bubbles of gas in gill and other tissues. This condition was related to heated water in which the shrimp were held and from which excess gas was not allowed to escape. These authors pointed out the potential threat of gas bubble disease to shrimp held in culture situations utilizing heated water. The extent of the threat of this disease in penaeid culture is unknown. This syndrome has not been reported in feral shrimp, but is a well-known disease in salmonid fishes that contact waters of varying temperatures and gaseous supersaturation.

"Shell Disease" and Black Gills

Blackened, pitted, and eroded exoskeleton is not uncommon in many decapod crustaceans as previously stated. These degenerative changes in cuticles of crabs, lobsters, and shrimps have been termed collectively "shell disease" (Rosen 1970). Lesions ranging from tiny, pinhead-size black holes in the cuticle to massive blackened, eroded area of the cuticle (Figure 6) are often observed in penaeid shrimps. Rosen (1970) reports that the disease is definitely contagious, but the identification of the infectious agents is not known for most species of decapods (see section on Bacteria, under Infectious Diseases). He believes that the necrotic pits in the cuticle act as "miniature niches" for several taxonomic groups of chitinoclastic microbes (bacteria and fungi). The only successful demonstration that chitinoclastic bacteria caused the disease was that of Bright et al.[15]. They isolated bacteria from lesions on Alaskan king crabs and introduced them into mechanical abrasions on healthy king crab and shell disease developed.

"Shell disease" may have many different causes in different species of crustaceans. Couch (1977) and Lightner (pers. commun.) found that blackening necrosis of gill tissues in pink shrimp (see Toxic Response Section—Cadmium), as well as blackened cuticular lesions occurred in shrimp exposed to cadmium, suggest that high concentrations of some heavy metals may cause a form of shell disease.

[15]Bright, D. B., F. E. Durham, and J. W. Knudsen. 1960. King crab investigations of Cook Inlet, Alaska. Unpubl. contract rep., Allen Hancock Found., Univ. South. Calif., Los Ang. to BCF Biol. Lab., Auke Bay, Alaska. Available Northwest and Alaska Fisheries Center Auke Bay Laboratory, Natl. Mar. Fish. Serv., NOAA, P.O. Box 155, Auke Bay, AK 99821.

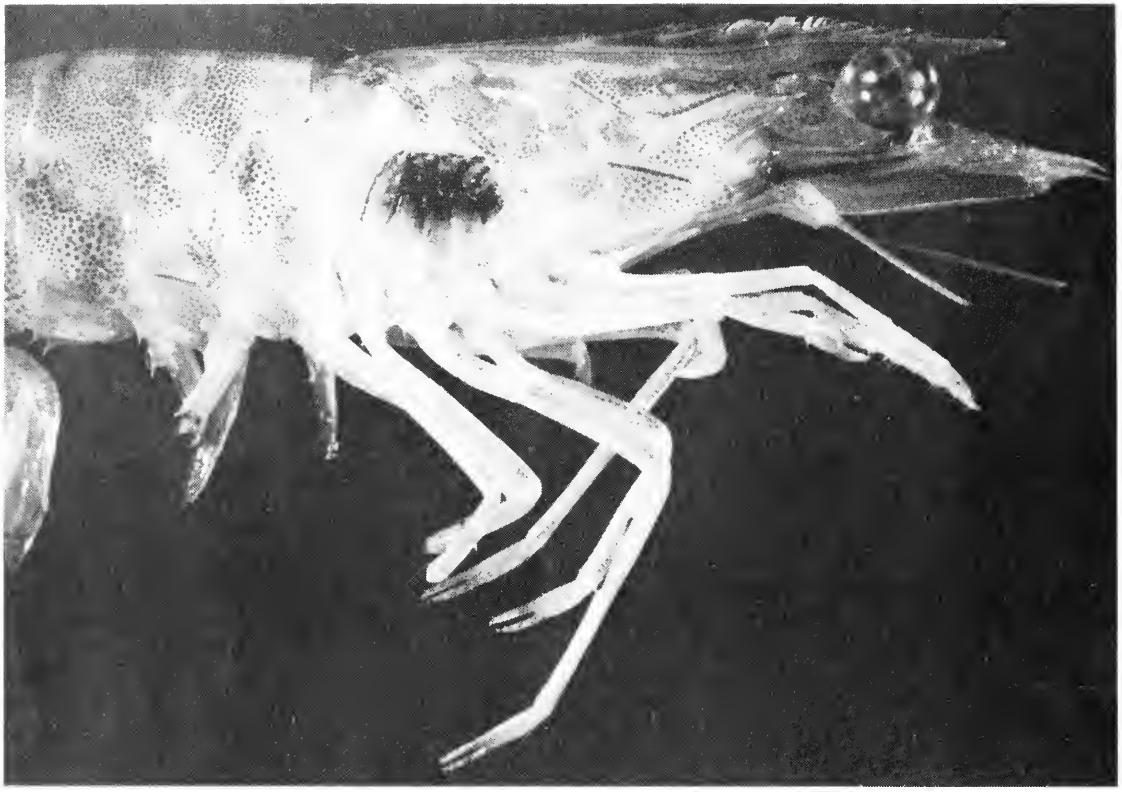


FIGURE 45.—Black gill in feral shrimp not exposed to any known pollutant; grossly resembles cadmium-associated black gill syndrome.

Black gills are often observed in shrimp taken from natural populations (Figure 45). Grossly, the black gills of feral shrimp and those of shrimp experimentally exposed to cadmium are indistinguishable. The cause of black gills in feral penaeids is unknown, but I have found shrimp heavily infested with apostome ciliate phoronts to have considerable areas of black gill. Therefore, black gill has been associated with heavy metal exposure, protozoan infestation, and with fungal infection (*Fusarium:* Solangi and Lightner 1976), suggesting multiple causes. Probably, any injury that causes death of cells in gills of shrimp could cause some form of blackened gill due to necrotic tissues, and, perhaps, melanization.

Broken-Back Syndrome

Shrimp suffering from severe salinity, cold temperature, and handling stresses in combination, display a characteristic dorsal separation of the pleural plates covering the third and fourth abdominal segments (Figure 46). This results in bulging of muscle through the separation. I have observed this in 100% of 1,800 captive pink shrimp dying from a sudden drop in salinity (15-18‰ to 3‰) combined with cold water (8°C). The separation of cuticular plates and bulging of muscle apparently results from uptake of water and severe flexures of the abdomen in shrimp attempting to escape unfavorable conditions.

OVERVIEW AND FUTURE RESEARCH

Some major problem areas in our knowledge of penaeid shrimp diseases become apparent in a review such as this. Although considerable parasitology has been done for penaeid shrimps, new protozoan and worm parasites, some pathogenic, continue to be found. Until recently no viruses were reported for shrimp; now at least one is known. Mycology and bacteriology have yet to contribute in major ways to our understanding of penaeid shrimp diseases and health. Relatively

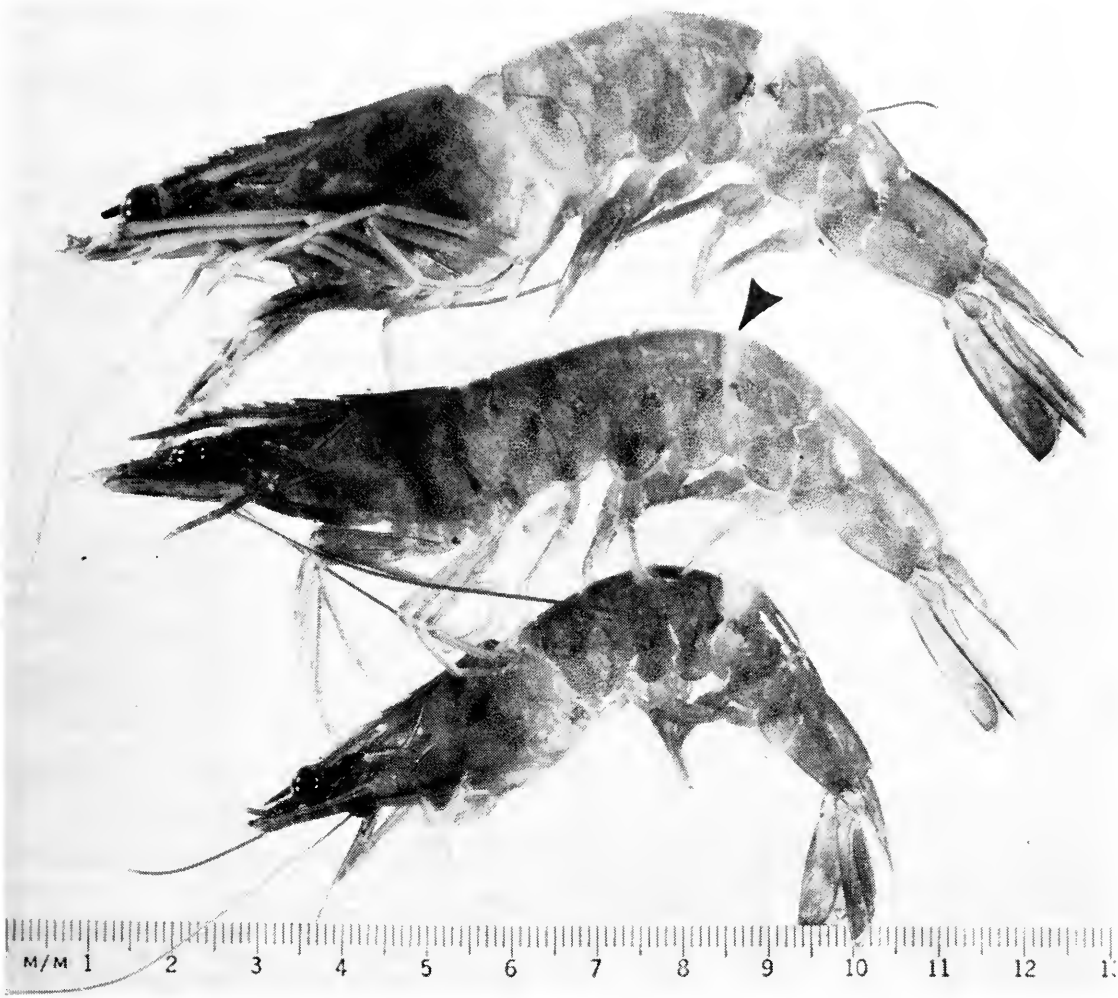


FIGURE 46.—Pink shrimp from mortality related to salinity drop and cold-water temperatures; note dorsal region between third and fourth pleural plates where muscle is protruding. Middle shrimp was still alive when photo was taken; note beginning break in dorsal cuticle (arrow). Top and bottom shrimp died just prior to photograph.

little is known of the toxic responses of penaeids to such environmentally abundant pollutants as oil, oil products, pesticides, heavy metals, industrial chemicals, and domestic sewage. The question of acquisition of resistance to infectious disease or toxicants in penaeid shrimps is unanswered. There is a pressing need to begin detailed studies of pathogenesis of disease and mechanisms of pathogenesis.

With the knowledge that penaeid shrimps have cosmopolitan distribution comes the realization that the disease problems of so narrow an area as encompassed in the review merely hint at the vastness of the potential problems of shrimp diseases worldwide. This is not the case for many other decapod Crustacea which have relatively restricted ranges (i.e., *Homarus americanus, Callinectes sapidus*) and which do not assume the worldwide commercial value of penaeid shrimps.

The old truisms concerning crowding of large numbers of penaeid shrimps in mariculture attempts and rapid spread of infectious diseases still apply as future problems to be studied. Along with this, continual need for better chemotherapeutic agents and an understanding of their effects on penaeid shrimps is apparent.

Because penaeid shrimps are components in the human food chain (wherein man is the final con-

sumer), a better knowledge of their accumulative, metabolic, and storage abilities of toxicants, particularly carcinogenic chemicals, from the environment is needed to safeguard human health as well as shrimp health. Penaeid shrimps are known to be very sensitive to certain classes of chemical pollutants such as organochlorines and heavy metals (e.g., cadmium) and, therefore, should be utilized more in the future as indicator organisms in environmental quality studies.

ACKNOWLEDGMENTS

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ESTIMATING NATURAL AND FISHING MORTALITIES OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE OCEAN, BASED ON RECOVERIES OF MARKED FISH

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ABSTRACT

In this paper I demonstrate the method of calculating estimates of fishing mortality (F) and natural mortality (M) occurring in the ocean for 1961 and 1962 brood Columbia River hatchery fall chinook salmon, *Oncorhynchus tshawytscha*, based on assumed values of the proportion of fish that mature annually (m) and on recoveries of marked fish.

The advantages of this method over the method of assuming fixed natural mortality rates and back calculating estimates are discussed. It was possible to develop estimates of 1962 Spring Creek data up to the fourth year of life and to compare these estimates with values for the 1961 brood whereas no estimates had been possible with the back calculation method. Thus, estimates of M_1 are higher for the 1962 brood; estimates of M_2 are very similar for the two broods and the estimates of M_3 are slightly higher for the 1962 brood. A major difference between the two methods is that natural mortality was assumed to be constant for the back calculation method whereas estimates of natural mortality were obtained separately each year using assumed proportions maturing. Thus, for the 1962 brood general marked fish, an $M = 0.60$ was used in the back calculation method while estimates of $M_1 = 5.814$, $M_2 = 0.510$, $M_3 = 0.653$, and $M_4 = 0.727$ were obtained by assuming varying proportions maturing.

A series of graphs are developed that permit a quick analysis of any combination of proportions of fish maturing, fishing mortality, and natural mortality and which clearly depict the relationship between these various factors.

Cleaver (1969) developed a method for estimating fishing mortalities and percentages of maturing fish for each age group of fall chinook salmon, *Oncorhynchus tshawytscha*,[2] from the Columbia River using selected values of natural mortality. Cleaver's estimates were based on data obtained from a cooperative marking experiment by fishery agencies along the Pacific Coast. This experiment started in 1962 and was designed to measure the contribution of fall chinook salmon from Columbia River hatcheries to the various fisheries. Cleaver's analysis was specifically directed towards returns for the 1961 brood year. The procedure used catches and escapements, by age, along with selected natural mortality values to back calculate, from year 5 to year 2, annual estimates of fishing mortality and proportion of fish that mature annually.

Henry (1971) utilized Cleaver's method to obtain similar estimates for the 1962 brood releases of Columbia River hatchery fall chinook salmon.

Lander and Henry (1973), in analyzing returns from marking experiments for Columbia River coho salmon, *O. kisutch*, pointed out two methods for estimating the various pertinent parameters mentioned above from salmon mark/recovery data: 1) assume selected values for M (natural mortality) and 2) assume selected values for m (proportion maturing).

Although both methods gave identical estimates of the parameters, their concepts differ. In selecting a value for natural mortality, as was done by Cleaver (1969) and Henry (1971), one has to start at the end of the life cycle and work backwards since the calculated parameters are sequentially dependent in that manner (Cleaver and Henry also assumed a constant M for all ages to simplify computations); by selecting values for the proportion of fish that mature annually, one begins at the younger age-groups and calculates the various parameters sequentially towards the end of the life cycle. This method more closely parallels the actual life history of the salmon. Furthermore, today's salmon management schemes are directed at preserving existing runs and their fisheries, i.e., changing diets, releasing fish at different times and at different sizes, transporting fish to avoid

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[2]Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall depending on the time of year that the adults enter the river to spawn.

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excessive mortalities (related to passage at dams and unfavorable environmental conditions caused by dams and reservoirs), or transporting fish to make a more direct input to a certain fishery. All of these efforts may affect the maturity, growth, fishing mortality, and the natural mortality for a particular stock of fish. In this paper, I describe a method by which such changes can be accounted for in the estimating procedure as soon as they are determined. Thus, the present method reduces the need for assumptions regarding constancy of natural mortality in salmon stocks, and the results may be more realistic, particularly if the maturity values selected are reasonable.

In discussing their method of selecting values for the proportion of fish that mature annually and then calculating the remaining parameters for coho salmon, Lander and Henry (1973) pointed out that the procedure also could be applied to chinook salmon, although they also noted that ". . . this gets to be very complicated to display graphically . . . .", since coho salmon have a much simpler life history than fall chinook salmon—m (proportion of fish that mature annually), M (natural mortality), and F (fishing mortality) need to be estimated for 1 yr only for each brood of coho salmon, but these parameters need to be estimated for three separate years for each brood of chinook salmon. Furthermore, the estimated values from this method are quite complicated to apply to chinook salmon. In fact for each m_1 (the subscript represents the different years of life covered by the calculations) value selected, there is a series of possible m_2 values, and for each of the possible m_2 values there is again a series of possible m_3 values. Thus, if n separate calculations are made for each m_i, and there are three of them, as for the chinook salmon, the total calculations potentially needed for a brood year would be $n_1 + n_2{}^2 + n_3{}^3$.

METHOD OF ESTIMATING PARAMETERS

In this paper I demonstrate the method of calculating estimates of fishing mortality (F) and natural mortality (M) based on assumed values of the proportion of fish that mature annually (m) for the 1961 and 1962 brood Columbia River fall chinook salmon. In particular, I compare data for the 1961 and 1962 broods of Spring Creek fish.

To aid in understanding the various parameters I estimate, in Figure 1 I have portrayed graphically certain features of the fall chinook salmon's life history, particularly the various parameters for the period from the release of the fish as smolts until final return to the Columbia River as adults—approximately 54 mo.

Figure 1 shows that as a result of this series of events, I end up with eight items of observed data: 1) number of smolts released (N_0); 2) number maturing as 2-yr-olds (E_1); 3) number caught by the ocean troll and sport fisheries as 3-yr-olds (C_1); 4) number maturing and returning to the river as 3-yr-olds (E_2); 5) number caught by the ocean troll and sport fisheries as 4-yr-olds (C_2); 6) number maturing and returning to the river as 4-yr-olds (E_3); 7) number caught by the ocean troll and sport fisheries as 5-yr-olds (C_3); and 8) number maturing and returning to the river as 5-yr-old fish (E_4). From these eight known values I want to estimate: 1) monthly fishing mortality rate on 3-, 4-, and 5-yr-old fish (F_1, F_2, and F_3, respectively) over the last 6-mo period of each year; 2) monthly natural

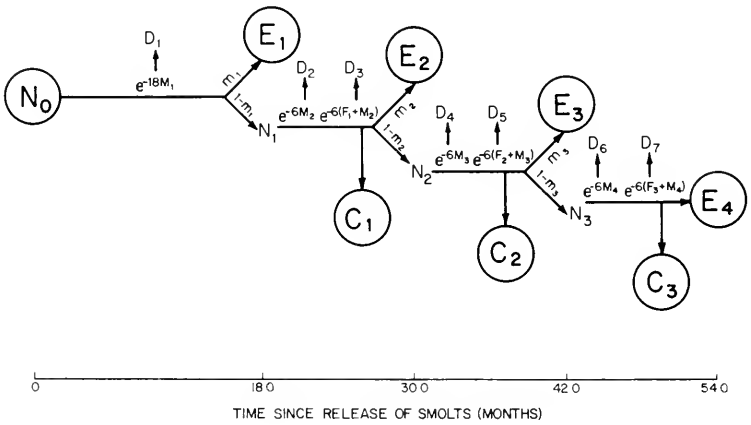

FIGURE 1.—Diagram depicting the life history of Columbia River fall chinook salmon for the period from release as smolts until their return to the Columbia River as adults—approximately 54 mo. Circled items indicate observed data. See text for identification of lettered symbols.

TABLE 1.—Estimated total recoveries of marked Columbia River hatchery fall chinook salmon of the 1961-62 broods.

	1962 Brood			1961 Brood		
	General mark	Spring Creek	Kalama	General mark	Spring Creek	Kalama
E_1	94	18	7	272	68	0
C_1	3,565	376	293	10,774	2,511	696
E_2	1,597	321	29	4,451	934	51
C_2	1,416	150	190	3,373	367	761
E_3	936	120	84	4,849	833	575
C_3	126	14	31	442	5	115
E_4	45	0	15	280	20	160
N_0	5,249,079	866,892	437,669	5,446,439	1,133,019	475,964

mortality rate for the 18-mo period from release as smolts until the mature 2-yr-old fish return to the river (M_1); 3) monthly natural mortality rates for each year as 3-, 4-, and 5-yr-old fish (M_2, M_3, and M_4, respectively); and 4) proportion maturing as 2-, 3-, and 4-yr-old fish (m_1, m_2, and m_3, respectively). A few of these fish are caught as 2-yr olds; however, to avoid further complicating the analyses I have included these in the estimate of M_1 for the first 18 mo at sea. The number of chinooks remaining at sea at the start of each year (N_1, N_2, and N_3) also can be calculated, but since this had already been done for certain parameters by Henry (1971), the calculations will not be repeated here. The D_i's shown represent the number of fish dying naturally. Thus, the entire initial group of smolts (N_0) is either caught (C), escapes into the river (E), or dies naturally (D), by the time $i = 7$. The fishing season runs generally from mid-April to mid-October.

Mark recovery data used in this paper are listed in Table 1. Catches of marked fish are estimates based on sampling (see Worlund et al. 1969). Each escapement is the total number of fish returning to the river and includes the river catch and returns to the hatchery for a given mark.

To expand the analysis used by Lander and Henry (1973) from coho salmon to chinook salmon, the events in Figure 1 can be depicted by a multinominal model with N_0 smolts falling into the following seven observed categories with certain probabilities O_i (i = 1-8) as follows:

Probabilities of

$$E_1 = \theta_1 = m_1 e^{-18M_1}. \tag{1}$$

$$C_1 = \theta_1 = (1-m_1)e^{-18M_1}e^{-6M_2}\frac{F_1}{F_1+M_2}(1-e^{-6(F_1+M_2)}). \tag{2}$$

$$E_2 = \theta_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-(F_1+M_2)}m_2. \tag{3}$$

$$C_2 = \theta_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)e^{-6M_3}\frac{F_2}{F_2+M_3}(1-e^{-6(F_2+M_3)}). \tag{4}$$

$$E_3 = \theta_5 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)\ e^{-6M_3}e^{-6(F_2+M_3)}m_3. \tag{5}$$

$$C_3 = \theta_6 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)$$
$$e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}\frac{F_3}{F_3+M_4}(1-e^{-6(F_3+M_4)}). \tag{6}$$

$$E_4 = \theta_7 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}(1-m_2)$$
$$e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)}. \tag{7}$$

$$D = \theta_8 = 1-\theta_1-\theta_2-\theta_3-\theta_4-\theta_5-\theta_6-\theta_7$$

where $D = D_1+D_2+D_3+D_4+D_5+D_6+D_7$ = Total fish dying naturally. (8)

The maximum likelihood estimators of the θ_i are:

$$\hat{\theta}_1 = E_1/N_0 \quad (9)$$

$$\hat{\theta}_2 = C_1/N_0 \quad (10)$$

$$\hat{\theta}_3 = E_2/N_0 \quad (11)$$

$$\hat{\theta}_4 = C_2/N_0 \quad (12)$$

$$\hat{\theta}_5 = E_3/N_0 \quad (13)$$

$$\hat{\theta}_6 = C_3/N_0 \quad (14)$$

$$\hat{\theta}_7 = E_4/N_0 \quad (15)$$

$$\hat{\theta}_8 = 1-\theta_1-\theta_2-\theta_3-\theta_4-\theta_5-\theta_6-\theta_7. \quad (16)$$

A maximum likelihood estimator of a function of the parameters θ_i is obtained by replacing the parameter values by the corresponding maximum likelihood estimates, θ_i (Graybill 1961). Beyond that, however, there exists no unique transformation, or function, to obtain maximum likelihood estimates of $m_1, m_2, m_3, F_1, F_2, F_3, M_1, M_2, M_3$, and M_4. Any given set of observed data can generate a variety of combinations of parameter estimates.

Since no unique solution exists, the only practical solution is to assume values for one of the unknown parameters and solve the equations for the remaining parameters. Thus Cleaver (1969) and Henry (1971) assumed values for M_i (natural mortality) for hatchery chinook salmon and calculated values for the remaining parameters. However, they assumed M to be constant (M_1) throughout the life of the salmon to simplify computations. Lander and Henry (1973), on the other hand, assumed values for m (proportion of fish that mature annually) for coho salmon and then calculated the remaining parameters.

Assuming fixed values for the proportion of fish that mature annually (m_i) permits a unique solution to Equations (1)-(8), combined with Equations (9)-(16), so that with:

$$m_1 = m_1 \text{ (fixed) } (\hat{\theta}_1 < m_1 < 1). \quad (17)$$

$$m_2 = m_2 \text{ (fixed) } (\hat{\theta}_3 < m_2 < 1). \quad (18)$$

$$m_3 = m_3 \text{(fixed) } (\hat{\theta}_5 < m_3 < 1). \quad (19)$$

$$M_1 = -\frac{1}{18} \ln \frac{\hat{\theta}_1}{m_1}. \quad (20)$$

$$\frac{\ln k_2+12M_2}{\ln k_2+6M_2}\left(1-e^{\ln k_2+6M_2}\right)e^{-6M_2} = k_1 \quad (21)$$

where $k_1 = \dfrac{\hat{\theta}_2}{1-m_1} e^{18M_1}$

$$k_2 = \frac{\hat{\theta}_3}{(1-m_1)m_2} e^{18M_1}$$

$$F_1 = -\frac{\ln k_2+12M_2}{6}. \quad (22)$$

$$k_2 e^{-6M_3} \frac{\ln k_4-\ln k_2+12M_3}{\ln k_4-\ln k_2+6M_3}$$

$$\left(1-e^{\ln k_4-\ln k_2+6M_3}\right) = k_3 \quad (23)$$

where $k_3 = \dfrac{\hat{\theta}_4}{(1-m_1)(1-m_2)} e^{18M_1}$

$$k_4 = \frac{\hat{\theta}_5}{(1-m_1)(1-m_2)m_3} e^{18M_1}.$$

$$F_2 = -\frac{\ln k_4-\ln k_2+12M_3}{6}. \quad (24)$$

$$k_4 e^{-6M_4} \frac{\ln k_6-\ln k_4+12M_4}{\ln k_6-\ln k_4+6M_4}$$

$$\left(1-e^{\ln k_6-\ln k_4+M_4}\right) = k_5 \quad (25)$$

where $k_5 = \dfrac{\hat{\theta}_6}{(1-m_1)(1-m_2)(1-m_3)} e^{18M_1}$

$$k_6 = \frac{\hat{\theta}_7}{(1-m_1)(1-m_2)(1-m_3)} e^{18M_1}.$$

$$F_3 = -\frac{\ln k_6-\ln k_4+12M_4}{6}. \quad (26)$$

The derivations of Equations (17)-(26) are verified in the Appendix. For a particular value of m_1 (Equation (17)), one solves Equation (20) explicitly for M_1. Then using these values of m_1 and M_1 plus a selected value for m_2 in Equation (18), M_2 in Equation (21) is found by iteration. Then F_1 is computed from Equation (22). Next, for a particular value of m_3 in Equation (19) plus the other values already determined, M_3 in Equation

(23) is found by iteration, and F_2 is calculated from Equation (24). Finally, M_4 in Equation (25) is found by iteration and F_3 is calculated from Equation (26).

In developing the computer program to do the above computations, I assigned a beginning value of 0.001 to m_1 and then computed the smallest m_2 possible that would give me nonnegative values for all the M's and F's. For these particular values of m_1 and m_2, I then incremented m_3 over a range of values as long as $m_3 < 1$ or the M_3, M_4, F_2, and F_3 values were nonnegative. The program would then go back and increment m_2 and compute another series of m_3 values and dependent parameters. When m_2 was incremented to a level where $m_2 = 1$ or that would no longer give positive values for either M_3, M_4, F_2, or F_3, the program would increment m_1 and the process would begin again. A sample of the printout for selected values is shown in Table 2.

COMPARISON OF TWO METHODS

To assist in comparing the results from: 1) assuming a given value for M_i (natural mortality) or 2) assuming given values for each m_i (proportion of fish that mature each year), I have listed in Table 3 the results for the 1962 brood data for the general marked fish based on assuming a given m. (The R_i shown in the table are equivalent to the N_i discussed in this paper.) One difficulty in making these comparisons is that the results from the two methods appear in quite different form. In Table 3, there are six lines of estimated values for six different levels of M. On the other hand, by assuming fixed values of m_i for the same data for the fish in the general mark category, the complete printout of results has a total of 48 groups of data, similar to the selected 10 groups shown in Table 2. Of course, the number of groups of data by the latter method is dependent on just how the m_i's are incremented.

One obvious difference in the two sets of results is that Table 3 (assuming fixed M) was computed using a single constant value for the M_i, whereas Table 2 (assuming fixed m_i) had separate estimates for each M_i. Although an exact comparison of the results is not possible since I did not use exactly the same m_i as shown in Table 3, many of my results are close enough to make useful comparisons. For example, for $M = 0.60$ in Table 3, I calculated $F_3 = 1.275, F_2 = 0.698, F_1 = 0.410, m_3 = 0.761, m_2 = 0.262$ and $m_1 = 0.006$. From Table 2 we can select values of m_i that are fairly comparable, i.e., $m_1 = 0.006$, $m_2 = 0.256$, $m_3 = 0.756$, which gives $F_1 = 0.405, F_2 = 0.669$ (0.11143 × 6), $F_3 = 1.177$ (0.19614 × 6) (F's are summed over 6 mo).

The major difference between the two sets of results is the natural mortality estimates with $M_1 = 5.814, M_2 = 0.510, M_3 = 0.653$, and $M_4 = 0.727$ (M_1 is summed over 18 mo, $M_{2\text{-}4}$ summed over 12 mo) from my calculations using estimates for the proportion of fish that mature annually compared with the $M = 0.60$ in Table 3. The comparatively large natural mortality in the first 18 mo of existence is not too surprising; however, the increasing values for M from M_2 to M_4 do not seem reasonable. Since the natural mortality values listed include the loss of "shakers" (fish released by fishermen because they are too small or out of season), one would expect the M_2 value to be largest because this is the time these fish would be most vulnerable to shaker losses. Estimates of shaker mortality have ranged from 15 to 45% (Wright[3]).

What these increasing estimates of M_i indicate is that the m_i's selected in this comparison are not realistic—m_i values for which the M_i's are at least equal, or even decreasing with increased age might be better. Although the relation shown between these values will vary depending on the value of m_2 (the M_3 value computed for a given m_3 value decreases as m_2 increases), at a certain value of m_3 or above, $M_4 \leq M_3$.

The relationship between the various parameters computed are shown more clearly in Figures 2-5 for the 1961 brood Spring Creek data. Thus, in Figure 2 is shown the relation between m_1 and M_1. As m_1 increases, M_1 also increases but at a diminishing rate. In Figure 3 is depicted the relation between F_1 and F_2 and m_1, m_2, and m_3. F_1 is affected by both the m_1 and m_2 values selected, whereas F_2 reacts to both the m_2 and m_3 values chosen. Both F_1 and F_2 increase as m_2 increases for a particular value of m_1 or m_3. Also, for a given value of m_2, both F_1 and F_2 increase with increasing m_1 and m_3 values, respectively. In Figure 4 is shown the relation between M_2 and M_3 for selected values of m_1, m_2, and m_3. With increasing m_2, M_2 increases but M_3 decreases. For a given m_2, M_3 increases with increasing m_3, and M_2 decreases with increasing m_1. Finally, in Figure 5 is shown

[3]Wright, S. 1970. A review of the subject of hooking mortalities in Pacific salmon. Wash. Dep. Fish., Manage. Res. Div., 38 p. (Report, prepared for the Salmon Research Staff of the Pacific Marine Fisheries Commission.)

TABLE 2.—Partial computer output for program designed to calculate fishing mortalities (F) and natural mortalities (M) for selected values of proportions of fish maturing (m)—1962 brood general marked Columbia River hatchery fall chinook salmon.

m_3	M_3	F_2	M_4	F_3	m_3	M_3	F_2	M_4	F_3
m_1 = 0.001000	M_1 = 0.22347	m_2 = 0.20999	M_2 = 0.01389	F_1 = 0.00735	m_1 = 0.003000	M_1 = 0.28450	m_2 = 0.106000	M_2 = 0.04519	F_1 = 0.03113
0.016000	0.01819	0.00378	0.57439	0.04353	0.121000	0.03339	0.02562	0.37489	0.08652
0.066000	0.13289	0.01056	0.43839	0.07066	0.171000	0.05879	0.03247	0.33569	0.09751
0.116000	0.17739	0.01555	0.37949	0.08530	0.221000	0.07709	0.03862	0.30449	0.10680
0.166000	0.20509	0.01988	0.33919	0.09646	0.271000	0.09119	0.04441	0.27779	0.11515
0.216000	0.22509	0.02376	0.30739	0.10586	0.321000	0.10269	0.04963	0.25389	0.12288
0.266000	0.24079	0.02706	0.28029	0.11439	0.371000	0.11229	0.05456	0.23169	0.13041
0.316000	0.25349	0.03037	0.25619	0.12212	0.421000	0.12059	0.05903	0.21059	0.13773
0.366000	0.26429	0.03325	0.23389	0.12959	0.471000	0.12769	0.06353	0.18999	0.14518
0.416000	0.27349	0.03620	0.21269	0.13696	0.521000	0.13409	0.06755	0.16959	0.15261
0.466000	0.28169	0.03871	0.19209	0.14432	0.571000	0.13969	0.07162	0.14879	0.16057
0.516000	0.28889	0.04130	0.17159	0.15195	0.621000	0.14479	0.07541	0.12729	0.16892
0.566000	0.29539	0.04371	0.15089	0.15976	0.671000	0.14939	0.07912	0.10449	0.17804
0.616000	0.30129	0.04602	0.12949	0.16805	0.721000	0.15369	0.08250	0.07969	0.18818
0.666000	0.30659	0.04843	0.10689	0.17700	0.771000	0.15759	0.08587	0.05179	0.19989
0.716000	0.31159	0.05050	0.08229	0.18710	0.821000	0.16119	0.08915	0.01889	0.21416
0.766000	0.31619	0.05255	0.05479	0.19858	0.871000	0.16449	0.09240	0.00000	0.21416
0.816000	0.32039	0.05468	0.02249	0.21257					
0.866000	0.32439	0.05660	0.00000	0.21257					
m_1 = 0.001000	M_1 = 0.22347	m_2 = 0.071000	M_2 = 0.11029	F_1 = 0.01758	m_1 = 0.006000	M_1 = 0.32301	m_2 = 0.256000	M_2 = 0.04249	F_1 = 0.06746
0.096000	0.05379	0.01944	0.39969	0.08017	0.306000	0.00329	0.06289	0.26079	0.12070
0.146000	0.08549	0.02592	0.35389	0.09241	0.356000	0.01259	0.06951	0.23819	0.12822
0.196000	0.10709	0.03180	0.31939	0.10227	0.406000	0.02039	0.07582	0.21679	0.13564
0.246000	0.12339	0.03707	0.29069	0.11110	0.456000	0.02719	0.08157	0.19619	0.14263
0.296000	0.13649	0.04171	0.26559	0.11902	0.506000	0.03309	0.08711	0.17569	0.15042
0.346000	0.14719	0.04632	0.24259	0.12673	0.556000	0.03829	0.09242	0.15509	0.15813
0.396000	0.15639	0.05042	0.22099	0.13418	0.606000	0.04289	0.09757	0.13389	0.16627
0.446000	0.16429	0.05444	0.20029	0.14136	0.656000	0.04709	0.10236	0.11149	0.17523
0.496000	0.17129	0.05815	0.17979	0.14889	0.706000	0.05099	0.10683	0.08739	0.18501
0.546000	0.17749	0.06175	0.15919	0.15667	0.756000	0.05439	0.11143	0.06059	0.19614
0.596000	0.18309	0.06516	0.13819	0.16462	0.806000	0.05759	0.11570	0.02939	0.20965
0.646000	0.18809	0.06858	0.11609	0.17337	0.856000	0.06059	0.11974	0.00000	0.20965
0.696000	0.19269	0.07181	0.09239	0.18297					
0.746000	0.19699	0.07477	0.06619	0.19386					
0.796000	0.20089	0.07778	0.03609	0.20671					
0.846000	0.20459	0.08054	0.00000	0.20671					
m_1 = 0.00100	M_1 = 0.22347	m_2 = 0.371000	M_2 = 0.23059	F_1 = 0.05256	m_1 = 0.009000	M_1 = 0.34554	m_2 = 0.361000	M_2 = 0.02449	F_1 = 0.09267
0.751000	0.00159	0.12610	0.06339	0.19503	0.686000	0.00159	0.11820	0.09729	0.18097
0.801000	0.00449	0.13105	0.03279	0.20813	0.736000	0.00489	0.12332	0.07169	0.19154
0.851000	0.00719	0.13574	0.00000	0.20813	0.786000	0.00789	0.12828	0.04259	0.20379
					0.836000	0.01069	0.13296	0.00759	0.21916
					0.886000	0.01329	0.13744	0.00000	0.21916
m_1 = 0.00200	M_1 = 0.26198	m_2 = 0.086000	M_2 = 0.06509	F_1 = 0.02423	m_1 = 0.010000	M_1 = 0.35139	m_2 = 0.326000	M_2 = 0.00889	F_1 = 0.08914
0.106000	0.04349	0.02190	0.38919	0.08280	0.541000	0.00449	0.09871	0.16129	0.15583
0.156000	0.07229	0.02870	0.34639	0.09440	0.591000	0.00909	0.10424	0.14029	0.16387
0.206000	0.09249	0.03464	0.31329	0.10409	0.641000	0.01329	0.10937	0.11839	0.17240
0.256000	0.10779	0.04026	0.28549	0.11263	0.691000	0.01699	0.11449	0.09489	0.18189
0.306000	0.12019	0.04519	0.26079	0.12070	0.741000	0.02039	0.11934	0.06899	0.19263
0.356000	0.13049	0.04982	0.23819	0.12822	0.791000	0.02339	0.12422	0.03939	0.20519
0.406000	0.13919	0.05432	0.21679	0.13564	0.841000	0.02629	0.12863	0.00359	0.22101
0.456000	0.14679	0.05848	0.19619	0.14283	0.891000	0.02889	0.13306	0.00000	0.22101
0.506000	0.15349	0.06242	0.17569	0.15042					
0.556000	0.15949	0.06612	0.15509	0.15813					
0.606000	0.16479	0.06987	0.13389	0.16627					
0.656000	0.16969	0.07329	0.11149	0.17523					
0.706000	0.17419	0.07653	0.08739	0.18501					
0.756000	0.17829	0.07973	0.06059	0.19614					
0.806000	0.18209	0.08281	0.02939	0.20965					
0.856000	0.18559	0.08584	0.00000	0.20965					
m_1 = 0.002000	M_1 = 0.26198	m_2 = 0.336000	M_2 = 0.16069	F_1 = 0.06016	m_1 = 0.010000	M_1 = 0.35139	m_2 = 0.376000	M_2 = 0.01659	F_1 = 0.09752
0.551000	0.00119	0.10083	0.15719	0.15730	0.761000	0.00010	0.12775	0.05769	0.19739
0.601000	0.00569	0.10631	0.13599	0.16555	0.811000	0.00299	0.13255	0.02599	0.21107
0.651000	0.00969	0.11163	0.11379	0.17431	0.861000	0.00559	0.13732	0.00000	0.21107
0.701000	0.01329	0.11676	0.08989	0.18401					
0.751000	0.01659	0.12164	0.06339	0.19503					
0.801000	0.01959	0.12639	0.03279	0.20813					
0.851000	0.02239	0.13088	0.00000	0.20813					

TABLE 3.—F, m, and R values for general marked fall chinook salmon of the 1962 brood; M is survival for 12 mo and F for 6 mo (adapted from Henry 1971).

Natural mortality	Fishing intensity			Proportion maturing			Recruitment		
M	F_3	F_2	F_1	m_3	m_2	m_1	R_5	R_4	R_3
0.24	1.346	0.781	0.535	0.810	0.332	0.009	220	3,216	10,441
.45	1.304	.733	.460	.783	.290	.007	260	3,912	13,681
.48	1.298	.727	.449	.779	.284	.007	266	4,028	14,238
.60	1.275	.698	.410	.761	.262	.006	293	4,516	16,736
.72	1.251	.671	.372	.743	.240	.005	323	5,076	19,831
.96	1.206	.616	.301	.705	.199	.003	393	6,438	28,320

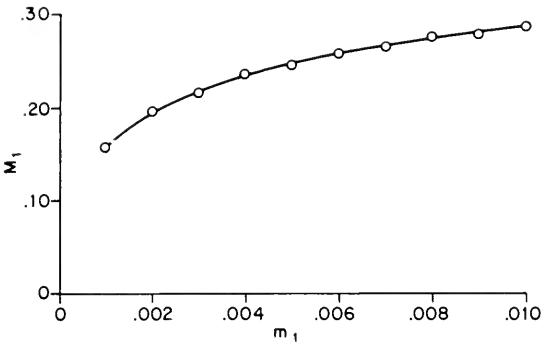

FIGURE 2.—Relation between computed monthly natural mortality (M_1) during the first 18 mo after release as smolts and selected values of proportions of salmon maturing after 18 mo (m_1)—1961 brood of fall chinook salmon from Spring Creek hatchery.

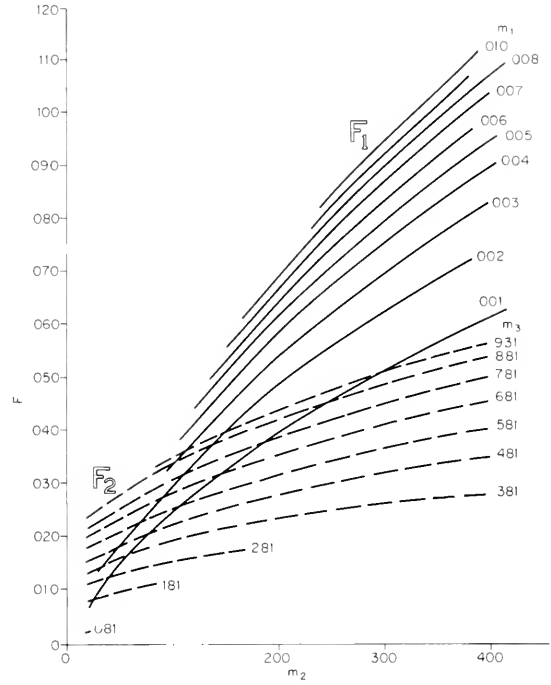

FIGURE 3.—Relations between certain computed monthly ocean fishing mortalities (F_1, F_2) and selected values of proportions of salmon maturing annually (m_1, m_2, m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

the relation between M_4, F_3, and m_3. As the m_3 value increases, F_3 also increases and M_4 decreases. It should be noted that for M_4 values <1.0 (summed over 12 mo), m_3 must be well over 0.800.

Although it is not possible to obtain unique estimates of the various parameters (only a range of estimated values) by selecting either the M_i or the m_i, the detailed relationships between the parameters—based on selecting m_i values—give a very good insight into the effect of each of these values on the other and the interrelationships between them. Furthermore, the graphic presentation of these relationships as shown in this paper permit any assumptions about the various parameters to be quickly examined. For example, to obtain estimates of the various parameters based on Cleaver's (1969) assumption that the M_i (i = 2-4) are equal for the 1961 Spring Creek data, we could go to Figure 5 and observe the m_3 and F_3 values for selected values of M_4.

Next, from Figure 4 for $M_4 = M_3 = M_2$ and the appropriate m_3 values, we could calculate the proper m_2 and m_1 values. Then from Figure 3 for these m_1, m_2, and m_3 values we could determine the proper F_1 and F_2 values and finally from Figure 2, the correct estimate of M_1. Of course, any other assumed relationships between the parameters also can be examined readily from these graphs.

COMPARISON OF 1961 AND 1962 BROOD SPRING CREEK DATA

I have selected the Spring Creek data to discuss in this paper because in my earlier paper (Henry 1971) I stated, "It is unfortunate that no analysis could be made for Spring Creek marks of the 1962 brood." This was due to the fact that there were no fifth year recoveries recorded for the river ($E_4 = 0$),

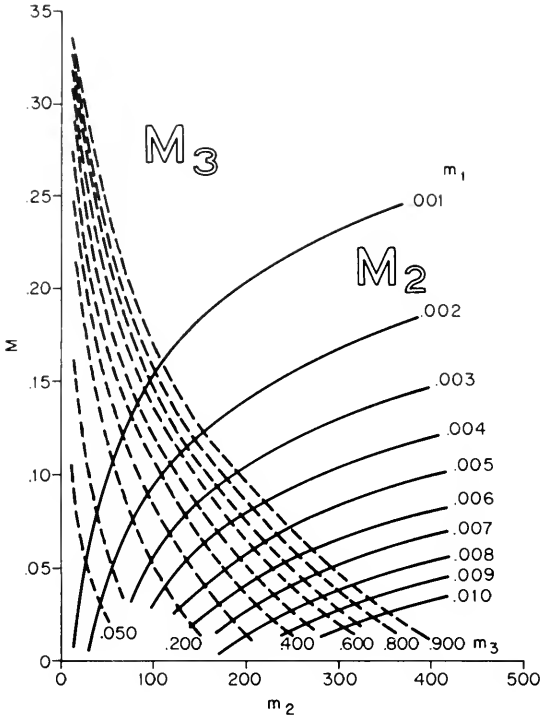

FIGURE 4.—Relations between certain computed monthly natural mortalities (M_2, M_3) and selected values of annual proportions of salmon maturing (m_1, m_2, and m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

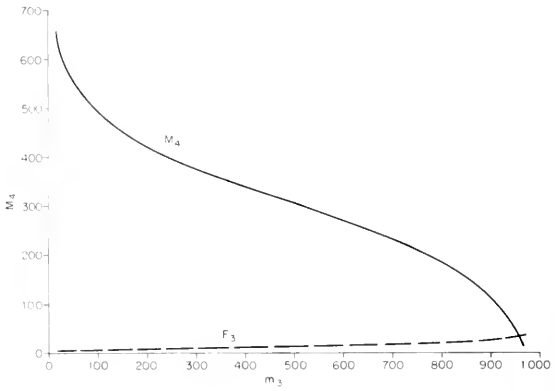

FIGURE 5.—Relations between computed last year of life monthly natural mortality (M_4) and last year of life ocean fishing mortality (F_3) for selected values of proportions of salmon maturing the previous year (m_3)—1961 brood of fall chinook salmon from Spring Creek hatchery.

so back calculations were not possible with the method of assuming a fixed value for M_1. However, by assuming fixed values of m_i and working from the early life history of the salmon onward, it is possible to calculate estimates of the various parameters up to the fifth year.

Although, as previously explained, it is not possible to compute M_4 and F_3 values (for the fifth year) for the 1962 Spring Creek data, estimates of the other parameters are possible. Therefore, the relations between m_1, m_2, m_3 and M_2, M_3, for the 1962 brood, are shown in Figure 6; between m_1, m_2, m_3 and F_1, F_2 in Figure 7; and finally, the relations between m_1 and M_1 are shown in Figure 8 for both the 1961 and 1962 broods.

Since it is now possible to calculate estimates of some of the parameters for the 1962 brood Spring Creek fish, it is interesting to compare some general conclusions I made (Henry 1971) with these estimates. I stated that ". . . the data suggest that the 1962 Spring Creek fish survived and entered the ocean fishery in about the same proportions as Kalama fish (Kalama 0.003, General 0.003) but in much smaller proportions than the 1961 Kalama brood (Kalama 0.011, Spring Creek 0.007)." In other words, I indicated that the first 18 mo of natural mortality after release as smolts for the Spring Creek fish was higher for the 1962 brood than for the 1961 brood. This tentative conclusion is now supported by the data shown in Figure 8 where the M_1 values for the 1961 and 1962 broods of Spring Creek fish are shown. It is apparent that for any given value of m_1, the estimate of M_1 is higher for the 1962 brood and it would require a considerably higher value of m_1 for the 1961 brood, compared with 1962, to have comparable estimates of M_1 for the two broods.

Another tentative conclusion made in my earlier paper, ". . . that the ocean fishery was less intense on the 1962 brood Spring Creek fish . . . ." also can be examined in greater detail with these new calculations. Thus, we see that when the data for the two brood years are compared, for fixed values of m_1, m_2, and m_3 (Table 4), the estimated fishing mortality for the 3-yr-old fish (F_1) from the 1962 brood was about half that for the 1961 brood. However, for the 4-yr-old fish (F_2) the estimated fishing mortality for the 1962 brood was about twice as large as that estimated for the 1961 brood. Since most of the catch was made as 3-yr-old fish (F_1) for both brood years, the overall catch (mortality) was less for the 1962 brood. These relations between the F_1 and F_2 values for the two broods can be more clearly seen by comparing Figure 3 (the 1961 brood) with Figure 7 (the 1962 brood).

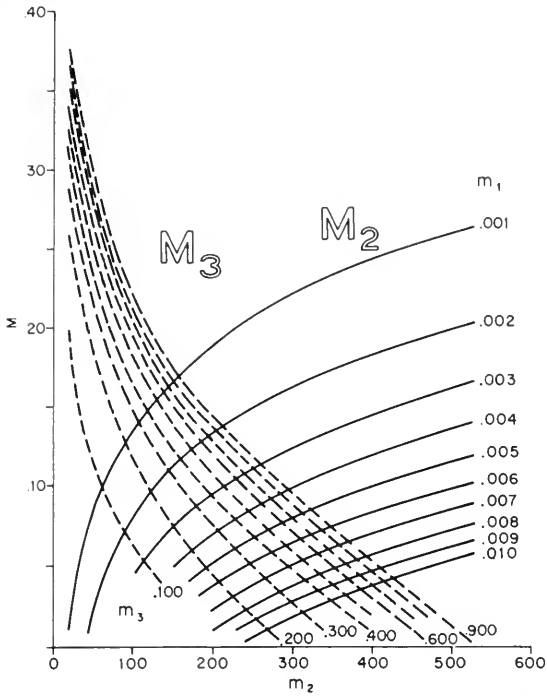

FIGURE 6.—Relations between certain computed monthly natural mortalities (M_2, M_3) and selected values of annual proportions of salmon maturing (m_1, m_2, and m_3)—1962 brood of fall chinook salmon from Spring Creek hatchery.

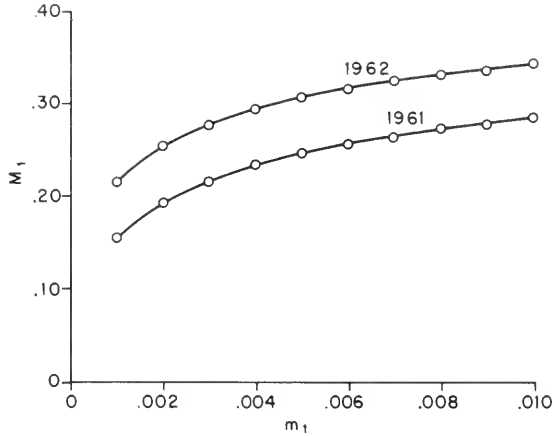

FIGURE 8.—Relations between computed monthly natural mortality (M_1) during the first 18 mo after release as smolts and selected values of proportions of salmon maturing after 18 mo (m_1)—1961 and 1962 broods of fall chinook salmon from Spring Creek hatchery.

TABLE 4.—Comparison of estimates of fishing mortality (F) for the 1961 and 1962 broods of marked fall chinook salmon from Spring Creek hatchery for fixed values of proportion of salmon maturing annually (m).

	1961 brood	1962 brood		1961 brood	1962 brood
m_1	0.001	0.001	m_3	0.600	0.600
m_2	.300	.300	F_2	.037	.078
F_1	.051	.026			

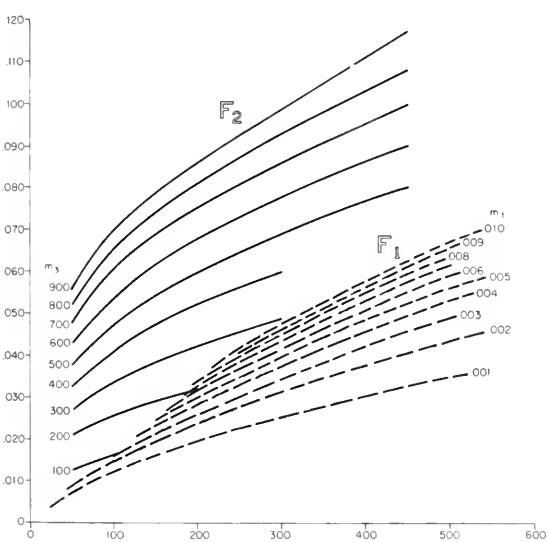

FIGURE 7.—Relations between certain computed monthly ocean fishing mortalities (F_1, F_2) and selected values of proportions of salmon maturing annually (m_1, m_2, and m_3)—1962 brood of fall chinook salmon from Spring Creek hatchery.

Thus, for a given value of m_2, the generally higher F_1 values compared with F_2 for the 1961 brood is quite different from the generally higher F_2 values compared with F_1 for the 1962 brood data shown in Figure 7.

A general comparison between the calculated M_2 and M_3 values can be obtained by comparing Figure 4 with Figure 6. There is considerable similarity between the pattern of mortality estimates for these two broods. In both cases, as m_2 increases, M_2 increases and M_3 decreases. However, for a given m_2 and m_3, the estimates of M_3 are slightly higher for the 1962 brood, whereas for a given m_2 and m_1, the estimates of M_2 are very similar for the two broods.

ACKNOWLEDGMENTS

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APPENDIX

Derivation of Text Equations

As pointed out in the text, the probabilities of

$$E_1\colon\ \theta_1 = m_1 e^{-18M_1}. \tag{1}$$

$$C_1\colon\ \theta_2 = (1-m_1)e^{-18M_1}e^{-6M_2}\ \frac{F_1}{F_1+M_2}\ (1-e^{-6(F_1+M_2)}). \tag{2}$$

$$E_2\colon\ \theta_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}m_2. \tag{3}$$

$$C_2\colon\ \theta_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}\ \frac{F_2}{F_2+M_3}\ (1-e^{-6(F_2+M_3)}). \tag{4}$$

$$E_3\colon\ \theta_5 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}m_3. \tag{5}$$

$$C_3\colon\ \theta_6 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}\ \frac{F_3}{F_3+M_4}\ (1-e^{-6(F_3+M_4)}). \tag{6}$$

$$E_4\colon\ \theta_7 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)}. \tag{7}$$

and maximum likelihood estimates of the θ_i are:

$$\hat{\theta}_1 = \frac{E_1}{N_0} \text{ or } \hat{\theta}_1 = m_1 e^{-18M_1} \text{ from Equation (1).} \tag{8}$$

$$\hat{\theta}_2 = \frac{C_1}{N_0} \text{ or } \hat{\theta}_2 = (1-m_1)e^{-18M_1}e^{-6M_2}\ \frac{F_1}{F_1+M_2}\ (1-e^{-6(F_1+M_2)}) \text{ from Equation (2).} \tag{9}$$

$$\hat{\theta}_3 = \frac{E_2}{N_0} \text{ or } \hat{\theta}_3 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}m_2 \text{ from Equation (3).} \tag{10}$$

$$\hat{\theta}_4 = \frac{C_2}{N_0} \text{ or } \hat{\theta}_4 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}\ \frac{F_2}{F_2+M_3}$$

$$(1-e^{-6(F_2+M_3)}) \text{ from Equation (4).} \tag{11}$$

$$\hat{\theta}_5 = \frac{E_3}{N_0} \text{ or } \hat{\theta}_5 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}\ e^{-6(F_2+M_3)}\ m_3 \text{ from Equation (5).} \tag{12}$$

$$\hat{\theta}_6 = \frac{C_3}{N_0} \text{ or } \hat{\theta}_6 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}e^{-6(F_2+M_3)}\ (1-m_3)e^{-6M_4}$$

$$\frac{F_3}{F_3+M_4}\ (1-e^{-6(F_3+M_4)}) \text{ from Equation (6).} \tag{13}$$

$$\hat{\theta}_7 = \frac{E_4}{N_0} \text{ or } \hat{\theta}_7 = (1-m_1)e^{-18M_1}e^{-6M_2}e^{-6(F_1+M_2)}\ (1-m_2)e^{-6M_3}$$

$$e^{-6(F_2+M_3)}(1-m_3)e^{-6M_4}e^{-6(F_3+M_4)} \text{ from Equation (7).} \tag{14}$$

Then for $m_i = m$ (fixed) $(\theta_1<m_1<1)(\theta_3<m_2<1)(\theta_5<m_3<1)$, text Equations (17) to (19), by rearranging Equation (8) and taking natural logarithms we obtain

$$-1/18 \ln\left(\frac{\hat{\theta}_1}{m_1}\right) = M_1 \text{ (text Equation (20)).}$$

Then Equation (10) can be rewritten as

$$\frac{\hat{\theta}_3}{(1-m_1)m_2}\ e^{18M_1} = e^{-6M_2}e^{-6(F_1+M_2)} = e^{-6M_2-6F_1-6M_2} = e^{-(6F_1+12M_2)} = k_2.$$

The natural logarithm of k_2

$$\ln k_2 = -(6F_1+12M_2) \tag{15}$$

which can be solved for F_1 as follows:

$$-6F_1 = \ln k_2+12M_2$$

$$F_1 = -\frac{\ln k_2+12M_2}{6} \text{ (text Equation (22)).} \tag{16}$$

Equation (9) can be written

$$\frac{\theta_2}{(1-m_1)}e^{18M_1} = e^{-6M_2}\ \frac{F_1}{F_1+M_2}\ (1-e^{-6(F_1+M_2)}) = k_1 \tag{17}$$

and since $e^{-6(F_1+M_2)} = e^{-6F_1-12M_2+6M_2} = e^{-(6F_1+12M_2)+6M_2} = e^{\ln k_2+6M_2}$ (from Equation (15))

and (from Equation (16))

$$\frac{F_1}{F_1+M_2} = \frac{-\frac{\ln k_2+12M_2}{6}}{\frac{\ln k_2+12M_2}{6}+M_2} = \frac{-(\ln k_2+12M_2)}{-(\ln k_2+12M_2)+6M_2} = \frac{\ln k_2+12M_2}{\ln k_2+12M_2-6M_2} = \frac{\ln k_2+12M_2}{\ln k_2+6M_2}$$

then Equation (17) becomes

$$\frac{\hat{\theta}_2}{(1-m_1)}\, e^{18M_1} = e^{-6M_2}\, \frac{\ln k_2+12M_2}{\ln k_2+6M_2}\, (1-e^{\ln k_2+6M_2}) = k_1 \text{ (text Equation (21)).}$$

Solve for M_2 by iteration.

Next, Equation (12) can be written as

$$\frac{\hat{\theta}_5}{(1-m_1)(1-m_2)m_3}\, e^{18M_1} = e^{-6M_2} e^{-6(F_1+M_2)} e^{-6M_3} e^{-6(F_2+M_3)} = e^{-(6F_1+12M_2)} e^{-(6F_2+12M_3)}$$

$$= k_2 e^{-(6F_2+12M_3)} = k_4.$$

The natural logarithm of k_4

$$\ln k_4 = -(6F_2+12M_3)+\ln k_2 \tag{18}$$

which can be solved for F_2 as follows:

$$-6F_2 = \ln k_4+12M_3-\ln k_2$$

$$F_2 = -\frac{(\ln k_4-\ln k_2+12M_3)}{6} \text{ (text Equation (24)).} \tag{19}$$

Since $e^{-6M_2} e^{-6(F_1+M_2)} = e^{-(6F_1+12M_2)} = k_2$,

Equation (11) can be written

$$\frac{\hat{\theta}_4}{(1-m_1)(1-m_2)}\, e^{18M_1} = k_2\, e^{-6M_3}\, \frac{F_2}{F_2+M_3}\, (1-e^{-6(F_2+M_3)}) = k_3 \tag{20}$$

and since $e^{-6(F_2+M_3)} = e^{-6F_2-12M_3+6M_3} = e^{-6(F_2+12M_3)+6M_3} = e^{\ln k_4-\ln k_2+6M_3}$ (from Equation (18))

and (from Equation (19))

$$\frac{F_2}{F_2+M_3} = \frac{-\left[\dfrac{\ln k_4-\ln k_2+12M_3}{6}\right]}{-\left[\dfrac{\ln k_4-\ln k_2+12M_3}{6}\right]+M_3} = \frac{-(\ln k_4-\ln k_2+12M_3)}{-(\ln k_4-\ln k_2+12M_3)+6M_3}$$

$$= \frac{\ln k_4-\ln k_2+12M_3}{\ln k_4-\ln k_2+12M_3-6M_3} = \frac{\ln k_4-\ln k_2+12M_3}{\ln k_4-\ln k_2+6M_3}$$

then Equation (20) becomes

$$\frac{\hat{\theta}_4}{(1-m_1)(1-m_2)}\, e^{18M_1} = k_2 e^{-6M_3}\, \frac{\ln k_4-\ln k_2+12M_3}{\ln k_4-\ln k_2+6M_3}\, (1-e^{\ln k_4-\ln k_2+6M_3}) = k_3 \text{ (text Equation (23)).}$$

Since $e^{-(6F_1+12M_2)} = k_2$ and $e^{-(6F_2+12M_3)} = \dfrac{k_4}{k_2}$

then, Equation (14) can be written as

$$\frac{\hat{\theta}_7}{(1-m_1)(1-m_2)(1-m_3)}\, e^{18M_1} = e^{-6M_2}e^{-6(F_1+M_2)}e^{-6M_3}e^{-6(F_2+M_3)}e^{-6M_4}e^{-6(F_3+M_4)}$$

$$= k_2 \frac{k_4}{k_2} e^{-6M_4}e^{-6F_3-6M_4}$$

$$= k_4 e^{-(6F_3+12M_4)} = k_6.$$

The natural logarithm of k_6

$$\ln k_6 = \ln k_4 - (6F_3+12M_4) \tag{21}$$

which can be solved for F_3 as follows:

$$-6F_3 = \ln k_6 - \ln k_4 + 12M_4$$

$$F_3 = \frac{-[\ln k_6 - \ln k_4 + 12M_4]}{6} \quad \text{(text Equation (26))}. \tag{22}$$

Equation (13) can be written

$$\frac{\hat{\theta}_6}{(1-m_1)(1-m_2)(1-m_3)}\, e^{18M_1} = k_2 \frac{k_4}{k_2} e^{-6M_4} \frac{F_3}{F_3+M_4} (1-e^{-6(F_3+M_4)}) = k_5 \tag{23}$$

and since $e^{-6(F_3+M_4)} = e^{-6F_3-12M_4+6M_4} = e^{-(6F_3+12M_4)+6M_4} = e^{\ln k_6 - \ln k_4 + 6M_4}$ (from Equation (21))

and (from Equation (22))

$$\frac{F_3}{F_3+M_4} = \frac{-\frac{\ln k_6 - \ln k_4 + 12M_4}{6}}{-\frac{\ln k_6 - \ln k_4 + 12M_4}{6} + M_4} = \frac{-[\ln k_6 - \ln k_4 + 12M_4]}{-(\ln k_6 - \ln k_4 + 12M_4)+6M_4}$$

$$= \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 12M_4 - 6M_4} = \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 6M_4}$$

then Equation (23) becomes

$$\frac{\hat{\theta}_6}{(1-m_1)(1-m_2)(1-m_3)}\, e^{18M_1} = k_4 e^{-6M_4} \frac{\ln k_6 - \ln k_4 + 12M_4}{\ln k_6 - \ln k_4 + 6M_4} (1-e^{\ln k_6 - \ln k_4 + 6M_4}) = k_5 \text{ (text Equation (25))}.$$

EFFECT OF SEVERAL DIETS ON SURVIVAL, DEVELOPMENT TIME, AND GROWTH OF LABORATORY-REARED SPIDER CRAB, *LIBINIA EMARGINATA*, LARVAE

THOMAS E. BIGFORD[1]

ABSTRACT

Survival, development time, and growth were determined for larvae of the spider crab, *Libinia emarginata*, reared with nine diet combinations of algae, rotifers, copepods, ciliates, and *Artemia*. Percent survival was greater and development times shorter for diets of *A. salina* nauplii, either alone or in combination with other food sources. Zoeal survival was higher in diets of *Artemia* at 6 nauplii/ml than at 3 nauplii/ml. Megalopal survival was more variable, being highest in cultures with *Artemia* and the rotifer *Brachionus plicatilis* as food. No significant differences were noted in carapace measurements of larvae reared on the six diets which supported development beyond stage I zoea.

The literature includes many descriptions of decapod crustacean larval culture in the laboratory. Much of this work has been directed at deriving culture techniques and optimum levels of factors such as temperature and salinity. The "standard" diet has been newly hatched *Artemia* nauplii, a highly successful, convenient, but increasingly expensive food source. Research trends have been to seek substitute or supplemental diets for the brine shrimp. Foods investigated have included barnacle nauplii (Ławiński and Pautsch 1969; Reed 1969), the rotifer *Brachionus plicatilis* (Brick 1974; Sulkin 1975; Sulkin and Epifanio 1975), various ciliates (Sulkin 1975), polychaete larvae (Roberts 1974; Sulkin 1975), and oyster larvae (Roberts 1974).

This study was designed to evaluate possible diets, in addition to *Artemia* nauplii, which will support larval development of the spider crab, *Libinia emarginata* Leach. Normal larval development of this species consists of two zoeal stages and one megalopa (Johns and Lang 1977). Parameters used to estimate diet success were survival of larvae to each stage, time to each molt, and carapace size.

Development of a satisfactory diet, in combination with the short larval development time, could establish *Libinia* as a very suitable bioassay organism. The culture methodology described is relatively simple, further increasing the potential for continued laboratory study.

MATERIALS AND METHODS

Ovigerous female *L. emarginata* were collected by otter trawl in Narragansett Bay, during July and August 1976. Females were placed in containers of aerated seawater and immediately transported to the laboratory; storage in the laboratory was in a 1.2-m diameter (195-l volume) Fiberglas[2] tank provided with flow-through ambient temperature (approximately 20°C) seawater. As the eggs ripened, the females were transferred into tubs containing 8 l of filtered seawater at 20° and 29-31‰. After hatching occurred the female was removed and the water changed.

Within several hours of hatching, the larvae were placed 5/dish in 8.75-cm diameter culture dishes containing 75 ml of filtered seawater. Temperature and salinity were maintained at 20°C and 29-31‰. This type of static system has been used commonly to rear other species of crabs (Brick 1974; Sulkin and Norman 1976; Sulkin et al. 1976). The density of 1 larva/15 ml was chosen to allow sufficient room for developing megalopae.

Food organisms used included newly hatched San Francisco Bay Brand *Artemia salina* nauplii, the ciliate *Euplotes vannus*, the copepod *Eurytemora affinis*, the green flagellate algae *Dunaliella viridis*, and the rotifer *Brachionus plicatilis* (Table 1). These organisms are available at the Environmental Research Laboratory (Narragansett, R.I.)

[1]U.S. Environmental Protection Agency, Environmental Research Laboratory, South Ferry Road, Narragansett, R.I.; present address: The Center for Natural Areas, 1525 New Hampshire Avenue, NW, Washington, DC 20036.

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

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TABLE 1.—Laboratory diets used in rearing *Libinia emarginata* larvae.

Diet symbol	Diet	Size (μm)	Concentration (no./ml)	Replicates and no. of larvae used
A_1	*Artemia salina*	350-400	3	2/80
A_2	*A. salina*	350-400	6	1/40
D	*Dunaliella viridis*	15-20	10^2-10^3	1/40
BD	*Brachionus plicatilis*	55-200	25	
	D. viridis	15-20	10^1-10^2	2/80
BD/ABD	Stage I			
	B. plicatilis	55-200	25	2/80
	D. viridis	15-20	10^1-10^2	
	Stage II - M			
	A. salina	350-400	3	
	B. plicatilis	55-200	15	
	D. viridis	15-20	10^1-10^2	
EED	*Eurytemora affinis*	140-243	5	
	Euplotes vannus	80-100	5	1/40
	D. viridis	15-20	10^1-10^2	
ABD	*A. salina*	350-400	3	
	B. plicatilis	55-200	15	2/80
	D. viridis	15-20	10^1-10^2	
ABDE	*A. salina*	350-400	3	
	B. plicatilis	55-200	15	
	D. viridis	15-20	10^1-10^2	1/40
	Eurytemora affinis	140-243	5	
S	Starved		0	2/80

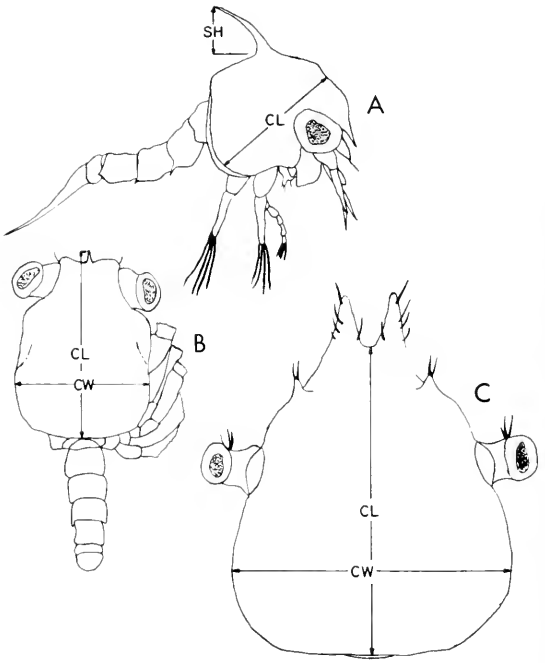

FIGURE 1. Body proportions of *Libinia emarginata* measured and the lines of measurement used. (A) zoea, (B) megalopa, (C) juvenile, (SH) spine height, (CW) carapace width, (CL) carapace length.

in mass cultures. Each species is an active swimmer, thereby satisfying the raptorial feeding requirements of *Libinia*. As noted in Table 1, several of the diets were replicated with 40 larvae (8 dishes of 5) in each of two trials; the remaining diets were investigated only once. Different trials utilized zoeae from different hatches; all 40 larvae in each diet replicate were from the same hatch. Concentrations of food organisms listed in Table 1 remained constant and were not adjusted as mortality occurred. One exception was diet BD/ABD, where the food organism composition was altered after the molt into stage II to include *Artemia* nauplii. Food and culture water were changed daily. Culture dishes were scrubbed clean in freshwater twice weekly. Larvae were transferred by wide-bore pipette to minimize body damage. Molts were recorded when exuviae appeared in the dishes and were verified under a compound microscope. The criteria for death was complete absence of a heartbeat.

Larvae and juvenile crabs were preserved in 10% buffered Formalin for carapace measurements. These measurements were determined with an ocular micrometer, with the carapace lengths and widths taken at maximum dimensions (Figure 1). Comparisons of development times and measurements were made by one-way analysis of variance, with significant differences ($P<0.05$) between diets tested by a Scheffe posterior comparison test (Nie et al. 1970).

RESULTS

Survival

Figure 2 shows the survival of spider crab larvae reared on each of the nine diets. Experiments continued for 25 days, at which time all larvae had either metamorphosed into the first crab stage or died. Survival data after each stage are shown in Table 2. Only six of the nine diets permitted development to proceed beyond stage I; in three diets (EED, D, and S) all zoeae died in the first stage.

Starved control larvae survived a maximum of 7 days, by which time mortality was 100% (Figure 2). After day 3, all larvae were moribund.

Addition of *Dunaliella viridis* (D) did not enhance either survival or molting. All stage I zoeae were motionless by day 4, but a heartbeat was observed up to day 10. No molts occurred. The dark red or orange chromatophores typically observed

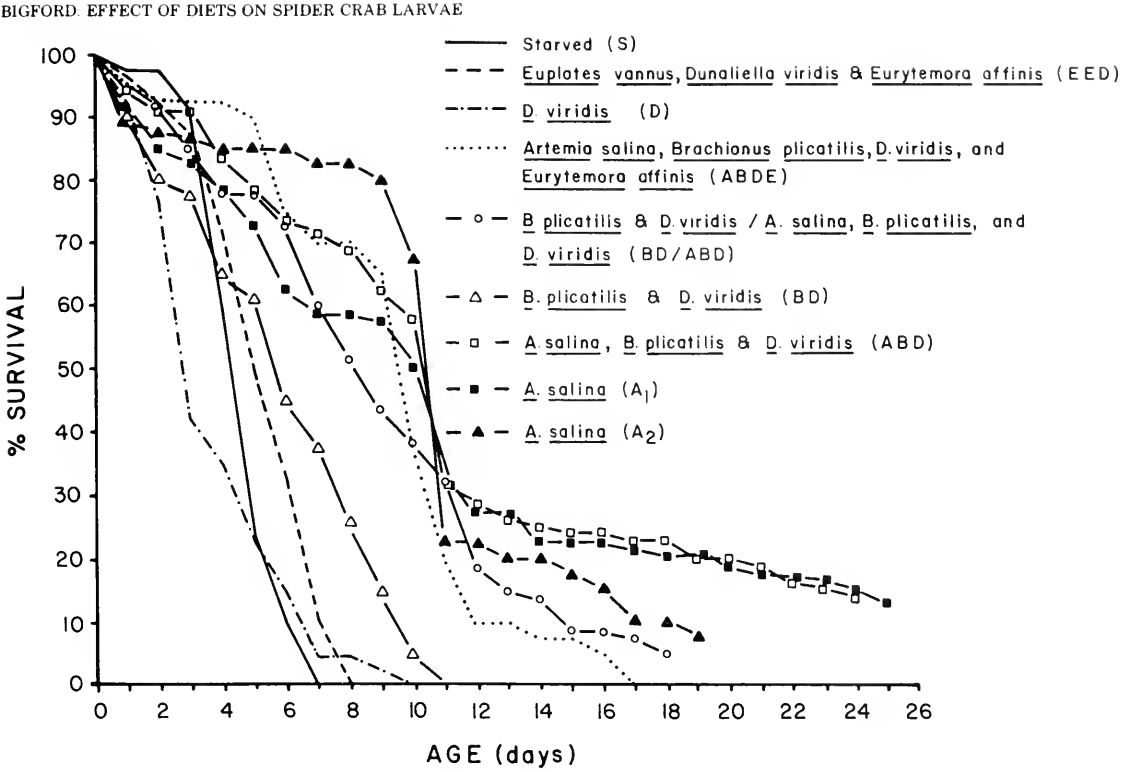

FIGURE 2. Percent survival at each day for *Libinia emarginata* larvae reared on nine laboratory diets. Refer to Table 1 for concentrations and sizes of food organisms in each diet.

TABLE 2.—Survival data and percentages to each stage of *Libinia emarginata* on the diets permitting larval development past stage I. N_I, N_{II}, and N_M represent number of larvae surviving to each stage; N_0 equals initial number.

	Molt					
	I→II		I→M		I→J	
Diet	N_I/N_0	%	N_{II}/N_0	%	N_M/N_0	%
A_1	59/80	74	34/80	43	8/80	10
A_2	33/40	83	30/40	75	3/40	8
ABD	58/80	73	40/80	50	10/80	13
BD/ABD	36/80	45	3/80	4	3/80	4
ABDE	32/40	80	18/40	47		
BD	29/80	36				

on the carapace were absent in nearly all larvae reared on diet D.

Survival on diet EED (ciliate, copepod, and algae) was only slightly higher than the starved controls (Figure 2). No molts were observed. Mortality was 100% by day 8.

A diet of *Brachionus* and *Dunaliella* (BD) allowed development into stage II. With this diet 36% (29/80) of the stage I zoeae molted into stage II, but all died by day 11.

Food organisms offered during stage I in diet BD/ABD were identical to diet BD. *Artemia* nauplii were added for all ensuing stages. Survival was 45% to stage II and 4% to both the megalopae and juvenile stages.

Diet ABD, identical to diet BD/ABD after stage I, allowed 73% survival to stage II, 50% to the megalopae, and 13% to the first crab stage.

Higher survival to stage II was achieved by diet ABDE, which included copepod subadults. On this diet, 80% of the zoeae molted successfully into stage II; 47% molted into megalopae. No larvae metamorphosed into the crab stage although several died during ecdysis.

Two diets of newly hatched *Artemia* nauplii were tested. Diet A_1, with 3 nauplii/ml, yielded 74% survival to stage II, 43% to megalopae, and 10% to the first stage crab. A second diet, A_2 (6 nauplii/ml), yielded higher survivals to stage II and megalopae, 83% and 75%, respectively, than any other diet. Survival to the juvenile stage was 8%.

Development Times

Diets supplying *Artemia* nauplii in stage I resulted in highest survival to stage II and the shortest development times (Table 3). Of the four diets grouped in the first subset (Table 4) for the molt into stage II, diet ABDE was the best. Diets BD and BD/ABD, although identical in content during stage I, were significantly different.

For the molt from zoeal stage II into megalopae diet ABDE again resulted in the shortest development time. Grouped with ABDE in homogeneous subset I was A_2, with the latter diet sufficiently similar in molt time to diet A_1 to also be included in subset II. As in the first molt, diet BD/ABD had the longest time to molt.

TABLE 3.—Development times of *Libinia emarginata* larvae from hatching to each molt for each diet. Diets EED, D, and S did not allow development past stage I.

Diet		Molt I→II	I→M	I→J
A_1	$\bar{x}$	4.66	10.29	18.86
	SD	0.60	1.14	2.48
	Range	4-7	9-14	16-22
A_2	$\bar{x}$	4.42	9.87	18.67
	SD	0.50	0.51	3.79
	Range	4-5	9-11	16-23
ABD	$\bar{x}$	4.62	10.30	19.00
	SD	0.64	0.85	2.21
	Range	4-6	9-12	16-24
BD/ABD	$\bar{x}$	6.56	13.00	21.67
	SD	1.36	1.73	3.06
	Range	5-9	11-14	19-25
ABDE	$\bar{x}$	4.25	9.39	
	SD	0.44	0.50	
	Range	4-5	9-10	
BD	$\bar{x}$	5.72		
	SD	1.28		
	Range	4-8		

In the last molt, from megalopae to the first crab stage, all four diets tested were grouped as one subset. Of the four, A_1 was ranked as the best in terms of development times and BD/ABD was the worst.

Carapace Measurements

Spine height, carapace length, and carapace width measurements were analyzed by a Scheffe posterior comparison test (Table 5). Zoeal stage II and juvenile crab measurements were not significantly ($P = 0.05$ level) different and were grouped into one homogeneous subset; carapace lengths of megalopae were similar in all diets. Only the carapace widths of megalopae proved statistically different, with two subsets describing the measurements of the larvae reared on different diets.

Ranking within each subset provides an indication of possible trends in size with respect to the diets tested. This trend is most evident in zoeal stage II; in both spine height and carapace length the ordering of diets was identical, with A_2 superior and ABD second. In megalopae and

TABLE 4.—Homogeneous subsets of diets tested on *Libinia emarginata* larvae as determined by analysis of variance and Scheffe posterior comparisons ($P < 0.05$) of development times. Shortest times are listed in subset I and longest in subset III.

Subset	Stage I→II	II→M	M→J
I	ABDE, A_2, ABD, A_1	ABDE, A_2	A_1, A_2, ABD, BD/ABD
II	BD	A_2, A_1, ABD	
III	BD/ABD	BD/ABD	

TABLE 5.—Carapace measurements for stage II, megalopa, and juvenile *Libinia emarginata* reared on various diets. Mean values (in millimeters) of spine height (SH), carapace width (CW), and carapace length (CL) are given in ranked order within each homogeneous subset of similar values. Roman numerals following the diet symbol denote replicate number, if applicable. Diets not represented, e.g., A_1 in stage II, could not be analyzed because of insufficient data.

Larval stage	Parameter measured	Subset	Ranked order of means					
Zoea II	CL	I	BD/ABD-II 0.859	ABDE 0.865	ABD-II 0.936	A_2 0.970		
	SH	I	BD/ABD-II 0.311	ABDE 0.316	ABD-II 0.338	A_2 0.360		
Megalopa	CW	I	A_1-II 0.938	A_2 1.037	A_1-I 1.044	ABD-I 1.100		
		II	A_2 1.037	A_1-I 1.044	ABD-I 1.100	ABDE 1.136	ABD-II 1.153	
	CL	I	ABDE 1.232	A_1-II 1.258	A_1-I 1.260	ABD-II 1.265	A_2 1.289	ABD-I 1.380
Juvenile	CW	I	BD/ABD-I 1.233	A_1-II 1.284	A_1-I 1.340	ABD-II 1.347	ABD-II 1.393	A_2 1.420
	CL	I	A_2 1.560	ABD-II 1.567	BD/ABD-I 1.575	A_1-II 1.644	ABD-I 1.690	A_1-I 1.705

juveniles, diet ABD (replicates I and II) often resulted in the largest measurements.

DISCUSSION

Survival

Based on survival, laboratory diets that included *Artemia salina* nauplii were better than diets consisting solely of rotifers, algae, ciliates, or copepod nauplii. However, when offered in combination with brine shrimp nauplii, rotifers and copepods may provide some nutritional value to the larvae. Survival percentages to zoeal stage II were very high with diet ABDE: diet ABD produced the best survival to the first stage juvenile. Johns and Lang (1977; unpubl. data), using an excess diet of *A. salina* and a compartmented box culture system, got 20% survival to first stage crab.

The success of *Artemia* nauplii as a laboratory diet is well documented (e.g., Brick 1974; Sulkin et al. 1976). Studies by Brick (1974) also showed that survival of *Scylla serrata* to megalopae increased as the concentration of *Artemia* nauplii was increased. Results showed a 25% survival to megalopae at concentrations of 5 nauplii/ml and 44% at 16 nauplii/ml.

Differences in survival on various diets is commonly observed in laboratory studies. Diets that permit partial development, e.g., diet BD in this study, normally yield correspondingly lower survival. This trend has also been observed in diet studies on larvae of the sand shrimp, *Crangon septemspinosa* (Bigford[3]).

Development Times

The diets resulting in the shortest development times closely parallel those yielding the highest survival percentages. These diets all include *Artemia* nauplii (Tables 3, 4).

For the molt from zoeal stage I to stage II the shortest development times were recorded for diets ABDE and A_2, which also are the diets yielding maximum survival to stage II. These same diets continue to rate high in terms of survival and molt time for the second molt also.

Division of molt times into three subsets during zoeal development infers that *L. emarginata* may prefer certain food types or sizes at different stages. Diets including *Artemia* also consisted of the largest size food particles, with copepods, rotifers, ciliates, and algae being smaller. This possible discriminate particle selection was not observed in megalopae; all diets were consumed equally and development times were similar. All larvae surviving to first stage crabs were reared on *Artemia,* alone or in combination, during stage II and megalopae.

The lack of development observed in diets D, EED, and S, plus the partial development in BD, is supported by the literature. Studies by Sulkin (1975) have shown that algae and ciliates do not satisfy the nutritional requirements of brachyuran zoeae. Broad (1957) concluded that various algal diets were similar to starved controls, with the addition of animal matter required for metamorphosis in grass shrimp, *Palaemonetes,* larvae. Particle size and biochemical composition, among other factors, may limit development and survival. Conversely, rotifers have been found to enhance survival and development of several other decapod larvae, most notably the blue crab, *Callinectes sapidus* (Sulkin and Epifanio 1975). Food size appears to be the controlling factor in selection of the rotifer as food for early stage zoeae of the blue crab.

Although ABDE was a successful diet in the zoeal stages, it did not sustain metamorphosis to the crab stage in this study. Perhaps at differing concentrations of *Artemia* and *Eurytemora* the diet would prove more successful for megalopae.

Carapace Measurements

There does not appear to be a significant difference in carapace size between the diets studied. Instead, the effects of diets were manifested in terms of development rate. Larvae apparently molt upon reaching a certain biomass, with the postmolt sizes similar in most cases.

Carapace length measurements for second stage zoeae and megalopae (Table 5) for diets A_1 and A_2 compare favorably with the values reported by Johns and Lang (1977) in their description of the larvae reared on excess concentrations of *Artemia.* Their mean measurements of 0.94 mm and 1.21 mm, respectively, were only slightly below the values reported here. Differences in measuring

[3]Bigford, T. E. 1975. The effects of diet on larval development of the early stages of the sand shrimp *Crangon septemspinosa* Say. Unpubl. manuscr. U.S. Environmental Research Lab., Narragansett, R.I.

techniques could account for the larger megalopa carapace lengths reported in this paper.

CONCLUSIONS

The results of this experiment suggest that a combined diet including at least 5 *Artemia* nauplii/ml would produce highest survival in the zoeae. Additional food organisms may be required by megalopae. Faster development times associated with diet A_2, compared with A_1, emphasize the importance of food concentration in addition to food type.

Limited success of diet ABDE in the zoeal stages implies that *Eurytemora affinis* subadults may provide some nutritional substance to spider crab larvae. Replication of the copepod diet alone would be required to verify the potential of *Eurytemora*.

Each of the diets permitting development to proceed through metamorphosis resulted in a low percent survival. This could be partially explained by the static dish system used to culture the larvae. Flow-through designs would control water quality and perhaps microbial infestations. With an improved culture design, a satisfactory diet, and the short development time, *L. emarginata* could prove to be a very satisfactory bioassay organism.

The biochemical content of *Artemia* nauplii may account for their value in the diet of spider crab larvae. As determined by Sulkin (1975), *A. salina* contain 30 total lipid/unit dry weight, a value far superior to that of *Brachionus plicatilis* (9%). A diet of fertilized polychaete *(Hydroides dianthus)* eggs, containing 20% total lipid, also sustained complete development of *Callinectes sapidus* in Sulkin's experiments. The lipid content of *Eurytemora* was not determined.

Each of the diets tested in this experiment resulted in a normal progression of larval development for *L. emarginata* (Johns and Lang 1977). No supernumerary stages or characters appeared

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DESCRIPTION OF REARED EGGS AND YOUNG LARVAE OF THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*

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ABSTRACT

Adult spotted seatrout, *Cynoscion nebulosus*, were induced to spawn in the laboratory by controlling temperature and photoperiod. Development of eggs and larvae, reared at 25°C, is described to 15 days after hatching. The pelagic, spherical eggs have a mean diameter of 0.77 mm, and usually contain one oil globule averaging 0.22 mm in diameter. Hatching occurs about 18 h after fertilization. Standard length at hatching is between 1.30 and 1.56 mm. Spotted seatrout average 4.4 mm standard length at notochord flexion. The larvae, which were fed the rotifer, *Brachionis plicatilis*, and nauplii of *Artemia* sp., grew to about 4.5 mm standard length in 15 days.

The spotted seatrout, *Cynoscion nebulosus*, is one of the most important fishes to both recreational and commercial fishermen in the Gulf of Mexico and southeastern United States. In the Gulf it ranks first in weight landed by sports anglers (Deuel 1973) and seventh by weight taken commercially (U.S. Department of Commerce 1975). Despite its value, the eggs and youngest larval stages have not been adequately described in previous literature.

Four early works (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Pearson 1929; Hildebrand and Cable 1934) provided descriptions of spotted seatrout development. Welsh and Breder (1923) described juvenile *C. nebulosus* as small as 28 mm, collected from North Carolina and Chesapeake Bay waters. Hildebrand and Schroeder (1928) illustrated a spotted seatrout presumably 120 mm long, apparently from Chesapeake Bay. Spotted seatrout from Texas as small as 7.8 mm were described by Pearson (1929). The most complete description of young spotted seatrout was by Hildebrand and Cable (1934). The smallest seatrout described by them was 1.8 mm long and was taken off North Carolina. The only other illustrations of larval spotted seatrout were of 3.0 and 5.0 mm SL fish from south Florida by Jannke (1971).

The first description of *C. nebulosus* eggs was by Miles (1950, 1951). He stated that eggs measured from 0.70 to 0.98 mm in diameter and contained one to four small oil globules. Later, Tabb (1966) stated that eggs were spherical and normally had one oil droplet, but sometimes two or three.

In this paper, we provide detailed descriptions of eggs and young larvae of spotted seatrout, based on laboratory spawned and reared specimens.

PROCEDURES

Adult spotted seatrout were caught by hook and line at Port Aransas, Tex., in August 1973. Eleven fish (seven males and four females) were brought into the laboratory and maintained in a 30,000-l seawater tank. The tank was constructed of fiber glass and measured 6 × 3 × 1.5 m. It contained seawater which was recirculated through a shell-and-gravel filter.

The fish were fed shrimp and fish, both live and dead. Temperature and photoperiod in the laboratory were adjusted to simulate spring and, subsequently, summer conditions. Spawning began 1 mo after conditions were stabilized at 15 h of light, 9 h of dark, and 26°C. Details of the methods to induce spawning by spotted seatrout are described by Arnold et al. (in press). In a 1-yr period, the spotted seatrout have spawned during each month for a total of 82 times. On several occasions more than one female spawned.

Eggs described in this paper were spawned by a single female on 8 September 1975. They were preserved hourly in 3% buffered Formalin[2] from

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

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the time of spawning until hatching. Larvae described in this report were from eggs spawned on 7 October 1975 and were transferred to rearing aquaria. Samples of larvae were preserved daily in 5% Formalin for 15 days.

Larvae were reared in 57-l aquaria which were filled with algae and rotifer culture water 2 days prior to the introduction of fish. Algal growth was enhanced by a constant light source above the aquaria. Seatrout were fed the rotifer, *Brachionis plicatilis*, daily at a rate of at least 20/ml of water for 4 days. On the fifth day rotifers and brine shrimp, *Artemia* sp., nauplii (3-5/ml) were both introduced. This combination was fed until larvae were 8 days old, then brine shrimp were used as the only food source. Temperatures in the aquaria were maintained at 24.0° to 26.0°C.

Eggs and larva were measured using an ocular micrometer in a dissecting microscope. Measurements included total length, standard length, snout to anus length, snout length, head length, eye diameter, and body depth. Illustrations are of preserved specimens. In discussing seatrout eggs, the three stages described by Ahlstrom and Ball (1954) are used.

EMBRYONIC DEVELOPMENT

Spotted seatrout eggs are pelagic and spherical, the chorion is clear and unsculptured, and the yolk is homogeneous. The perivitelline space in live eggs is narrow, occupying approximately 4% of the egg diameter. One hundred live eggs and 100 Formalin-preserved eggs were measured at various stages of development. No differences in diameters of eggs or oil globules were noted at different stages of development. Diameters of both live and preserved eggs averaged 0.77 mm. The diameter of live eggs ranged from 0.73 to 0.82 mm while diameters of preserved eggs ranged from 0.70 to 0.85 mm.

The eggs usually contain one yellow oil globule, but some eggs (2%) have two or three globules. Oil globules in preserved eggs range from 0.18 to 0.26 mm in diameter, with a mean of 0.22 mm. Oil globules in live eggs range from 0.22 to 0.27 mm in diameter, with a mean of 0.23 mm. When more than one globule is present, sizes vary greatly.

Early Stage Eggs

Duration of the early stage is about 8 h. Eggs preserved in Formalin have yellowish oil globules, opaque cells, and, in this early stage, a shrunken and disorganized yolk (possibly due to poor preservation). Eggs float with the oil globule(s) on top and the developing cells on the bottom.

Development proceeds as follows: 1½ h, 16- or 32-cell stage; 2 h, morula stage; 3 h, blastula stage; 4 h, gastrulation begins; 6 h, gastrula encircles two-thirds of the yolk and primitive streak is evident; 8 h, blastopore closure. At the onset of gastrulation, numerous small droplets form around the oil globule. By blastopore closure, optic vesicles are visible in most eggs and the notochord can be seen in some. Myomeres are not discernable and no pigmentation is present on the egg or embryo.

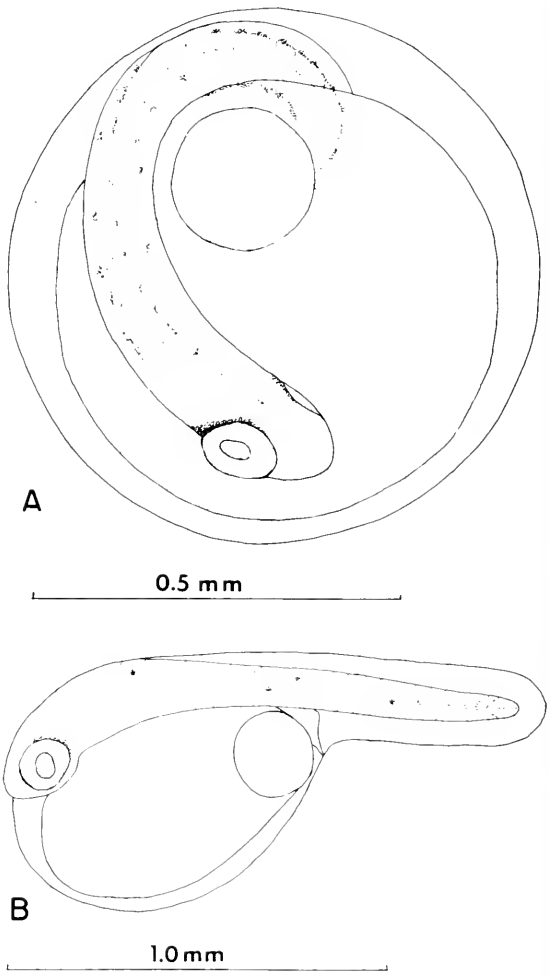


FIGURE 1.—Spotted seatrout embryos: A) 15 h after fertilization; B) at hatching (SL 1.46 mm).

Middle Stage Eggs

Duration of the middle stage is about 4 h. At 9 h after fertilization, the notochord develops further and the forebrain begins to develop. Small melanophores are present for the first time around the optic vesicles and in no apparent pattern along the body. In the 10th hour, six to eight myomeres can be seen with difficulty on the posterior one-third of the embryo. By the 12th hour, the embryo extends over about one-half the circumference of the egg.

Late Stage Eggs

The tip of the tail of the embryo has separated from the yolk and the finfold is evident on both the posterior dorsal and ventral caudal regions at 13 h. Eighteen to 20 myomeres are present. Melanophores, which are present over the entire body of the embryo, are concentrated around the dorsal surfaces of the eyes, on either side of the notochord, and along the base of the finfold. At 15 h (Figure 1A), the tail of the embryo is well past the oil globule and has developed a marked curve. The finfold surrounds the posterior half of the embryo and 24 to 25 myomeres can be counted. Internal organs show some differentiation, while anteriorly the eyes are pronounced and the hindbrain is developing. One hour later, the embryo occupies three-fourths of the circumference of the egg. Twenty-five myomeres are apparent.

Hatching occurs 16 to 20 h after fertilization, when incubation temperatures are approximately 25°C. In other experiments, hatching occurred in 15 h at 27°C and in 21 h at 23°C.

LARVAL DEVELOPMENT

Hatching (Figure 1B)

Standard lengths of 20 newly hatched larvae ranged from 1.30 to 1.56 mm and averaged 1.46 mm. At hatching the oil globule is located at the posterior end of the yolk sac. Some scattered melanophores like those in the embryos are still found, but most are indistinct, especially those along the finfold. No pigment is visible in the yolk or on the oil globule.

Sixteen Hours Posthatching (Figure 2A)

At 16 h, larval standard lengths ranged from 1.89 to 2.10 mm and averaged 2.03 mm. The finfold is large and clear with no fin differentiation. The mouth is undeveloped, only a little yolk remains, and the oil globule is still in a posterior position. Otocysts are faintly visible within the otic capsule. Pectoral fin buds are evident for the first time. The alimentary canal is straight, terminating at the anus in the anterior half of the body.

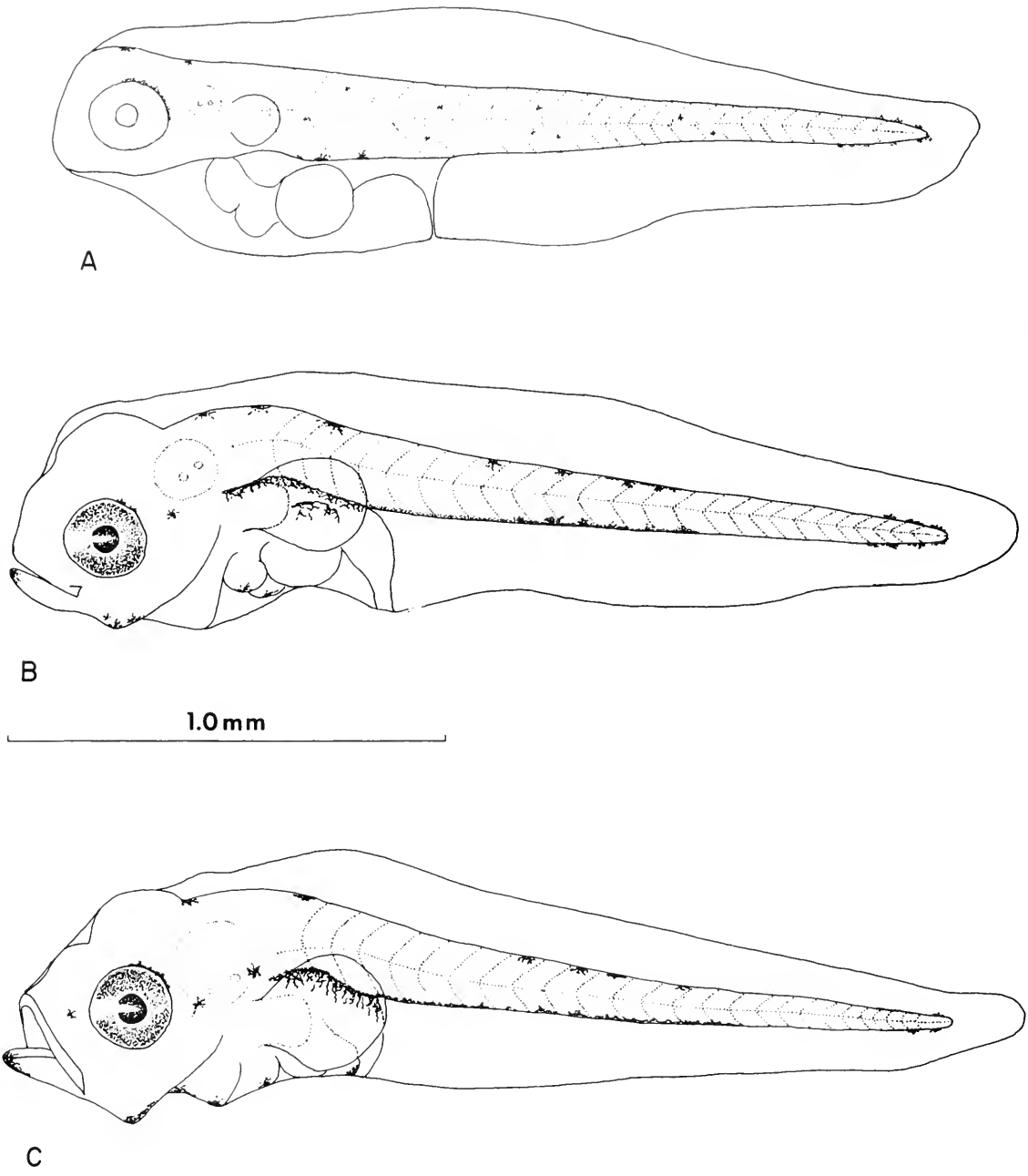
Body pigments are in four vertical bands located above the abdomen, above the anus, and one-third and two-thirds of the distance from the anus to the tip of the notochord. Small melanophores are concentrated in these bands, but many disappear with preservation. The most prominent of the bands is located one-third of the way from the anus to the notochord tip. Pigmentation in preserved specimens is most distinctive in the head region. Several small dendritic melanophores are located above and behind the eye. Two dendritic melanophores are located on the dorsomedial surface of the head. Some slight black pigmentation is visible above the abdomen where the first pigment band is located. Numerous granular melanophores are also found on the finfold at the dorsal and ventral body margins at the notochord tip.

Forty Hours Posthatching

At 40 h, the larvae average 2.10 mm SL, the mouth is formed, and the yolk sac is almost completely gone. The head has grown very deep, and the brain appears dorsally over the eyes. In preserved fish the eye is totally black, and pectoral fins stand out from the sides. Internal organs are increasing in size and complexity, but the alimentary canal is still straight, although thicker than at hour 16.

Pigmentation undergoes distinctive changes prior to 40 h of age. The four vertical bands which occur on the 16-h larva are absent, and only one wide, diffuse band is found just forward of the half-way point between the anus and the tip of the notochord. Melanophores are intensifying along the dorsal and ventral body margins within the band and anteriorly over the abdomen. The granular melanophores on the finfold at the tip of the notochord are somewhat fewer in number. Dendritic melanophores are on the dorsal surface of the abdomen. Pigmentation on the lower jaw is heaviest at the angle and posteriorly. A few small melanophores are anterior to this and at the tip of the lower jaw.

The pigment which remains least distinct and disappears after a short period in Formalin is that



around the eye and dorsal surface of the head. Concentrations of small amber chromatophores are found ventral and posterior to the eye, while several larger yellow chromatophores are found above the eye. Several amber chromatophores are also located medially on the dorsal surface of the head.

Sixty-Four Hours Posthatching (Figure 2B)

Larvae at 64 h past hatching range from 2.06 to 2.15 mm SL and average 2.12 mm SL. The yolk is completely absorbed, the gut has become convoluted, and the intestine is very thick.

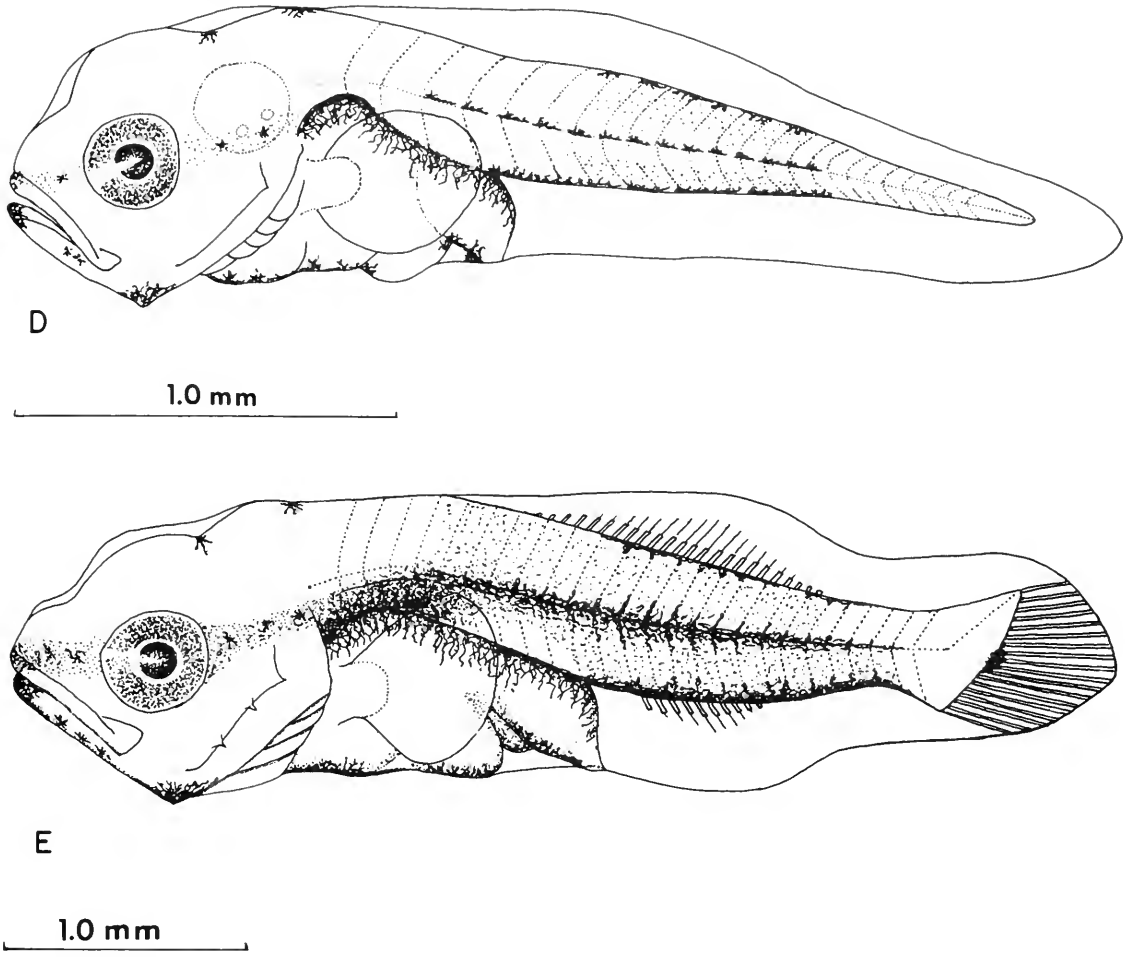


FIGURE 2.—Spotted seatrout larva: A) 16 h posthatching (SL 2.03 mm); B) 64 h posthatching (SL 2.12 mm); C) 112 h posthatching (SL 2.12 mm); D) 232 h posthatching (SL 2.71 mm); E) 328 h posthatching (SL 4.21 mm).

Eye pigmentation is complete and very reflective. The diffuse band found in 40-h fish is still present but is indistinct. Basic pigment patterns and melanophore placement remain similar to 40-h fish except in the following cases. Pigment is increasing along the dorsal surface of the abdomen, and anteriorly towards the eye. The melanophores on the tip of the lower jaw are more distinct. Some pigment is also present on the ventral surface of the abdomen.

Four and Five Days Posthatching (Figure 2C)

In a typical spotted seatrout 112 h old, standard lengths vary from 2.04 to 2.15 mm and average 2.12 mm. The mouth is well-developed and the maxillary is prominent.

Dendritic melanophores are found from the upper surface of the abdomen posteriorly to two-thirds of the length of the tail along the ventral midline. They radiate ventrally over the outer abdominal surface. Melanophores on the tail radiate dorsally from the ventral margin and ventrally from the dorsal margin. Large dark melanophores are present on the preserved larvae at this age but are somewhat variable. One is found immediately ahead of the anus (an important characteristic in sciaenid larvae), and two to three more occur anteriorly below the abdomen. Another is located at the angle of the lower jaw. One or two are on the

dorsal surface of the body above the abdomen. Melanophores on the finfold at the tail vary greatly; they are found both on the dorsal and ventral body margins in varying numbers. A single dendritic melanophore is present anterior to the eye, and two or three more are posterior to the eye.

Six Through Eight Days Posthatching

At this age, there is little difference in body form and structure from that in Figure 2c. Standard lengths at 160 h average 2.06 mm and range between 1.80 and 2.23 mm. The preopercle can be seen on some larger specimens.

Pigmentation has become more intense and is expanding. Principal changes in the dendritic pigments involve the ventral expansion of melanophores on the upper surface of the abdomen, and the coalescence of tail pigmentation into dark stripes. Indistinct pigment occurs from the eye to the tip of the snout. Melanophores are still found anterior to the anus and have increased in number below the abdomen. A melanophore spot is still found on the tip of the lower jaw.

Nine Through Eleven Days Posthatching (Figure 2D)

During this 3-day period the larvae begin to grow appreciably in length. By 11 days, standard lengths average 2.92 mm and range from 2.37 to 3.48 mm. Six small teeth are present on the upper jaw and four on the lower jaw at this age. The preopercle is more evident and a small spine can be seen. Branchiostegal rays are present for the first time. The pectoral fin is still membraneous. Some larvae have a presumptive hypural plate below the notochord tip, but no notochord flexion is observed.

Pigmentation undergoes only minor changes in this period. Principal body pigment gives the appearance of a dark stripe from snout to tail. Melanophores are now evident on the lateral line giving the impression of a series of dashes. Tiny melanophores are present on the midlateral tail region and both ahead of and behind the eye within the pigment stripe.

Twelve Through Fifteen Days Posthatching (Figure 2E)

Standard lengths at 12 days average 3.35 mm, and increase to 4.59 mm at 15 days. The preopercular spine is prominent, and on the larger specimens second and third spines are visible below the first. By the 14th day (at a size of 4.4 mm SL) notochord flexion has occurred in all specimens. As many as 18 caudal rays are first seen at 13 days (4.0 mm SL), and by 15 days (4.4 mm SL), 25 dorsal rays and 10 anal rays are evident. Teeth are found on both jaws (10 on the upper and 6 on the lower).

At this age, the pigmentation still gives the appearance of a stripe from the snout through the eye to the upper abdomen, and on the lateral line and ventral tail surface. Melanophores are still located at the tip and posterior to the angle of the lower jaw, on the tip of the upper jaw, and along the ventral margin of the abdomen. The spot anterior to the anus is indistinct. Pigmentation around the eye is localized in an anterior and posterior position within the pigment stripe. The dendritic melanophores on the upper abdominal surface are still large and distinct. Dendritic melanophores are heavily concentrated along the lateral line and also along the ventral margin of the tail. The dorsal tail margin has less pigmentation. A single large dendritic melanophore is found on the base of the caudal fin. Other pigmentation is widely scattered over the entire tail. Seatrout preserved for long periods seem to lose the melanophore on the caudal fin but other body melanophores remain visible.

GROWTH

Larval spotted seatrout grew from about 1.5 mm SL at hatching to about 4.5 mm SL in 15 days. A. K. Taniguchi (pers. commun.) at the University of Miami has observed faster growth of larval spotted seatrout. He raised larvae at various temperatures and fed them copepods. At 2 wk of age, we noted cannibalism in our seatrout larvae even though ample food of appropriate size appeared to be present.

Measurements were made of preserved larvae. The data were tabulated according to size and age (Table 1). Standard lengths of larvae were consistently 93 to 95% of the total length until flexion of the notochord occurred at 14 or 15 days; then the standard length decreased to 88% of total length.

Preanal lengths at 1 day posthatching were 44% SL, 36% SL at 5 days, and 54% SL at 15 days. This indicated that the preliminary decrease in gut length appeared to be associated with yolk absorption. After 5 days, the gut length steadily in-

TABLE 1.—Average age (hours) and measurements (millimeters) of preserved larval spotted seatrout of known size.

Standard length range	Age	Number of specimens	Snout to anus length	Snout length	Head length	Eye diameter	Body depth
1.70-1.89	118	4	0.79	0.09	0.43	0.21	0.50
1.90-2.09	92	32	0.85	0.10	0.44	0.22	0.53
2.10-2.29	122	52	0.91	0.12	0.49	0.23	0.54
2.30-2.49	216	6	1.22	0.17	0.69	0.28	0.65
2.50-2.69	248	3	1.38	0.21	0.83	0.30	0.75
2.70-2.89	244	4	1.41	0.20	0.82	0.31	0.77
2.90-3.09	253	7	1.47	0.21	0.88	0.32	0.80
3.10-3.29	274	8	1.60	0.26	1.01	0.34	0.90
3.30-3.49	290	7	1.72	0.29	1.06	0.35	0.91
3.50-3.69	304	3	1.78	0.27	1.08	0.35	0.96
3.70-3.89	316	4	1.95	0.35	1.20	0.40	1.01
3.90-4.09	323	5	2.06	0.34	1.29	0.42	1.07
4.10-4.29	323	5	2.20	0.40	1.37	0.38	1.13
4.30-4.49	344	3	2.46	0.41	1.50	0.45	1.24
4.50-4.69	—	0	—	—	—	—	—
4.70-4.89	352	1	2.56	0.43	1.63	0.48	1.35
4.90-5.09	342	5	2.68	0.45	1.68	0.48	1.36
5.10-5.29	—	0	—	—	—	—	—
5.30-5.49	352	1	3.05	0.47	1.84	0.52	1.48

creased relative to standard length. Snout length increased relative to standard length from 3% at 1 day to 9% at 15 days. Similarly, head length increased relatively from 19-20% SL to 34% SL. Both these changes were due to rapid development of the mouth and head. Eye diameter and body depth varied only slightly during development. Eye diameter was between 9 and 11% SL at all stages, while body depth varied from 22 to 28% SL at all ages.

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PHYSICAL AND CHEMICAL CHANGES OF PINK SHRIMP, *PANDALUS BOREALIS*, HELD IN CARBON DIOXIDE MODIFIED REFRIGERATED SEAWATER COMPARED WITH PINK SHRIMP HELD IN ICE

FERN A. BULLARD AND JEFF COLLINS[1]

ABSTRACT

Pink shrimp, *Pandalus borealis*, were held in carbon dioxide modified refrigerated seawater for 12.5 days and in ice for 11.5 days. Chemical tests for spoilage indicated that shrimp held in carbon dioxide modified refrigerated seawater were acceptable up to 9.5 days and those held in ice up to 6.5 days. Data on weight, yield, solids, carotenoids, protein, salt, and pH are given. When expressed on a constant basis (salt-free, 75% moisture), the yield of cooked product calculated from the gross weight of whole shrimp decreased rapidly during the first few days in either system. The yield of cooked meats from the carbon dioxide modified refrigerated seawater system decreased from 18.3% at 0.5 day to 15.3% at 4.5 days but varied in the ice system between 14.0 and 15.5% over the useful holding period of 6 days.

The advantages and disadvantages of the refrigerated seawater system (RSW) for holding fish and shellfish are well documented and were recently discussed by Barnett et al. (1971) and by Nelson and Barnett (1971). Based on bacteriological measurement and sensory evaluation, these authors showed that rockfish, *Sebastodes flavidus*, can be held in the RSW system modified by the addition of carbon dioxide (MRSW) for longer periods of time than in ice. The purpose of this study was to obtain detailed information on the physical and chemical changes that occur during time of holding of pink shrimp in the MRSW system compared with that of pink shrimp held in ice.

EXPERIMENTAL

Preparation of Pink Shrimp

Pink shrimp, *Pandalus borealis*, when received by the laboratory, had been held for 2 h at ambient temperature of -1.7°C (29°F) without ice aboard a commercial fishing vessel. Shrimp were separated from fish and after a brief rinse in cold freshwater were placed in fiber glass-coated hardware cloth baskets and rinsed again in cold tapwater for 2 min. The shrimp were then drained for 30 min and the weight of each sample was adjusted to contain 2,100 g (4.63 lb). It had been established that draining for 30 min resulted in nearly constant weight.

The MRSW holding portion of the experiment was conducted as follows. Baskets of shrimp and loose shrimp were alternately placed in the MRSW tank containing a 3.5% brine at -1.7°C, previously treated with carbon dioxide to 3.92 pH. The final loading ratio of shrimp to brine was 1:1.4 (wt/wt).

The ice holding portion of the experiment was conducted as follows. Samples of shrimp for ice holding were similarly rinsed, drained for 30 min, and adjusted to 2,100 g each before being placed in single layer cheese cloth "baskets" and covered with ice and 38.5 kg (85 lb) loose shrimp. Loose shrimp were mixed with ice to more closely simulate boat holding conditions. Fresh ice was placed on the ice-held samples daily to insure a minimum 15-cm (6-in) cover over any given sample.

Holding Tank and Refrigeration Unit

A 568-l (150-gal) fiber glass holding tank was connected to a refrigeration unit by three 3.81-cm (1½-in) flexible plastic hoses. The brine was circulated at 151 l/min (40 gal/min) through a shell and tube heat exchanger with the capacity to chill 454 kg (1,000 lb) of shrimp and brine from 10° to -1.7°C (50° to 29°F) in 3 h. Refrigeration was provided by a conventional Freon[2] 12 condensing unit. The

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

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

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FISHERY BULLETIN: VOL. 76, NO. 1, 1978.

tubes in the heat exchanger were made of titanium to avoid corrosion. Carbon dioxide was metered into the suction side of the pump for maximum diffusion; at a rate of 0.2 l/min (0.2 ft^3/h), the pH was lowered from 7 to 4 in 5 h. In this 14-day experiment, 8.8 kg (4 lb) of carbon dioxide were used.

A chest-type home freezer was used as an insulated box to hold shrimp in ice. One day before its use the refrigeration was disconnected and the door raised to allow the ice to begin to melt in order to simulate conditions in a boat's hold.

SAMPLING

Sampling Procedure

In this comparative holding experiment, a sample was taken daily from each holding system and allowed to drain for 30 min before weighing (iced shrimp were first rinsed briefly in cold water to remove ice). Four subsamples were prepared from each sample—three to represent commercial practices and the fourth for laboratory analyses to determine chemical changes in the shrimp. The subsamples, stored at -34°C (-30°F) for later analyses, are as follows.

Subsampling Procedure

1. Whole shrimp: The total weight of whole shrimp was determined at each period of holding to simulate the weight of shrimp landed at the dock and to determine yield of products. Water uptake was determined by a solids analysis in a blended sample.
2. Hand-peeled, raw shrimp meats: This laboratory sample was used to determine basic chemical changes, mainly spoilage.
3. Hand-peeled, raw, washed shrimp meats: This sample simulated a machine peeled raw frozen product. Washing was required to approximate the leaching action of commercial machine peelers. The hand-peeled meats were washed gently in cold water for 2 min, drained on hardware cloth for 10 min, then weighed, and frozen for later analyses.
4. Hand-peeled, washed, cooked shrimp meats: This sample simulated a cooked frozen product. A portion of the washed meats after frozen storage, as in 3 above, was thawed and cooked in boiling water for 2 min at a 12:1 ratio, drained 1 min, cooled 5 min, and blended for analyses.

To prepare subsamples 2 and 3 for analyses, they were removed from the freezer left at room temperature for 2 h, stored in a refrigerator overnight to thaw, and then blended.

Analytical Techniques

After the frozen samples were thawed and blended, the following analyses were performed: total nitrogen, solids, total chloride (Horwitz 1975), total volatile base (TVB; Stansby et al. 1944), total volatile acid (TVA; Friedemann and Brook 1938), trimethylamine (TMA; Dyer 1945), and carotenoids (Kelley and Harmon 1972). Sodium and potassium were determined by using a Beckman Model B hydrogen-oxygen flame photometer on appropriate dilutions of a 20-g sample digested with nitric and perchloric acids. The pH of the brine was determined daily.

RESULTS AND DISCUSSION

Whole Shrimp

The change in weight of whole shrimp held in these systems has commercial importance. The yield of product obtained in a processing plant is calculated from the weight of whole shrimp landed at the dock. The time of holding and the holding system affect the weight of landed shrimp (Table 1) and, therefore, the yield of the final product. Whole shrimp held in MRSW gained 5% in gross weight during the first 1.5 days and slowly gained an additional 2% during the next 7 days. A much

TABLE 1.—Change in gross weight and percentage solids with time of holding 2,100 g of whole pink shrimp in modified refrigerated seawater (MRSW) and ice and pH of the brine.

		MRSW system		Ice system	
Holding time (days)	pH	Gross weight (g)	Solids (%)	Gross weight (g)	Solids (%)
0.5	6.85	2,173	22.1	2,215	20.7
1.5	6.50	2,198	18.8	2,333	18.6
2.5	6.40	2,191	19.0	2,333	17.6
3.5	6.40	2,165	18.8	2,365	18.7
4.5	6.10	2,214	18.6	2,330	17.5
5.5	6.30	2,214	18.0	2,323	17.2
6.5	6.40	2,212	18.3	2,355	16.8
7.5	6.35	2,226	18.0	2,315	16.9
8.5	6.30	2,250	18.3	2,331	17.1
9.5	6.50	2,200	17.8	2,254	16.0
10.5	6.70	2,177	17.6	2,263	16.3
11.5	6.67	2,245	17.7	2,239	14.5
12.5	6.57	2,221	17.7		

higher gain in weight was observed in the ice-held shrimp. The ice-held whole shrimp gained 11% in the first 1.5 days, maintained this weight for 8.5 days, and decreased thereafter. These gross changes in weight were caused by changes in the water, solids, and salt content of whole shrimp with time of holding (Collins 1960, 1961).

The pH of the brine was 3.92 at the beginning of the experiment and rose to 6.85 during the first 12 h but varied between 6.1 and 6.9 during the remainder of the experiment. The flow of carbon dioxide was regulated at approximately 0.2 l/min but was shut off occasionally to reduce excess loss of carbon dioxode to the environment and buildup of foam.

Hand-Peeled, Raw, Pink Shrimp Meats

Gross weights of hand-peeled, raw meats increased rapidly in both holding systems (Table 2). The salt and sodium content of the raw peeled meats from the MRSW system increased rapidly during the first 2 days to 2% and 0.85%, respectively, and remained at this level over the remainder of the holding period. Potassium decreased during the holding period (MacLeod et al. 1960). In the ice system, however, the meats slowly lost salt, presumably due to the leaching effect of the ice melt.

Based on chemical tests, the quality of shrimp held in the MRSW system was considered acceptable through 9.5 days. There was a slight increase in the total volatile acid value at 9.5 days and in the trimethylamine value at 10.5 days, suggesting that quality deteriorated slightly after 8.5 days. In the ice system, quality was acceptable up to 6.5 days, borderline at 7.5 days, and unacceptable thereafter.

Because of the large excess of ice used in this holding experiment, the commercial limit for holding shrimp on ice would probably be less than 6.5 days. In this study, it appears that pink shrimp held in the MRSW system can be held for several days longer than in ice.

Hand-Peeled, Raw, Washed, Pink Shrimp Meats

The solids content (Table 3) for the hand-peeled, raw, washed meats when expressed as percentage composition, was nearly equal from the two holding systems after the effects of salt were removed by subtraction. In both systems there was a rapid decrease in percentage solids (increased moisture) for the first 5 days, but the percentage solids remained about equal thereafter. Salt, sodium, and potassium followed the same trend as the raw, peeled meats but at a lower level due to the washing.

The data on gross weight and composition (Table 3) are not useful for direct comparison of recovery of meat between the two holding systems because of differences in moisture and salt content. When recalculated on a constant basis (salt-free, 84% moisture), recoveries of raw, washed meats were much higher for the ice system than for the MRSW system (Figure 1). This observation was confirmed when recoveries of protein were compared for the two systems (Figure 1). The sharp drop in recovery at 6.5 days for the ice system suggested that soluble proteins were retained through the mild washing technique used in this experiment until spoilage became evident (the 6.5 day break point). In the MRSW system, however, the soluble proteins were leached gradually into the aqueous system.

TABLE 2.—Change in weight and analytical values with time of holding 2,100 g of hand-peeled, raw, pink shrimp meats in modified refrigerated seawater (MRSW) and ice.

	MRSW system								Ice system							
Holding time (days)	Gross weight (g)	Solids (%)	NaCl (%)	Na (%)	K (%)	TVA (meq H^+/ 100 g)	TVB (mg N/ 100 g)	TMA (mg N/ 100 g)	Gross weight (g)	Solids (%)	NaCl (%)	Na (%)	K (%)	TVA (meq H^+/ 100 g)	TVB (mg N/ 100 g)	TMA (mg N/ 100 g)
0.5	759	19.6	1.5	0.66	0.16	0.04	10.2	0.1	743	19.0	0.6	0.26	0.27	0.10	11.0	0.0
1.5	797	19.0	1.9	0.78	0.10	0.05	4.8	0.3	787	18.0	0.5	0.26	0.25	0.10	4.0	0.3
2.5	790	18.3	2.0	0.83	0.09	0.06	2.8	0.3	815	17.1	0.5	0.25	0.21	0.08	4.5	0.2
3.5	803	18.0	2.1	0.85	0.08	0.16	7.2	0.2	819	16.9	0.6	0.26	0.21	0.06	8.8	0.2
4.5	807	17.7	2.1	0.85	0.08	0.28	7.0	0.4	827	16.5	0.6	0.25	0.21	0.21	10.8	0.2
5.5	793	17.5	2.1	0.84	0.09	0.26	7.0	0.6	822	16.6	0.6	0.26	0.20	0.15	10.9	0.3
6.5	812	17.5	2.2	0.85	0.09	0.39	6.6	0.5	830	15.7	0.5	0.24	0.18	0.32	12.4	0.3
7.5	814	17.6	2.2	0.84	0.08	0.31	7.2	0.5	837	15.7	0.5	0.23	0.18	0.46	12.8	1.1
8.5	822	17.5	2.2	0.90	0.09	0.21	7.0	0.8	853	15.9	0.5	0.24	0.18	0.51	18.5	3.2
9.5	812	17.3	2.2	0.90	0.09	0.43	6.8	0.8	855	15.2	0.4	0.20	0.15	0.58	18.9	5.1
10.5	805	17.1	2.2	0.90	0.09	0.40	7.3	1.1	850	15.2	0.5	0.21	0.16	0.87	26.2	11.4
11.5	836	16.9	2.2	0.91	0.09	0.50	9.1	1.1	848	13.0	0.2	0.11	0.07	0.50	15.8	6.5
12.5	827	16.3	2.1	0.85	0.08	0.46	7.5	1.1								

TABLE 3.—Change in weight and analytical values with time of holding 2,100 g of hand-peeled, raw, washed, pink shrimp meats in modified refrigerated seawater (MRSW) and ice.

	MRSW system						Ice system					
Holding time (days)	Gross weight (g)	Solids (%)	Protein (%)	NaCl (%)	Na (%)	K (%)	Gross weight (g)	Solids (%)	Protein (%)	NaCl (%)	Na (%)	K (%)
0.5	749	17.8	15.4	1.2	0.48	0.14	761	16.4	15.2	0.5	0.21	0.20
1.5	827	17.6	13.7	1.7	0.65	0.08	820	15.9	14.7	0.5	0.21	0.19
2.5	816	16.6	13.6	1.8	0.69	0.07	844	15.3	14.1	0.4	0.21	0.17
3.5	783	16.5	13.5	1.8	0.70	0.07	862	15.1	13.8	0.5	0.22	0.16
4.5	799	16.1	13.1	1.9	0.71	0.07	859	14.9	13.8	0.5	0.22	0.16
5.5	809	15.8	12.8	1.9	0.69	0.06	859	15.0	13.9	0.5	0.25	0.17
6.5	812	16.1	12.9	1.9	0.73	0.07	846	14.3	13.1	0.4	0.21	0.14
7.5	801	16.4	13.3	1.9	0.69	0.07	856	14.3	13.3	0.4	0.20	0.14
8.5	828	16.2	13.0	1 9	0.70	0.07	866	14.4	13.2	0.4	0.20	0.14
9.5	794	16.1	13.1	2.0	0.71	0.07	864	13.9	12.6	0.4	0.17	0.12
10.5	793	15 9	11.1	2.0	0.72	0.07	850	14.0	12.8	0.4	0.17	0.13
11.5	807	15.7	12.6	2.0	0.71	0.07	825	12.2	11.2	0.2	0.09	0.05
12.5	796	16.0	12.8	2.1	0.75	0.07						

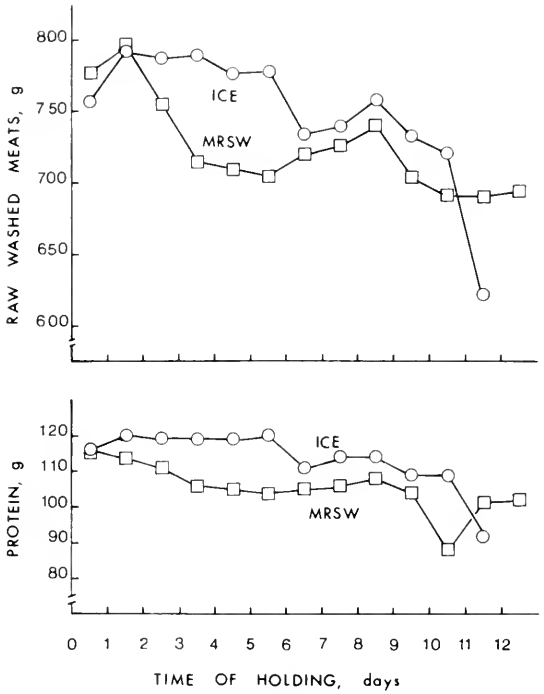

FIGURE 1.—Recovery of hand-peeled, raw, washed pink shrimp meats with time of holding 2,100 g of shrimp in modified refrigerated seawater (MRSW) or ice, expressed on a salt-free, 84% moisture basis and protein.

Commercial shrimp peelers exert a strong mechanical and washing action on the shrimp, which leaches out soluble proteins. In part therefore, the final yield would be a function of the gross weight of the landed whole shrimp and of the amount of soluble protein present, which would be influenced by the time and extent of action by bacteria or enzymes. Because the MRSW system reportedly extends holding time, ex-vessel shrimp—processed at an equal stage of quality (say, 4-day ice and 8-day MRSW) and at an equal water content—should give equal yields. In actual practice, however, machine peeling efficiency tends to be the controlling factor for yield. For example, if shrimp were to peel too easily on the machines, yields would be low because the meats would be rubbed off on the rollers. Yields would also be low if the shrimp were too difficult to peel because some unpeeled shrimp would be discarded at the inspection belt. Nelson and Barnett[3] obtained a 19% raw meat yield from pink shrimp held in the MRSW system and processed through a Laitram (Model A) machine peeler.

Hand-Peeled, Washed, Cooked, Pink Shrimp Meats

The gross weights for hand-peeled, washed, cooked meats obtained from the 2,100 g of whole shrimp were considerably higher from the ice-held shrimp than from the MRSW-held shrimp (Table 4). Under commercial processing conditions, infill weights must be adjusted to compensate for the high moisture content which would otherwise cause low drained weights after retorting or freezing. Consequently, to equalize the variable water content between holding systems and samples, we calculated the weight on a constant basis (salt-free, 75% moisture) and found that the two holding systems gave nearly identical recoveries except for low recoveries during the first several days in

[3]Nelson, R. W., and H. J. Barnett. Improved shrimp quality by the use of RSW modified with CO_2 gas. Unpubl. manuscr. Northwest and Alaska Fisheries Center Utilization Research Division, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

TABLE 4.—Change in weight and analytical values with time of holding 2,100 g of hand-peeled, washed, cooked, pink shrimp meats in modified refrigerated seawater (MRSW) and ice.

	MRSW system							Ice system						
Holding time (days)	Gross weight (g)	Solids (%)	Protein (%)	Carotenoid index	NaCl (%)	Na (%)	K (%)	Gross weight (g)	Solids (%)	Protein (%)	Carotenoid index	NaCl (%)	Na (%)	K (%)
0.5	413	24.8	22.3	0.065	0.7	0.35	0.09	353	24.2	22.6	0.047	0.3	0.16	0.14
1.5	389	25.6	22.6	0.077	1.1	0.49	0.06	395	23.3	21.5	0.062	0.3	0.17	0.14
2.5	352	27.6	24.1	0.089	1.2	0.49	0.05	390	22.6	20.5	0.058	0.3	0.17	0.13
3.5	284	28.1	24.6	0.084	1.1	0.46	0.04	373	22.4	20.9	0.067	0.3	0.17	0.12
4.5	309	28.6	24.6	0.089	1.1	0.46	0.04	399	21.6	20.1	0.064	0.3	0.16	0.11
5.5	286	29.6	25.8	0.091	1.1	0.46	0.04	367	23.1	21.3	0.068	0.3	0.17	0.12
6.5	298	30.2	26.1	0.086	1.1	0.43	0.04	374	22.0	20.3	0.068	0.3	0.16	0.13
7.5	280	29.9	26.9	0.092	1.1	0.42	0.04	383	21.9	20.0	0.074	0.3	0.15	0.10
8.5	289	29.9	25.6	0.098	1.1	0.43	0.04	398	22.0	20.2	0.074	0.3	0.16	0.11
9.5	291	29.8	25.7	0.096	1.1	0.46	0.04	396	21.8	20.0	0.075	0.2	0.16	0.08
10.5	275	30.5	26.6	0.093	1.1	0.44	0.04	387	21.5	19.9	0.077	0.2	0.14	0.09
11.5	258	30.0	26.4	0.090	1.1	0.44	0.04	348	21.8	19.9		0.1	0.13	0.09
12.5	262	29.9	26.1	0.094	1.1	0.44	0.04							

ice caused by poor peeling characteristics. These adjusted weights and the protein data (Figure 2) showed a rapid decrease from both holding systems to 4.5 days, a leveling off to 10.5 days, and another decrease at 11.5 days.

Under commercial fishing and processing conditions, payment for landed shrimp is based on weight, and weight depends upon time of holding and system used. In our equipment, ice-held shrimp gained more weight and gave a greater recovery of cooked meats than shrimp in the MRSW system. Based on the weight of whole shrimp (Table 1) and the weight of cooked meats (Table 4), therefore, MRSW-held shrimp gave much lower yields than ice-held shrimp, averaging 13.9 and 16.4%, respectively. This difference in yield between systems would be reduced when the processor adjusts the weight of infill for a proper cut-out weight. Overall, the only difference in yield between systems is that caused by changes in water and salt content in the whole shrimp, i.e., landed weight. Under production conditions, MRSW has a slight advantage over ice because whole shrimp gain less in MRSW than in ice. It is believed that the laboratory data on the MRSW system would be representative of an MRSW holding system on a boat, but icing techniques may vary considerably from laboratory to boat, and the results obtained in the laboratory may differ from those in commercial practice.

Sodium chloride, sodium, and potassium followed the same general trends as the previous subsamples. The lower levels (1.1% NaCl, MRSW; 0.3% NaCl, Ice) were caused by cooking.

The carotenoid index, previously used to indicate comparative quality between production variables (Collins and Kelley 1969), showed an increase with increase in time of holding shrimp in

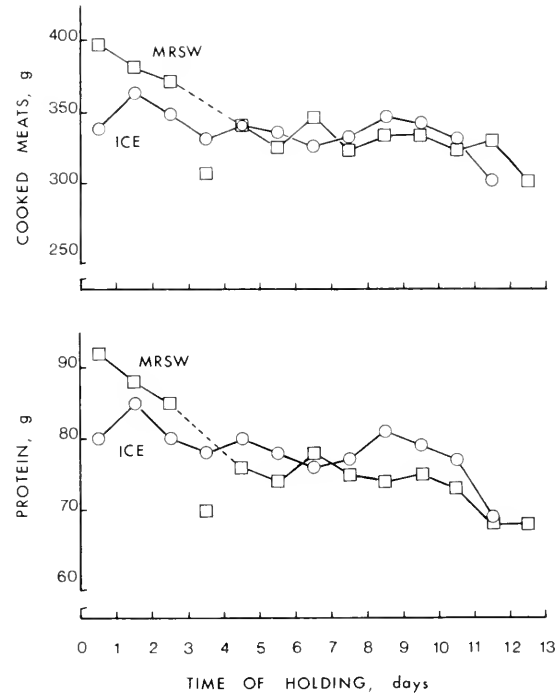

FIGURE 2.—Recovery of hand-peeled, cooked pink shrimp meats with time of holding 2,100 g of shrimp in modified refrigerated seawater (MRSW) or ice, expressed on a salt-free, 75% moisture basis and protein.

both systems. The index, expressed on a dry basis, unexpectedly increased rather than decreased with holding time. We suggest that the peeling-washing technique used in this experiment was less severe than that used during commercial machine peeling and that the 26% loss of protein in cooked meats over the holding period caused a pseudoincrease in the carotenoid content. In

agreement with Nelson and Barnett (1971), the color of shrimp held in MRSW was much better than that for shrimp held in ice.

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TAXONOMY AND DISTRIBUTION OF *ROULEINA ATTRITA* AND *ROULEINA MADERENSIS* (PISCES: ALEPOCEPHALIDAE)[1]

DOUGLAS F. MARKLE[2]

ABSTRACT

Three Atlantic species of *Xenodermichthys* and *Rouleina* are recognized: *X. copei*, *R. attrita*, and *R. maderensis*. *Bathytroctes mollis* and *B. aequatoris* are considered junior synonyms of *R. attrita*. *Anomalopterus megalops* is considered incerta sedis.

Diagnostic characters for *R. attrita* are: no photophores, convoluted testes, 43-48 lateral line scales, 43-46 preural vertebrae, papillae on body near lateral line, and maturation at a size around 250-300 mm standard length. Diagnostic characters for *R. maderensis* are: photophores present, lobate testes, 50-56 lateral line scales, 47-50 preural vertebrae, papillae usually peripheral to photophores on fins and fin bases, and maturation at a size around 200-250 mm standard length.

The two species are sharply segregated by depth: 91% of all *R. maderensis* were from bottom trawls made between 595 and 1,200 m while 88% of all *R. attrita* were from bottom trawls fished between 1,400 and 2,100 m.

The Alepocephalidae are moderate to large deep-sea salmoniform fishes, most commonly encountered below 1,000 m. In terms of biomass and species diversity, the family is one of the most important in the deep sea. Recent exploratory trawling has discovered commercial concentrations of alepocephalids west of the British Isles (Anonymous 1974) and in the northwestern Atlantic (Savvatimskii 1969). Off northwestern Africa, Golovan (1974) found about 20 species of alepocephalids and labeled the zone below about 1,000 m as "the kingdom of fishes of the family Alepocephalidae." As might be expected in a diverse group of deep-sea fishes, there are still many problems with identification and nomenclature.

One group of naked alepocephalids, those with approximately equal and opposite dorsal and anal fins, has been the subject of numerous descriptions and much confusion. Roule (1915) recognized two genera, *Rouleina* (=*Aleposomus* of Roule) and *Xenodermichthys*, the latter distinguished by a greater number (more than 25) of dorsal and anal fin rays.

The two known species of *Xenodermichthys*, *X. nodulosus* and *X. copei*, have caused few taxonomic problems and are easily diagnosed. Both have photophores arranged approximately in quincunx on the body and fin bases, two pyloric caeca, and no lateral line scales in adults. *Xenodermichthys copei* has 27-31 dorsal and 26-30 anal fin rays, 46-50 vertebrae, and an unrestricted gill opening; *X. nodulosus* has 32-33 dorsal and anal fin rays, 50 vertebrae, and a dorsally restricted gill opening which begins at the upper base of the pectoral (Markle 1976). The nomenclature of the Atlantic species, *X. copei*, has been confused because the oldest of the three available names, *Aleposomus copei* Gill 1884, was originally described as: "an Alepocephalid, with the body as well as heads caleless (sic), which I shall describe as *Aleposomus copei*." Grey (1959) and Krefft (1973) have considered *A. copei* Gill 1884 a nomen nudum, but Gill's (1884) sentence clearly refers to an alepocephalid with a naked head and body, and in 1884 that was a sufficient amount of information to clearly distinguish it from all known alepocephalids, with the possible exception of *X. nodulosus*. In any case the inadequate statement satisfies Articles 11 and 12 of the International Code of Zoological Nomenclature and the name has been used frequently since 1884. Gill's holotype (USNM 33551) was subsequently described and figured by Goode and Bean (1895).

The taxonomy of *Rouleina* is more confused, in part because there are 15 nominal species, many based upon damaged or poorly preserved specimens. All known species of *Rouleina* can be distinguished from *Xenodermichthys* by having less than 25 anal fin rays, more than two pyloric caeca,

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and modified ringlike lateral line scales in the adults. Photophores are present or absent: their loss appears secondary. For example, in *R. funebris* the size and arrangement of photophores are identical to *Xenodermichthys*: in *R. maderensis* the photophores are smaller; in *R. harperi* only dark spots remain; and in *R. attrita* there are no photophores. The purpose of this paper is to discuss the taxonomy and distribution of the two known Atlantic species, *R. attrita* and *R. maderensis*.

METHODS

Standard taxonomic measurements and counts were made (Hubbs and Lagler 1958) with the following clarifications and additions. Caudal vertebrae were distinguished from precaudal vertebrae by the presence of a haemal arch and spine in the former. On radiographs there is a sharp demarcation, characterized by a reduction in the length of the pleural rib on the last precaudal vertebra and/or the apparent intersection of the last pleural rib with the first haemal spine. The last caudal vertebra counted is that which articulates with the parahypural, even if fused to a ural centrum. The one or more ural centra are variable in alepocephalids and were not counted.

The high water content and postpreservation shrinkage plus the damage inflicted on most alepocephalids during capture, causes a noticeable amount of variation in most measurements of a species or even in repeated measurements of an individual. The precision of alepocephalid morphometrics is therefore relatively low. In addition, most alepocephalid morphometrics exhibit definite allometry (Parr 1949, 1956, 1960). Before the allometry of morphometrics will be useful in identifying larvae and small juveniles, more smaller and less damaged specimens than are presently available will be needed.

MATERIAL

The following type-material of *Rouleina* was examined from the U.S. National Museum of Natural History, Washington, D.C. (USNM); Museum National d'Histoire Naturelle, Paris (MNHN); Zoological Museum, University of Copenhagen (ZMUC); Zoological Museum, Berlin (ZMB); and Museu Municipal do Funchal, Madeira (MMF): *Bathytroctes attrita*, MNHN 85-166 and 85-169; *B. mollis*, MNHN B-2219; *B. aequatoris*, USNM 44085; *B. harperi*, USNM 92333; *B. welshi*, USNM 92332; *Xenodermichthys funebris*, USNM 99534, *Anomalopterus megalops*, USNM 170957; *Aleposomus nudus*, ZMB 17426; *A. lividus*, ZMB 22398; *R. danae*, ZMUC P1778; and *R. maderensis*, MMF 50, 2395, and 2396.

Additional material was examined from the British Museum (Natural History), London (BMNH); University Museum, Tokyo (UMT); Institute of Oceanographic Sciences, Wormley, England (IOS); Museum of Comparative Zoology, Harvard (MCZ); Field Museum of Natural History, Chicago (FMNH); Rosenstiel School of Marine and Atmospheric Sciences, Miami (UMML); Institut für Seefischerei, Hamburg (ISH); and Virginia Institute Marine Science, Gloucester Point (VIMS). These collections included four specimens of *R. guentheri* cataloged as BMNH 1898.7.13.19 and UMT 5785, 5785′, and 20983; one specimen of *R. danae*, USNM 215490; 69 specimens of *R. attrita*, USNM 215479-215489 and 44085; ISH 123/73, 124/73, 950/73, 141/74, 163/74, 511/74, 512/74, 835/74, 844/74, 212/75, 234/75, and one uncatalogued; VIMS 3539, 3540, 3542, and 3543; FMNH 65711; UMML 22353; MCZ 40609; and IOS Discovery 8512#1; and 35 specimens of *R. maderensis*, USNM 215471-215478; ISH 130/75; VIMS 3541; MCZ 39349; BMNH 1945.7.20.5; IOS Discovery 7431, 7432, and 7436; and ZMUC Dana 1183[1].

RESULTS

The species of *Rouleina* separate conveniently into two groups. The first group, which lacks photophores or their remnants, contains *R. attrita* and *R. danae*. *Rouleina danae* differs from *R. attrita* by its reduced maxillary dentition and much larger orbit (43.5% of head length (HL) vs. 24-29% HL at about 100 mm standard length (SL)). The second group, which has photophores, contains *R. maderensis* and several Indo-Pacific species which differ from it in having fewer anal fin rays (16-19 vs. 20-22).

Although the two North Atlantic species, *R. attrita* and *R. maderensis*, are easily distinguished with undamaged material, most specimens are damaged and the two species are very similar in gross morphology. The following key summarizes characters which have been found useful to separate these species.

Key to North Atlantic Species of *Rouleina*

1a. No photophores: testes ribbonlike with many convolutions in mature specimens but folds always connected, never with separate lobes (Figure 1); lateral line with 43-48 modified ringlike scales, undetectable in specimens less than 155 mm SL; preural vertebrae 19-22 (precaudal) + 22-26 (caudal) = 43-46 (total); papillae on body especially near lateral line, along bases of vertical fins, and along all fin rays; mature around 250-300 mm SL ..... *R. attrita* (Vaillant 1888)

1b. Flat superficial photophores present, commonly abraded; testes discrete, separate lobes even when immature (Figure 1); lateral line with 50-56 modified ringlike scales, undetectable at 131 mm SL; preural vertebrae 20-22 (precaudal) + 26-28 (caudal) = 47-50 (total); papillae restricted to fins and fin bases, usually peripheral to photophores which are more numerous below lateral line; mature around 200-250 mm SL ..... *R. maderensis* Maul 1948

Rouleina attrita (Vaillant 1888)

Figure 2A

Bathytroctes attritus Vaillant 1888:158, fig. 2 (holotype, MNHN 85-166 only; lat. 37°35′N, long. 29°26′W, 1,442 m; paratype, MNHN 85-169, is *Bellocia koefoedi*).

Bathytroctes mollis Koehler 1896:517, pl. 26, fig. 2 (holotype, MNHN B-2219, Bay of Biscay, 1,700 m).

Bathytroctes aequatoris Goode and Bean 1896:44, fig. 50 (holotype, USNM 44085, lat. 01°03′N, long. 80°15′W, 1,355 m).

Nomenclature

Quéro (1974) suggested that *R. attrita* be treated as a nomen dubium since Vaillant (1888:158), using a 55-mm shred of skin from the caudal peduncle, had estimated 40-50 scale rows on the body and since Vaillant's dorsal and anal fin ray counts are wrong for *Rouleina*. The source of the problem is the nature of the skin of *Rouleina* and the fact that the remaining type-material represents two different genera (Vaillant originally listed four specimens, but two could not be located

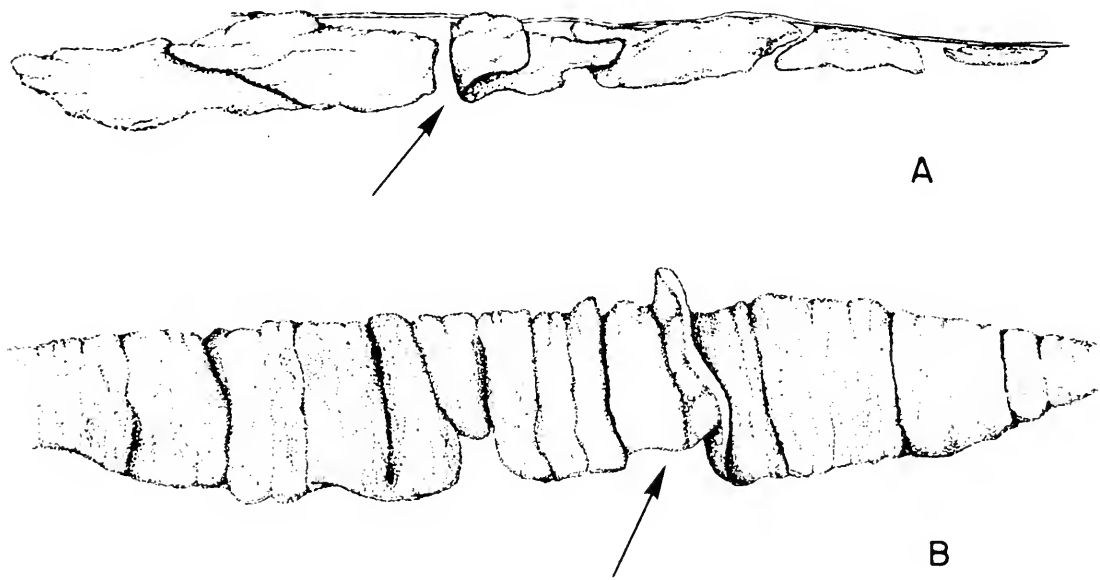

FIGURE 1.—A. *Rouleina maderensis*, USNM 215476, about 275 mm SL, testes, showing completely separated lobes (arrow). B. *Rouleina attrita*, USNM 215483, 369 mm SL, testes, showing convolutions without the formation of separate lobes (arrow).

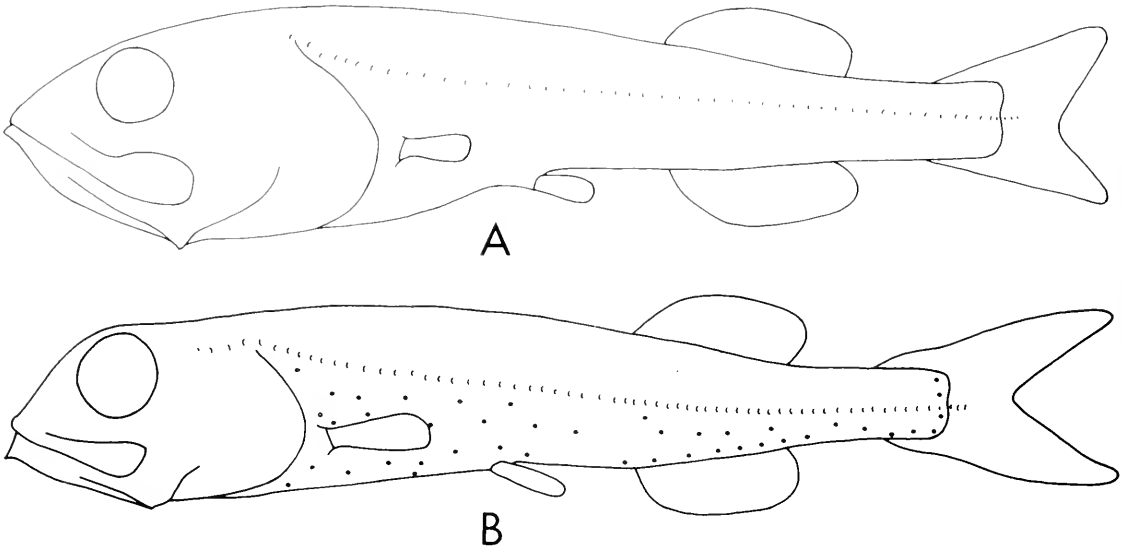

FIGURE 2.—A. *Rouleina attrita*, redrawn from Koefoed (1927, plate 3, fig. 5). B. *Rouleina maderensis*, redrawn from Maul (1948, fig. 1), with photophore distribution based upon USNM 215478, 131 mm SL.

in MNHN). Fortunately, Vaillant clearly indicated that the description of each species is based on a unique individual chosen from the collection (Bauchot et al. 1971). On the bottom of page 159, following a list of measurements of a 250-mm specimen, Vaillant (1888) made the notation "No. 85-166, Coll. Mus.," a clear designation of a holotype. This specimen is now in very poor condition but a piece of skin clearly shows the typical ring-like lateral line scales (Figure 3) and indications of fluid-filled dermal compartments typical of *Rouleina*. The latter could be mistaken for scale poc-

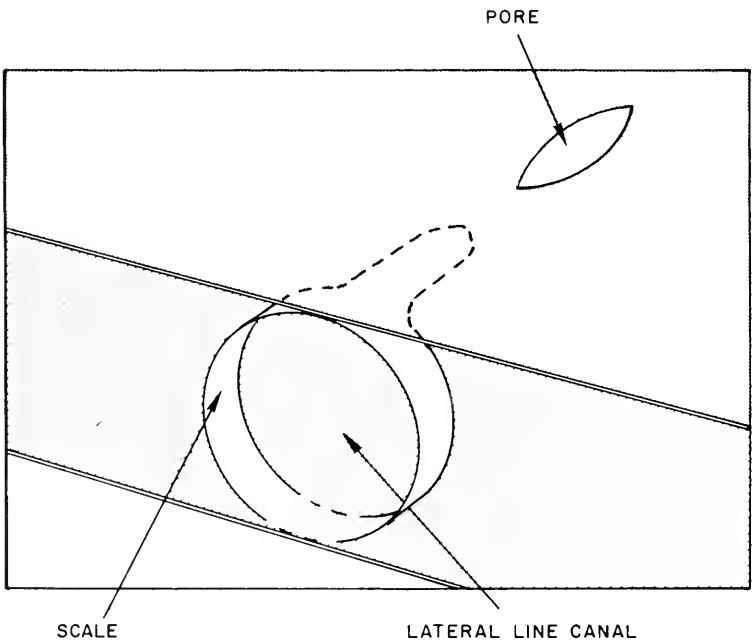

FIGURE 3.—*Rouleina attrita*, schematic of lateral line scale and subsequent pore from the midbody region.

kets and are very similar to the dermal compartments in *Xenodermichthys* as illustrated and described by Best and Bone (1976).

Vaillant (1888, pl. 12, fig. 2) illustrated otoliths and gave a vertebral count (Vaillant 1888,159) "Il y a 20 vertebres dorsales et 25 caudales." A radiograph of the contents of the jar containing MNHN 85-166 showed that the otoliths were intact and there were 20 + 24 vertebrae. It is likely therefore that both observations came from the missing paratypes. A comparison of the illustrated otoliths with recently collected material of *Alepocephalus agassizii*, *Xenodermichthys copei*, *Bathytroctes microlepis*, *Narcetes stomias*, and *Rouleina attrita* shows they were undoubtedly taken from a *Rouleina*. Haedrich and Polloni (1974) found unstated "significant differences" between their *Rouleina* otoliths and Vaillant's, but their description and my examination of their specimens (ISH 950/73) shows them to be *R. attrita*. Therefore, the vertebral counts, lateral line scales, Vaillant's estimate of number of (lateral line) scales, and otoliths indicate that the holotype and probably the missing paratypes agree with recently collected material of *R. attrita*.

The remaining paratype, MNHN 85-169 (lat. 15°48′N, long. 20°23′W, 3,655 m), is a specimen of *Bellocia koefoedi* Parr 1951. This identification is based on examination of the type series of *B. koefoedi* in the Zoological Museum, Bergen, and the presence of the following diagnostic characters in MNHN 85-169: palatine teeth present, gill rakers 4-1-14 on first arch, body scaled, dorsal inserted in advance of anal, and a radiograph shows 22 + 18 = 40 vertebrae, 11 anal fin rays, and about 16 dorsal fin rays. The radiograph also shows otoliths in the skull and a standard length of no more than 220 mm (Quéro 1974 stated about 230 mm). The length, intact otoliths, and vertebral count indicate that Vaillant (1888) was not basing his description of *R. attrita* on MNHN 85-169. However, since its condition is somewhat better than the holotype, Vaillant's reference to scale rows and a minimum of 11 anal fin rays may have been based on comparison with this specimen.

Description

Accurate descriptions and illustrations can be found in Goode and Bean (1895, as *B. aequatoris*), Koehler (1896, as *B. mollis*), Koefoed (1927, as *Talismania mollis*), Grey (1959), Haedrich and Polloni (1974), and Pakhorukov (1976). Important diagnostic meristic characters are in Table 1. In addition, the present material showed the following meristic variation (number of specimens in parentheses): $P_1$6-7 (26), $P_2$6-7 without a splint bone (27), gill rakers on first arch [7-8] + 1 + [15-20] = [23-28] (23), branchiostegal rays 6 (5), and pyloric caeca 7-11 (16). Teeth are present only on the dentary, premaxillary, maxillary, third and fourth infrapharyngobranchials, fourth epibranchial, and fifth ceratobranchial.

Twenty-six specimens of *R. attrita*, 57.1-378 mm SL, showed much morphometric variation and no noticeable differences with 19 *R. maderensis*, 86.7-323 mm SL. In both species smaller specimens have relatively shorter caudal peduncles. In addition, smaller specimens of *R. attrita* (<155 mm SL) lacked lateral line scales and the papillae on the body were relatively longer and more noticeable than in larger specimens.

In one well-preserved large specimen, 347 mm SL (USNM 215481), the branchiostegal membranes, gill cavity, orbit, and bases of fins are bluish. The rest of the body is covered by thin black skin, under which is a network of longitudinally aligned, fluid-filled, oblong dermal compartments (Best and Bone 1976). The lateral line, which extends onto the caudal fin, is a tube supported by

TABLE 1.—Selected counts of *Rouleina attrita* and *R. maderensis* (superscript prefix indicates type material of: A—*Bathytroctes attritus*, B—*R. maderensis*, C—*B. aequatoris*, and D—*B. mollis*).

Species	Lateral line pores													
	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
R. attrita	1	1	4	2	1										
R. maderensis								2		1	1	1	B_1	2	B_1

	Precaudal vertebrae					Caudal vertebrae						Total vertebrae						
	19	20	21	22	22	23	24	25	26	27	28	43	44	45	46	47	48	49	50
R. attrita	4	$^{A.C.D}22$	7	2	1	D_1	$^{A.C}13$	15	4			D_1	$^{A.C}13$	15	7				
R. maderensis		2	B_{17}	17					B_{19}	B_{15}	3					B_8	B_{22}	8	1

	Dorsal fin rays					Anal fin rays					
	18	19	20	21	22	18	19	20	21	22	
R. attrita	5	D_{10}	C_{10}	1		D_7	10	C_9	1		
R. maderensis			3	B_8	B_5			5	B_6	4	

modified ringlike scales with pores usually situated midway between and not touching the scales (Figure 3). The skin along the dorsal midline, above the supracarinalis muscle, is typically split open, exposing dense fat deposits and mucus. Ventrally, the skin overlying the lower hypaxial muscles is also split open. In addition, the area ventral to the heart, between the cleithra, contains a mucus-filled network of connective tissue.

Testes are thin ribbonlike structures in immature males and become thick and convoluted in mature specimens. The convolutions, however, never become separate lobes (Figure 1). The ovaries, back to about the level of the pelvics, are completely enclosed by ovarian tunic medially and the body wall laterally. Posteriad the lateral ovarian surface is exposed. The ovary contains few eggs up to 3.2 mm in diameter.

Rouleina maderensis Maul 1948

Figure 2B

Rouleina maderensis Maul 1948:7, fig. 1 (holotype, MMF 2398, Madeira, 600-1,600 m depth range for type series).

As a supplement to Maul's (1948) description, Table 1 summarizes important diagnostic meristic characters. In addition, the present material showed the following meristic variation (number of specimens in parentheses): $P_1$5-7 (13), $P_2$5-6 without a splint bone (13), gill rakers on first arch [6-8] + 1 + [15-21] = [22-30] (8), branchiostegal rays 6 (12), and pyloric caeca 10-11 (7). Dentition similar to *R. attrita*.

Lateral line scales were absent in the two specimens <131 mm SL but were present in a 177-mm SL specimen. Photophores were present on the smallest specimen, 86.7 mm SL. Generally, photophores are more difficult to find in larger specimens.

Black papillae are distributed along the base of the caudal, on primary caudal rays, dorsal and anal rays, on the supratemporal, and from the interorbital area to the snout. An irregularly arranged row of papillae lies between the lateral line and dorsal profile. Small flat photophores are mostly located below the lateral line; a paratype (MMF 50) has nine photophores along the anal fin, two on the base of the lower caudal and one or two on the upper caudal base; body photophores are arranged approximately in quincunx. The superficial layer of black skin covers longitudinally aligned, fluid-filled, oblong, dermal compartments and is frequently split along the midline as in *R. attrita*. The modified ringlike lateral line scales have a relatively broad and long posterior tab. Lateral line pores are usually at the end of the scale tab of the preceding lateral line scale, approximately midway between scales but touching the anterior scale.

Testes, even when immature, are always lobed (Figure 1). The ovary is similar to that in *R. attrita*. Eggs are large, up to 3.7 mm.

Incerta sedis

Anomalopterus megalops Beebe 1933

An examination of Beebe's damaged and contorted holotype (USNM 170957), now about 25 mm SL, indicates that it might be a *Rouleina*. The dorsal and anal origins appear approximately opposite in contrast to Beebe's (1933) statement that the anal origin was under the middle of the dorsal. The "numerous small tubercles" which Beebe found abundant on the head and less so on the body are no longer visible. Beebe's (1933) description, the best source for deciphering the identity of the specimen, agrees with *Rouleina*, especially *R. maderensis*. However, the seven branchiostegal rays and anal fin extending well posteriad of the end of the dorsal fin are characters which are unknown in the available North Atlantic *Rouleina*. Identification of this specimen should be postponed until more larval and juvenile material are available.

ECOLOGY

Direct sighting of two *R. attrita* <1 m from the bottom at 1,800 m off Virginia was made during DSRV *Alvin* dive 575, 4 June 1975. The moderate-sized individuals had a more rounded head than the more commonly sighted alepocephalid, *Alepocephalus agassizii*. The dorsal and ventral profiles of the snout and lower jaw regions are approximately equal arcs in *R. attrita* (Figure 2A), while in *A. agassizii* the ventral profile of the lower jaw is straighter. The skin of *R. attrita* also appears smoother since it is mostly scaleless, but both are about equally black in situ.

An unexpected observation was that the two *R. attrita* had shredded sheets of mucus hanging from their jaws and body. The two individuals drifted

motionless by the observation port, one head down, the other more or less on its side. *Alepocephalus agassizii* was observed in similar motionless positions and were seen to move when disturbed, so that the motionless positions are probably not a sign of death. The observation of mucus is, as yet, uncorroborated by others. However, Koehler (1896:518) described the fresh condition of the holotype of *B. mollis* as being flaccid as a holothurian and retrieved from the trawl in a thick mucus. The split skin along the dorsal and ventral midline commonly observed in preserved specimens of *Rouleina* may be related to fat and mucus concentrations in these regions of the body. The function of these concentrations and the mucus sheets is unknown.

All of the *R. attrita* and most of the *R. maderensis* were from bottom trawls, but two of the smaller *R. maderensis,* 86.7 and 177 mm SL, were from nonclosing midwater trawls. It is possible that the rather amorphous and almost degenerate photophores (based on microsections from a 236-mm SL specimen) of demersal adult *R. maderensis* represent organs which are functional only in mesopelagic juveniles.

DISTRIBUTION

Both species are known from the southeastern Pacific and North Atlantic, while *R. attrita* is also known from the South Atlantic and southwestern Indian Ocean (Figure 4). The two species have been caught in the same net once in the western Atlantic and once in the southeast Pacific. Although the geographic distributions are similar, *R. attrita* and *R. maderensis* segregate sharply by depth. Thirty of 33 specimens (91%) of *R. maderensis* were from bottom trawls fished between 595 and 1,200 m. In contrast, 66 of 75 specimens (88%) of *R. attrita* were from bottom trawls fished between 1,400 and 2,100 m.

Off the east coast of the United States, the most consistent physical characteristic between 1,200 and 1,400 m is the 4°C isotherm (VIMS unpubl. data, Churgin and Halminski 1974a). However, in the Gulf of Mexico (Churgin and Halminski 1974b) and eastern North Atlantic (Lenz 1975), the 4°C isotherm is considerably deeper. A characteristic feature of the demersal ichthyofauna on the continental slope off Virginia is a sharp increase in mean weight of individual fish around 1,500 m (Markle 1976; C. A. Wenner and J. A. Musick pers. commun.). Consistent with this phenomenon is the observation of generally larger body size in the deeper dwelling *R. attrita* compared with its shoaler dwelling congener, *R. maderensis*. Although this suggests a possible biological factor in their distribution, a lack of appropriate ecological data for most of the available collections precludes such a statement. Without comprehensive ecological information for all collections, the mechanism of bathymetric segregation in the two Atlantic species of *Rouleina* remains unknown.

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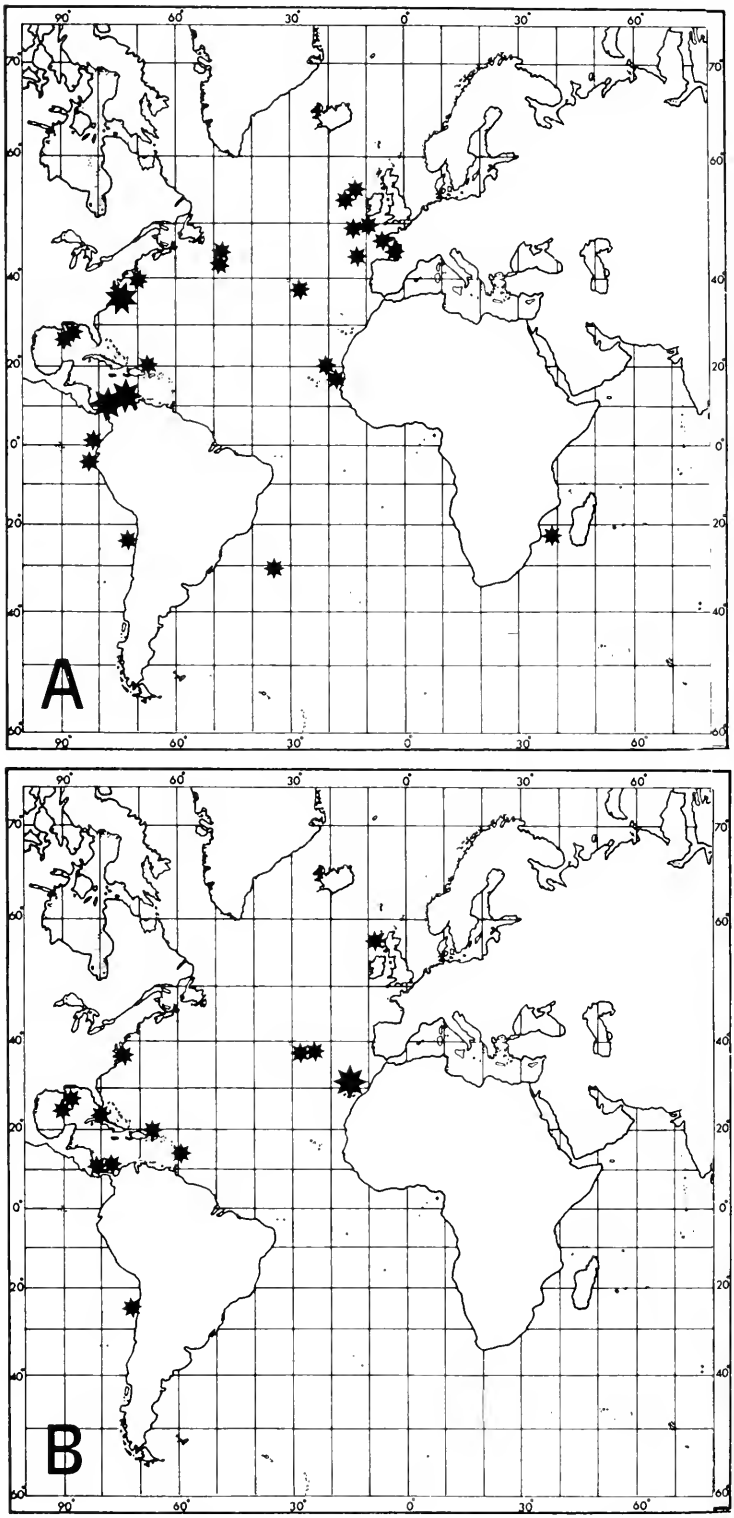

FIGURE 4.—A. *Rouleina attrita*, geographic distribution of collections examined plus recent capture in South Atlantic of Pakhorukov (1976). B. *Rouleina maderensis*, geographic distribution of collections examined. Larger symbols indicate multiple captures.

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FOOD AND FEEDING HABITS OF JUVENILE ATLANTIC TOMCOD, *MICROGADUS TOMCOD*, FROM HAVERSTRAW BAY, HUDSON RIVER

STEPHEN A. GRABE[1]

ABSTRACT

Juvenile Atlantic tomcod from Haverstraw Bay (Hudson River, N.Y.) were found to have a May-June diet of copepods and a July-December diet of amphipods, *Neomysis americana*, and isopods. This dietary shift occurred when mean length reached 90 mm during July. Growth paralleled feeding intensity: elevated during June, October, and November, and depressed July through September; feeding intensity decreased prior to spawning (December). Feeding and growth were inhibited at temperatures >24°C and dissolved oxygen <7mg/l.

The Atlantic tomcod, *Microgadus tomcod* Walbaum, is an inshore marine fish whose range extends from southern Labrador (Bigelow and Schroeder 1953) south to Virginia (Massman 1957); freshwater populations are localized in Quebec and Newfoundland (Scott and Crossman 1973). The Hudson River may represent the southern extent of the tomcod's breeding range since it has not been reported from the Delaware River estuary (de Sylva et al.[2]) and its status in New Jersey waters is uncertain (Miller 1972; Heintzelman[3]). In the Hudson River tomcod were formerly considered to be a seasonal, migratory species (Curran and Ries 1937; Clark and Smith[4]); more recent work, however, suggests that tomcod remain in the estuary for their entire life cycle (Lawler et al.[5]).

Tomcod spawn as young-of-the-year and yearlings (Lawler et al.[6]) with egg deposition typically occurring during December and January (Bigelow and Schroeder 1953; Booth 1967). First year growth, while initially rapid, slows in midsummer (Howe 1971) and resumes in early fall (Lawler et al. see footnote 5; Texas Instruments[7]; Dew and Hecht[8]).

Young-of-the-year Hudson River tomcod undergo a dietary shift, from calanoid copepods to *Gammarus* spp. amphipods, as they increase in size (Texas Instruments see footnote 7). My objectives were to define the diet and feeding intensity of juvenile tomcod within the vicinity of Haverstraw Bay, Hudson River, N.Y.

MATERIALS AND METHODS

Stomach contents of 577 juvenile tomcod were analyzed as part of the postoperational biological monitoring program for a fossil fuel steam electric generating station located at Hudson River milepoint 37.5. The study area (Figure 1) encompassed Hudson River milepoints 37.5-41.5, as measured from the Manhattan Battery.

Tomcod were collected once monthly June-December 1973 and 1974 by a 9.1-m otter trawl with a 64-mm mesh cod end liner, towed against the tide at 1.5-2.0 m/s. Collections of plankton and juvenile fishes were made twice monthly June-August 1974 with a 1-m diameter plankton net of 571-μm mesh mounted in an epibenthic sled and towed against the tide at 0.9-1.2 m/s. Tomcod from May and December 1975 trawl collections were also analyzed to provide a larger data base for these months.

[1]Lawler, Matusky and Skelly Engineers, Pearl River, N.Y.; present address: 95 Ash Street, Piermont, NY 10968.

[2]de Sylva, D. P., F. A. Kalber, and C. N. Schuster, Jr. 1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper water. Del. Board Fish Game Comm., 164 p.

[3]Heintzelman, D. S. (editor). 1971. Rare or endangered fish and wildlife of New Jersey. N.J. State Mus. Sci. Notes 4, 23 p.

[4]Clark, J. R., and S. E. Smith. 1969. Migratory fish of the Hudson River. *In* G. P. Howells and G. J. Lauer (editors), Hudson River ecology, p. 293-319. N.Y. State Dep. Environ. Conserv.

[5]Lawler, Matusky and Skelly Engineers. 1975. 1974 Hudson River aquatic ecology studies. Bowline Point and Lovett Generating Stations. Prepared for Orange and Rockland Utilities, Inc.

[6]Lawler, Matusky and Skelly Engineers. 1976. Environmental impact assessment-water quality analysis: Hudson River. National Comm. on Water Quality. NTIS PB-251099.

[7]Texas Instruments, Inc. 1975. Hudson River ecological study in the area of Indian Point: 1974 annual report (draft). Prep. for Consolidated Edison Co. of N.Y., Inc.

[8]Dew, C. B., and J. H. Hecht. 1976. Ecology and population dynamics of Atlantic tomcod (*Microgadus tomcod*) in the Hudson River estuary. *In* Hudson River ecology. Hudson River Environ. Soc., Inc.

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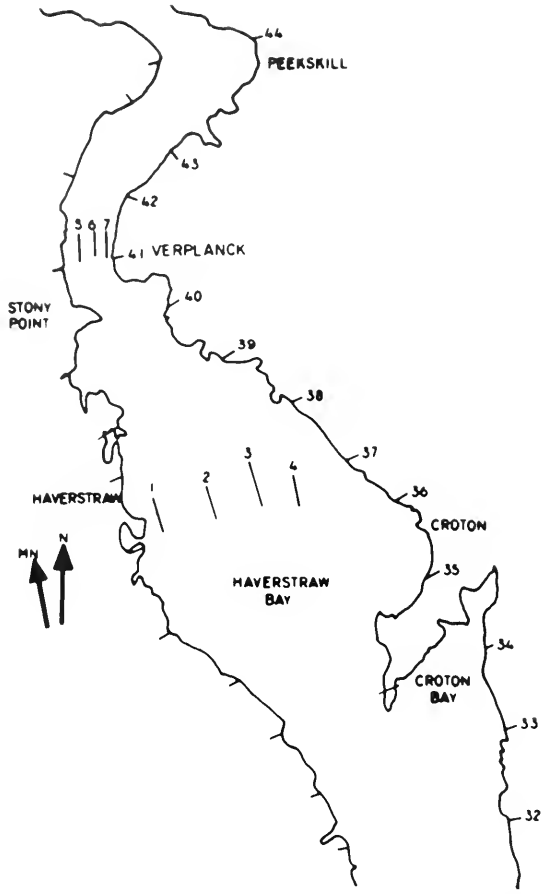

FIGURE 1.—Sampling stations, depths, and collection methods for Atlantic tomcod, Haverstraw Bay 1973-75. Numbers along river indicate mile points above the Manhattan Battery. Station 1: 6.7 m; trawl, epibenthic sled. Station 2: 12.2 m; epibenthic sled. Station 3: 7.6 m; trawl. Station 4: 3.0 m; epibenthic sled. Station 5: 18.3 m; trawl, epibenthic sled. Station 6: 16.8 m; epibenthic sled. Station 7: 13.7 m; trawl, epibenthic sled.

Bottom temperature (Figure 2), dissolved oxygen, and salinity (Table 1) were measured at station 2 (depth 12.2 m).

Fish were preserved in 5% (epibenthic sled collections) or 10% (trawl collections) buffered Formalin.[9] Total length of each fish was measured to the nearest millimeter. Fish >50 mm were weighed to the nearest 0.1 g; fish <50 mm were weighed to the nearest 0.01 g. Stomachs were removed and transferred to a 70% solution of ethanol prior to analysis. One everted fish stomach, indicative of regurgitation, was excluded. Food organisms were identified, counted, and the entire contents, excluding obvious nonfood items (e.g., pebbles), of 401 stomachs were dried to a constant weight at 103°C.

Only postlarval juveniles were studied; the distinction between larval and juvenile tomcod was the completed differentiation of the fins (Balon 1975). Lower limits of adult fin ray counts were taken from Bigelow and Schroeder (1953). Application of this criterion showed that a total body length of 25 mm represented the lower size limit of juveniles. During 1973, young-of-the-year were distinguished from yearlings by examination of length-frequency histograms of larger sample sizes of tomcod (Lawler et al. see footnote 6; Lawler et al.[10]). Fish collected during November and December 1973, 148 and 160 mm, respectively, were considered to represent upper size limits of young-of-the-year. All fish collected during 1974 and December 1975 were condsidered young-of-the-year.

Stomach content data were pooled by month and quantitative results for each taxon calculated as percent occurrence, percent composition, and importance (Windell 1971):

$$\text{Importance} = \sqrt{(\%\ \text{composition})\ (\%\ \text{occurrence})}.$$

Percent relative importance was calculated by summing importance values at the lowest taxonomic level and dividing individual importance values by that sum. A modified similarity index (Windell 1971) was then calculated to compare monthly changes in percent relative importance of various food items, at the lowest comparable taxonomic level. Consecutive months were compared by selecting the lesser of two relative importance values for each food item and then summing them. This sum is the index of similarity and it may range from 0 to 100%.

An index of fullness (I_f) (Nikolsky 1963; Windell 1971), indicative of feeding intensity, was calculated for each fish:

$$I_f = \frac{\text{stomach content biomass (g)} \times 10^4}{\text{weight (g) of fish}}.$$

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

[10]Lawler, Matusky and Skelly Engineers. 1974. 1973 Hudson River aquatic ecology studies: Bowline Point and Lovett Generating Stations. Prepared for Orange and Rockland Utilities, Inc.

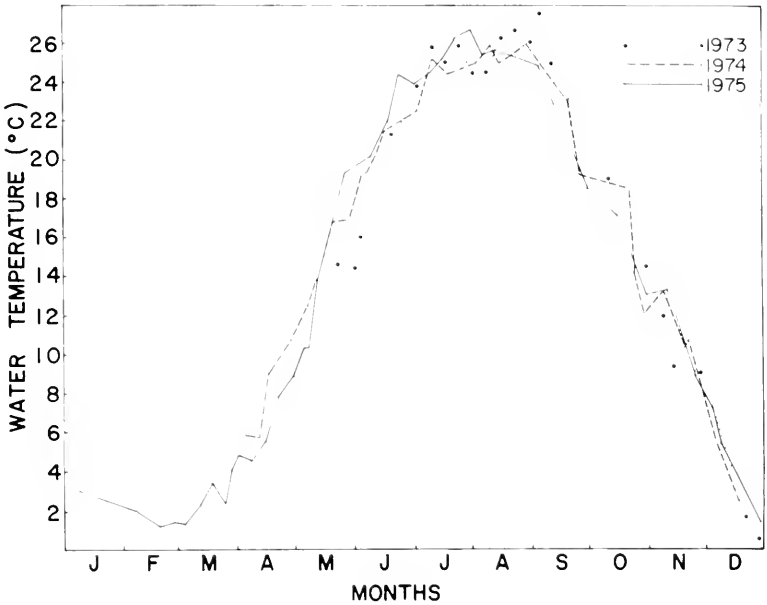

FIGURE 2.—Bottom water temperatures at Station 2, Haverstraw Bay (mile point 37.5).

TABLE 1.—Mean monthly bottom dissolved oxygen and salinity measurements at Station 2, Haverstraw Bay (mile point 37.5) 1973-75.

Month	Dissolved oxygen (mg/l)			Salinity (‰)		
	1973	1974	1975	1973	1974	1975
Jan.	(1)	(1)	9.0	(1)	<0.03	2.65
Feb.	(1)	(1)	12.5	(1)	<0.03	2.92
Mar.	(1)	(1)	12.8	(1)	<0.03	0.97
Apr.	(1)	9.6	12.1	(1)	<0.03	1.16
May	7.8	9.3	9.5	(1)	<0.03	0.93
June	7.1	7.8	6.7	<0.03	1.44	1.48
July	5.9	7.7	5.8	1.32	3.07	3.34
Aug.	5.8	5.5	5.1	(1)	4.14	4.48
Sept.	6.9	9.1	7.8	2.98	1.72	1.39
Oct.	8.6	8.5	7.8	5.72	2.02	0.87
Nov.	9.2	10.2	8.1	3.51	0.85	0.03
Dec.	12.4	12.2	11.7	<0.03	0.04	0.30

(1)Data not available.

RESULTS

Ranking dominant food items by importance (Table 2) revealed two distinct dietary regimes: a May-June diet of copepods and a July-December diet of amphipods, mysids, and isopods. The similarity index for consecutive months emphasized this shift by a markedly low value (39%) for June-July compared with a range of 54-80% for other months.

Pooling June and July fish by 10-mm length intervals indicated that copepod importance decreased and that of amphipods increased as mean length increased. At 90 mm, transition to an amphipod-dominated diet was complete (Table 3).

A seasonal feeding cycle was distinguished by trends in I_f, percentage of empty stomachs, and average number of food items per stomach (Table 4), with feeding greatest during May, June, October, and November, and lowest during July-September. Feeding also decreased during December. Growth of the 1974 year class paralleled seasonal alterations in I_f (Figure 3).

The trends of the above parameters suggested that seasonally fluctuating environmental variables (e.g., temperature and dissolved oxygen) might be affecting feeding intensity and, therefore, growth. Statistical tests to discriminate the

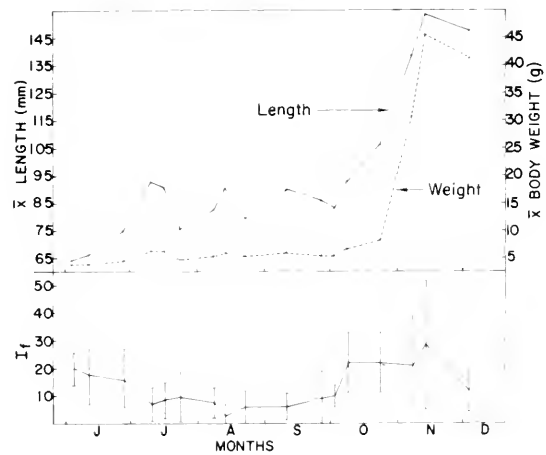

FIGURE 3.—Index of fullness (I_f) and growth of juvenile Atlantic tomcod, Haverstraw Bay, June-December 1974.

TABLE 2.—Monthly summary of five most important food items of juvenile Atlantic tomcod from Haverstraw Bay, 1973-75.

Month	Sample size	Taxon	Percent occurrence	Percent composition	Index
May	38	Copepoda	100.0	99.2	99.6
		Eurytemora affinis			
		Ectocyclops sp.			
		Halicyclops sp.			
		Gammarus daiberi	10.5	0.6	2.5
		Monoculodes edwardsi	2.6	0.1	0.5
		Ostracoda	2.6	0.1	0.5
June	210	Copepoda	54.8	82.4	67.2
		E. affinis			
		Cyclopoida			
		Harpacticoida			
		Unidentified nauplii			
		G. daiberi	64.8	6.9	21.2
		M. edwardsi	37.6	2.7	10.0
		Bosmina sp.	22.4	3.0	8.2
		Neomysis americana	19.5	0.9	4.3
July	69	*G. daiberi*	63.8	38.9	49.8
		N. americana	30.4	19.8	24.5
		M. edwardsi	31.9	18.4	24.2
		Cyathura polita	23.2	4.7	10.5
		Scolecolepides viridis	11.6	3.0	5.9
Aug.	58	*M. edwardsi*	37.9	45.8	41.7
		G. daiberi	41.4	18.2	27.4
		N. americana	25.9	15.0	19.7
		Edotea triloba	22.4	5.2	10.8
		C. polita	12.1	3.1	6.1
Sept.	43	*G. daiberi*	72.1	53.1	61.9
		M. edwardsi	34.9	28.6	31.6
		N. americana	20.9	5.4	10.6
		C. polita	14.0	2.1	5.4
		Chaoborus punctipennis	11.6	1.8	4.6
Oct.	43	*G. daiberi*	93.0	70.9	81.2
		M. edwardsi	34.9	20.2	26.5
		C. polita	25.6	2.2	7.6
		Rhithropanopeus harrisii	14.0	1.5	4.6
		Corophium lacustre	2.3	0.6	1.2
Nov.	42	*G. daiberi*	73.8	86.8	80.0
		Crangon septemspinosa	40.5	7.1	16.9
		N. americana	11.9	3.3	6.3
		R. harrisii	16.7	1.4	4.8
		M. edwardsi	4.8	0.3	1.2
Dec.	74	*G. daiberi*	95.9	68.9	81.3
		Copepoda	9.4	24.9	15.3
		M. edwardsi	16.2	2.3	6.1
		Chironomidae larvae	18.9	1.4	5.1
		Cyathura polita	16.2	0.7	3.3

TABLE 3.—Importance values of copepods, amphipods, and *Neomysis americana* in stomachs of June and July juvenile Atlantic tomcod pooled by 10-mm size intervals.

Size interval (mm)	Sample size	Copepods	Amphipods	*Neomysis americana*
40-49	3	36.3	47.9	0.0
50-59	48	65.9	29.8	3.5
60-69	65	74.9	27.3	5.7
70-79	80	59.7	29.8	6.7
80-89	40	39.6	38.9	4.5
90-99	38	0.0	83.7	16.8
>100	5	8.8	75.5	0.0

effects of temperature from those of dissolved oxygen were not applied since the two parameters were highly correlated ($r = -0.96$). I_f was, however, lowest when water temperatures were >24°C and dissolved oxygen (DO) <7 mg/l and increased at temperatures <19°C and DO >7 mg/l (Table 5).

DISCUSSION

Howe (1971) characterized tomcod as opportunistic feeders; the data presented here qualify that hypothesis. Smaller tomcod, present during May and June, preyed upon copepods (Table 2) which have been the most abundant zooplankters collected by 76- and 150-μm mesh nets in this reach of the Hudson River (Lawler et al. see footnotes 5, 10; Lawler et al.[11], Lauer et al.[12]). When total length reached 80-90 mm (June-July), food preference shifted to larger prey, e.g., amphipods (Table 3). Such a shift has been documented in a variety of species (Nikolsky 1963; Stickney et al. 1974; Werner 1974; Stickney 1976), including the related species *Gadus morhua* (Kohler and Fitzgerald 1969). This shift did not appear to be a response to changes in prey density, since abundance of copepods increased while that of amphipods decreased during June-August 1973-75 (Lawler et al. see footnotes 5, 10, 11).

Copepods were a supplementary prey during December, occurring as frequently as the larger decapods *Crangon septemspinosa* (5.4%) and *Rhithropanopeus harrisii* (4.1%) which were relatively important during November (Table 2). Selection of smaller prey with the concomitant decrease of larger prey may be a response to the constriction of the alimentary canal by maturing gonads noted by Schaner and Sherman (1960). In Hudson River tomcod, gonadal biomass prior to spawning averages between 15 (males) and >30% (females) of the body weight minus the gonad weight. In contrast, female gonads in Hudson River *Morone americana* (Lawler et al. see footnote 10) average about 8%, *Alosa sapidissima* about 22% (calculated from Lehman 1953), *Trinectes maculatus* less than 6% (calculated from Koski 1974), while those of *Tautogolabrus adspersus* from Long Island Sound averaged about 7% (Dew 1976) of the body weight minus the gonad weight.

A decrease in prey (*C. septemspinosa*) availability was not considered a factor in this change. In the Haverstraw Bay area, *C. septemspinosa*

[11]Lawler, Matusky and Skelly Engineers. 1976. 1975 Hudson River aquatic ecology studies: Bowline Point and Lovett Generating Stations. Prepared for Orange and Rockland Utilities, Inc.

[12]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), Proceedings of the second entrainment and intake screening workshop, Feb. 5-9, 1973, p. 37-88. Johns Hopkins Univ., Baltimore, Md.

TABLE 4.—Mean length, weight, index of fullness, number of food items per stomach, and percent frequency of empty stomachs for juvenile Atlantic tomcod from Haverstraw Bay 1973-75.

Month	Number[1]	Total length (mm) Mean	SD	Weight (g) Mean	SD	Index of fullness Mean	SD	Number of food items per stomach Mean	SD	Frequency of empty stomachs (%)
May[2]	36/38	28.9	3.2	0.3	0.1	21.809	14.630	29.3	14.1	0.0
June[3]	100/210	68.8	11.0	3.5	1.8	17.224	9.645	68.4	178.5	0.0
July[3]	68/69	86.8	11.0	6.9	2.4	7.272	6.214	7.2	7.4	5.8
Aug.[3]	39/58	86.5	10.2	6.3	2.2	5.387	5.333	5.0	6.2	10.3
Sept.[3]	30/43	90.9	9.9	7.4	2.8	7.820	7.453	9.2	9.4	2.3
Oct.[3]	40/43	98.6	12.2	9.8	3.7	25.317	41.485	18.7	16.9	2.3
Nov.[3]	42/42	139.2	14.2	33.0	11.8	24.403	22.657	15.2	17.0	2.4
Dec.[4]	46/74	143.8	12.9	35.2	12.2	12.902	7.550	55.4	67.7	2.7

[1]Number of stomachs analyzed for index of fullness/total number of stomachs.
[2]Two dates, 1975 only
[3]1973 and 1974
[4]1973-75; no index of fullness for 1973 fish.

TABLE 5.—Index of fullness of 1974 juvenile Atlantic tomcod, bottom water temperatures, and dissolved oxygen measurements, Haverstraw Bay.

Date	Sample size	Index of fullness Mean	SD	Temp (°C)	Dissolved oxygen mg/l	% saturation
4 June	17	20.195	6.226	17.5	8.2	85
11 June	44	16.839	10.040	20.3	8.4	91
26 June	25	17.977	12.066	21.7	7.2	82
29 June	14	13.482	5.499	(1)	(1)	(1)
10 July	24	7.062	5.872	24.8	7.1	85
16 July	7	8.694	6.593	24.8	7.0	83
23 July	9	9.798	9.264	24.8	6.8	81
8 Aug.	12	7.895	5.986	25.9	6.9	84
13 Aug.	18	3.288	3.667	25.5	5.6	68
22 Aug.	9	6.241	6.087	26.7	5.4	79
10 Sept.	13	6.261	4.610	23.4	6.8	79
26 Sept.	14	9.394	9.583	19.4	6.7	72
2 Oct.	4	10.194	3.634	18.9	7.6	81
8 Oct.	13	22.336	10.859	17.9	7.8	82
23 Oct.	11	22.065	11.226	14.2	9.8	94
5, 8 Nov.	14	20.695	18.794	14.6	9.4	91
13 Nov.	13	27.898	22.372	12.2	10.2	94
3 Dec.	22	12.370	8.107	5.6	11.6	92

[1]Data not available.

were relatively abundant in trawl collections August through November 1973 and 1974 (Lawler, Matusky and Skelly Engineers unpubl. data). Haefner (1976) found that greatest abundance of *C. septemspinosa* in channel areas of the York River and lower Chesapeake Bay occurred when water temperatures were 5°-10°C and was a result of migration from littoral areas to deeper, more saline areas; such a temperature regime occurs in Haverstraw Bay between mid-November and mid-December (Figure 1).

Feeding intensity and growth followed similar seasonal patterns. Rapid growth and relatively intense feeding occurred during May, June, October, and November (Table 4; Figure 3); growth and feeding were depressed during July-September. Prey density was not considered limiting during summer months since *Neomysis americana* was generally abundant. Also, resumption of feeding and growth occurred during October when macrozooplankton standing crop was lower than previous months (Lawler et al. see footnotes 5, 10, 11; Lauer et al. see footnote 12). Seasonally fluctuating abiotic factors, then, may be affecting growth and feeding. Food consumption in other species of gadids has been observed (Tyler 1970) or postulated (Sikora et al. 1972) to be inhibited at temperatures >20°C.

Tomcod are considered to have a low thermal optimum (Huntsman and Sparks 1924; Bigelow and Schroeder 1953; Howe 1971). Retardation of growth during summer months when water temperatures exceed 24°C has been observed in the Hudson River (Lawler et al. see footnote 5; Texas Instruments see footnote 7; Dew and Hecht see footnote 8) and Weweantic River, Mass. (Howe 1971), populations. Growth of juveniles from the Woods Hole area during 1962 (maximum surface water temperature = 21.1°C) did not appear to cease during midsummer (Lux and Nichy 1971); however, only 22 young-of-the-year fish were caught between June and August.

Concomitant with elevated water temperature is decreased dissolved oxygen. In separate reviews of dissolved oxygen requirements, Doudoroff and Shumway (1970) noted that feeding and growth responses to low DO levels have been variable, while Davis (1975) suggested that inhibition occurred at 50% of air saturation. Warren et al. (1973) found that growth and feeding of *Oncorhynchus kisutch* and *O. tshawytscha* were inhibited when saturation was <100%, but that only a 10% decrease in production would occur at 70% saturation. Thatcher (1975; cited in McKim et al. 1976) found that *O. kisutch* acclimated at 15°C did not reduce food consumption or growth when DO was >5 mg/l (49% saturation).

Tomcod feeding, measured by I_f, was minimal at DO <7 mg/l during 1974; July-September percent saturation ranged from 68 to 85% (Table 5). In light

of the above studies on salmonids, it seems unlikely that DO levels encountered in Haverstraw Bay are the primary variable affecting feeding and growth. The summer temperature regime of the Hudson River, then, appears to be near maximum for this species and may be capable of inhibiting feeding and retarding growth.

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EGGS AND LARVAE OF *SCOMBER SCOMBRUS* AND *SCOMBER JAPONICUS* IN CONTINENTAL SHELF WATERS BETWEEN MASSACHUSETTS AND FLORIDA

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ABSTRACT

Larval *Scomber scombrus* and *Scomber japonicus* from the western North Atlantic Ocean are compared. At 4 to 11 mm *S. japonicus* are deeper bodied, and at 3 to 15 mm have greater preanus lengths than *S. scombrus* of comparable sizes. *Scomber scombrus* larvae are more heavily pigmented than *S. japonicus*, particularly on the dorsal trunk surface and at the cleithral sympysis.

In continental shelf waters between Martha's Vineyard, Mass., and Palm Beach, Fla., 1966-68, *S. scombrus* eggs occurred north of Cape Hatteras, N.C., mostly in the shoreward half of shelf waters, during spring and summer. Surface temperatures associated with egg occurrences varied from 6.3° to 16.9°C. *Scomber japonicus* eggs were taken south of Cape Hatteras, in the outer half of shelf waters, during winter and spring cruises. Surface temperatures associated with egg occurrences ranged from 20.4° to 25.4°C.

Larval *S. scombrus* occurred north of Cape Hatteras during spring and summer with concurrent surface temperatures ranging from 12.3° to 20.7°C. With the exception of three specimens, *S. japonicus* larvae occurred south of Cape Hatteras and were taken where the surface temperature ranged from 16.0° to 29.4°C.

Despite an abundance of publications describing the young stages of Atlantic mackerel, *Scomber scombrus* Linnaeus, and their occurrences in the western North Atlantic (Dannevig 1919; Sette 1943; Bigelow and Schroeder 1953; Berrien 1975), very little information exists on young of the congeneric chub mackerel, *Scomber japonicus* Houttuyn, from the same area. There are no descriptions of *S. japonicus* eggs, larvae, or juveniles from the western North Atlantic, although there are excellent descriptions of specimens from the Pacific Ocean (Fry 1936a; Orton 1953; Uchida et al. 1958; Kramer 1960; Watanabe 1970) and some brief descriptions of this species from European waters (Ehrenbaum 1924; Padoa 1956). Ehrenbaum (1924), Padoa (1956), and Dekhnik (1959) compared larvae of the two species. Reports of young *S. japonicus* in the western North Atlantic are limited to those by Anderson and Gehringer (1958), Dooley (1972), Fahay (1975), and de Sylva.[2] Although adults of *S. japonicus* are known to range from the Gulf of St. Lawrence (Leim and Scott 1966) to Bermuda and the Gulf of Mexico (Briggs 1958) in the western Atlantic, they occur irregularly along the U.S. east coast. In various years they have been abundant, uncommon, or absent (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). This species apparently inhabits warmer waters than does *S. scombrus* (Bigelow and Schroeder 1953; Matsui 1967).

The purposes of this paper are: 1) to present descriptive, comparative information on two species of *Scomber* larvae, in order to facilitate their identification; and 2) to compare the spawning areas of the two species as indicated by occurrences of *Scomber* young taken between Massachusetts and Florida.

Specimens utilized in this study were taken primarily during ichthyoplankton survey cruises by the RV *Dolphin* in continental shelf waters from December 1965 to February 1968 between Martha's Vineyard, Mass., and Palm Beach, Fla. Some larvae in the descriptive section were taken on other cruises during April 1971 and June 1972, within the same area.

PROCEDURES

Sampling

Eight plankton sampling cruises were conducted between December 1965 and December

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[2]de Sylva, D. P. 1970. Ecology and distribution of postlarval fishes of southern Biscayne Bay, Florida. Prog. Rep. to Div. Water Qual. Res., Water Qual. Off., U.S. Environ. Prot. Agency Contract FWQA 18050 Div. Rosenstiel School Mar. Atmos. Sci., Univ. Miami, 198 p. (Unpubl. manuscr.)

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1966 aboard the RV *Dolphin* in continental shelf waters, between Martha's Vineyard and Cape Lookout, N.C. Four cruises were made between May 1967 and February 1968 between New River Inlet, N.C., and Palm Beach (Figure 1). Gulf V samplers, with 0.4-m mouth and 0.52-mm mesh openings, were used for plankton tows. The tows were 0.5 h long at a speed of 9.3 km/h (5 knots) in a step-oblique pattern. Normally the nets were lowered in six 3-m depth increments and towed for 5 min at each depth. One Gulf V net (net 1) sampled from 0 to 15 m, and a second net sampled from 18 to 33 m. While setting and retrieving net 2, contamination above 15 m was inevitable, since the nets were not equipped with closing devices. Plankton samples were preserved in 5% Formalin[3] buffered with borax. Sampling time, whether day or night, was essentially random, in that there was no prearranged time schedule. At each station we measured surface water temperature, made a bathythermograph cast to a maximum depth of 275 m, and measured salinity with an in situ induction salinometer at 5-m intervals down to include the plankton sampling depth. Additional details on the sampling scheme and gear used, as well as temperatures, salinities, zooplankton volumes, and midwater trawl catches, were summarized by Clark et al. (1969, 1970).

Identification of Eggs and Larvae

Scomber scombrus eggs were identifiable using criteria summarized by Berrien (1975). Briefly, distinguishing features of this species' eggs are: they are spherical and have a diameter of about 1.0 to 1.3 mm; they have a single yellowish oil globule about 0.3 mm in diameter; and after blastopore closure, melanophores occur on the head, trunk, and oil globule. Pigment is absent from the yolk except just prior to hatching when one melanophore occurs near each side of the embryo, immediately posterior to the head.

Despite a lack of information on *S. japonicus*

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

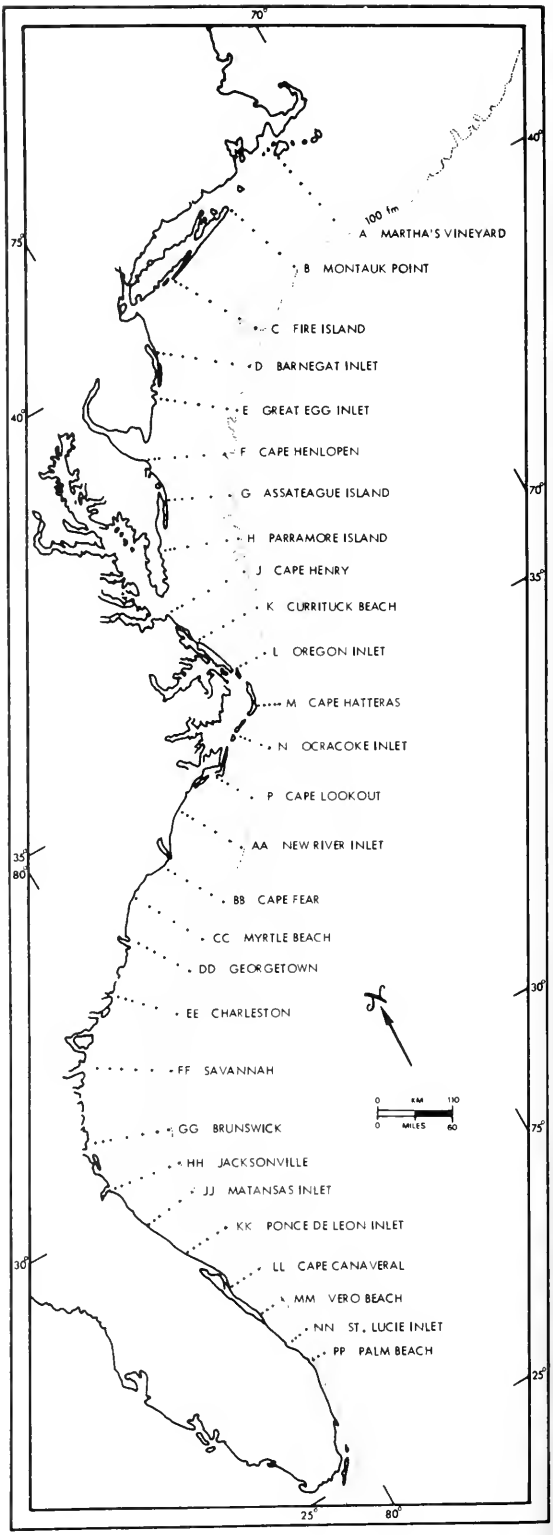


FIGURE 1.—Ichthyoplankton survey area; transects designated by single letters were sampled eight times, December 1965 to December 1966; those with two letters were sampled four times, May 1967 to February 1968. Stations starting at 1 on the inshore end of each transect were numbered consecutively, progressing oceanward.

eggs from the Atlantic Ocean, they have been well described from the Pacific Ocean, and are similar to eggs of *S. scombrus* in size and appearance (Fry 1936a; Kramer 1960; Watanabe 1970). The most obvious difference between eggs of the two species is the amount of pigment found on the yolk surface during the late or third stage in development. *Scomber japonicus* develops several melanophores on the yolk while *S. scombrus* has, at most, a pair of melanophores, as described above. Due to similarity of early-stage eggs of the two *Scomber* species, their identification must depend upon other information, such as spawning area, and the proximity of older identifiable stages.

In separating *Scomber* spp. larvae from larvae of other fishes I found the descriptions and illustrations by Bigelow and Schroeder (1953), Kramer (1960), and Watanabe (1970) to be especially helpful. *Scomber* spp. larvae are characterized by the following: 1) they have 31 myomeres and lack preopercular spines, unlike other scombrid larvae in the western North Atlantic which have more myomeres and possess strong spines; 2) melanophores are present above the forebrain, midbrain, and gut, and along the postanus ventral edge of the trunk; 3) prominent recurved teeth form in larvae by about 4 mm, and are present well into the juvenile stage although somewhat embedded and obscured at sizes above about 15 mm; and 4) a large portion of *Scomber* spp. larvae between about 7 and 15 mm have noticeably subterminal mouths.

Other larval fishes found along the U.S. east coast which grossly resemble one or the other of the two *Scomber* spp. include *Sebastes marinus, Pomatomus saltatrix, Centropristis striata,* and *Stenotomus chrysops*. Despite pigmentation similarities myomere counts alone will separate *Scomber* larvae (with 31 myomeres) from *P. saltatrix* (with 26) and *C. striata* and *Stenotomus chrysops* (each with 24 myomeres). *Sebastes marinus* can have the same number of myomeres (with 30 to 32) as *Scomber* and is pigmented in most of the same body areas as both species of *Scomber*. However, at lengths less than about 9 mm *Sebastes marinus* lack teeth and have dorsal and ventral trunk melanophores which are close enough together to appear as dorsal and ventral lines of pigment. Comparably sized *Scomber* larvae have prominent teeth and discrete dorsal and ventral trunk melanophores. Also *Sebastes marinus* larvae are more slender and have shorter snout-to-anus lengths than *Scomber* larvae. The presence of temporal and preopercular spines on *Sebastes marinus* and their absence on *Scomber* larvae separate the two species at lengths >9 mm, before fin-ray counts are distinguishable.

Treatment of Specimens and Data

Measurements, as defined by Kramer (1960), made in this study include: standard length (SL = anterior tip of snout to tip of notochord, or to posterior edge of the hypurals after notochord flexure); preanus length (PAL = anterior tip of snout to the most posterior edge of the anus); and body depth (BD = the vertical distance from the dorsal surface of the body directly above the dorsal point of the cleithrum to the ventral point of the cleithrum). Length measurements in this paper are standard lengths, unless otherwise stated.

Osteological characters in developing *Scomber* larvae were investigated by examination of bone-stained specimens (Hollister's method in Clothier 1950) and radiographs.

All *Scomber* eggs in samples containing <400 eggs were identified and tabulated. In larger samples, the numbers of *S. scombrus* eggs were estimated from a random subsample of 200. To test the validity of this procedure *S. scombrus* eggs were identified from seven aliquots of 200 eggs from one sample. No significant differences were found between aliquots (chi-square = 5.415, $P = 0.5$).

Lengths for length-frequency diagrams were measured to the nearest 0.1 mm in fish <15 mm and to the nearest 0.5 mm in those >15 mm. Measurements were taken of all specimens from samples of 100 or fewer fish and of 50 to 75 randomly selected specimens from larger samples.

The numbers of *Scomber* spp. eggs and larvae taken during survey cruises are presented on charts. For these charts the catches from net 1 (0-15 m) and net 2 (18-33 m) were combined at stations where both were towed. Before these numbers were plotted some were adjusted in an attempt to standardize the catches. Because net 2 spent an estimated 3 min of the ½-h tow being set and retrieved through the upper 15 m, the catch by net 2 was reduced by 10% of the net 1 catch to correct for contamination. In cases where there was insufficient water depth to allow lowering the plankton net for the standard of six 3-m depth increments, the towing scheme was altered. During these tows we sampled for 15 min at each of two levels, or for 10 min at each of three levels. The resulting catch was reduced to one-third when two

levels were sampled or to one-half when three levels were sampled. Fahay (1974) explained this procedure in more detail.

COMPARISON OF TWO SPECIES OF *SCOMBER* LARVAE

Scomber larvae occurred in samples from our northernmost transect, off Martha's Vineyard to our southernmost transect off Palm Beach. The larvae were of two types, the distinction between the two being more obvious in larvae smaller than 15 mm. One type, collected north of Cape Hatteras, predominantly over the inshore and central portions of the continental shelf, during May, June, and August 1966, was tentatively identified as Atlantic mackerel, *S. scombrus*. A second type collected south of Cape Hatteras was tentatively identified as chub mackerel, *S. japonicus*. It occurred predominantly in samples taken near the offshore edge of the continental shelf, during May and July 1967 and January and February 1968. The identities of the two types were confirmed by examination of some meristic characters of the large larvae and juveniles.

Because of the similarity and possible confusion of these two species, the following descriptions and comparisons were compiled to facilitate future identifications. Three study areas were considered in larval development: meristic characters, morphology, and pigmentation.

Meristic Characters

Of the 12 characters listed by Matsui (1967, table 5) as distinguishing between the species of *Scomber*, four were found to be useful in identifying young stages dealt with here. These were: 1) first-dorsal-fin spine counts; 2) counts of precaudal and caudal vertebrae; 3) counts of first-dorsal-fin ptergiophores and the arrangements in relation to neural spines; and 4) the relative position of the first haemal spine and the first anal pterygiophore.

Scomber japonicus has 9 or 10 first-dorsal-fin spines and *S. scombrus* has 11 to 14 (Matsui 1967). Examination of Formalin-preserved specimens under a dissecting microscope revealed that counts of 9 or 10 were attained by a length of 18.5 mm in *S. japonicus* and counts of 11 to 15 by 21.0 mm in *S. scombrus*. However, bone-stained specimens of both species had higher counts and earlier formation of spines than indicated in the above. Apparently some of the minute, posterior spines in the first dorsal fin, observed in bone-stained specimens, were obscured in nonstained specimens by surrounding muscle and epithelial tissue and by their position in the longitudinal groove. I observed a complement of 10 or 11 spines in *S. japonicus* as small as 11.9 mm long and 12 to 17 spines in *S. scombrus* 18.2 mm and greater (Table 1).

Counts of vertebrae were made to help identify the two species of *Scomber* larvae. *Scomber japonicus* is reported to have 14 precaudal and 17 caudal vertebrae and *S. scombrus* to have 13 precaudal and 18 caudal vertebrae (Matsui 1967). The first caudal vertebra is the most anterior vertebra which has an elongate pointed haemal spine and lacks ribs. In *Scomber* larvae the haemal spine on the first caudal vertebra is noticeably longer than the haemal arch on the last precaudal vertebra. Also, rib articulation surfaces on haemal arches of posterior precaudal vertebrae are distinctly flattened or truncated, rather than pointed as are haemal spines on caudal vertebrae. In my work counts of precaudal vertebrae were distinguishable in bone-stained *S. japonicus* as small as 7.6 mm (indeterminate at 6.7 mm) and on radiographs by 9.3 mm. Precaudal counts characteristic of *S. scombrus* were observable in bone-stained larvae at 8.6 mm (indeterminate at 7.6 mm) and on radiographs by 11.2 mm (Table 1). A few of the *S. scombrus* specimens had precaudal and caudal vertebral counts different from those reported by Matsui (1967). Six of the 136 *S. scombrus* specimens bone-stained or X-rayed large enough for determination had 12 precaudal and 19 caudal vertebrae. In two other specimens the 28th and 29th vertebrae were fused together, as evinced by a total count of 30 and by the presence of two neural and two haemal spines on the 28th vertebra. One additional larva was observed with partial fusion of the same two vertebrae.

The numbers of first-dorsal-fin pterygiophores separate the two species of *Scomber*. Matsui (1967) reported *S. japonicus* has 12 to 15 first-dorsal-fin pterygiophores and *S. scombrus* has 21 to 28. Full complements of pterygiophores, 13 or 14 in *S. japonicus* and 22 to 25 in *S. scombrus*, were found in bone-stained *S. japonicus* as small as 20.2 mm and on radiographs by 33.3 mm; they were found in bone-stained *S. scombrus* at 32.0 mm and on radiographs at 38.8 mm (Table 1). Because anterior pterygiophores ossify before posterior ones and because there is a difference

TABLE 1.—Some meristic characters in *Scomber japonicus* and *S. scombrus* young as determined in bone-stained (and two X-rayed) specimens. D_1 refers to the first dorsal fin; pterygiophore counts were made between successive neural spines, starting in the second interneural space. (— = count was indeterminate. X = X-rayed specimen. * = pterygiophore series completed. M = mutilated, spine(s) lost in handling.)

Scomber japonicus				*Scomber scombrus*			
SL (mm)	Vertebrae	D_1 spines	D_1 pterygiophores	SL (mm)	Vertebrae	D_1 spines	D_1 pterygiophores
6.7	—	—	—				
7.6	14 + —	—	—	7.6	—	—	—
7.7	14 + 17	1	—				
8.4	14 + —	6	—				
8.5	14 + 17	7	—	8.6	13 + —	—	—
9.0	14 + 17	4	—				
9.1	14 + 17	6	—	9.3	13 + —	—	—
10.2	14 + 17	8	—				
10.5	14 + 17	9	—	10.5	13 + 18	—	—
				10.7	13 + 18	—	—
				11.4	13 + —	—	—
11.7	14 + 17	8	11121	11.6	13 + 18	—	—
11.9	14 + 17	11	1121				
12.4	14 + 17	11	11121	12.3	13 + 18	2	—
13.8	14 + 17	11	112111	13.4	13 + 18	5	—
14.0	14 + 17	10	11121	14.8	13 + 18	6	—
16.5	14 + 17	10	11121111	16.0	13 + 18	10	—
17.7	14 + 17	10	1112111	18.2	13 + 18	17	1122
20.2	14 + 17	11	11211111121*	19.8	12 + 19	15	1123
22.1	14 + 17	10	1112111120211*	22.1	13 + 18	16	112221
24.7	14 + 17	11	11121111	24.3	13 + 18	13	11222
26.3	14 + 17	11	11121111112*	26.0	13 + 18	14	1122221
				28.2	13 + 18	14	11222222
28.6X	14 + 17	10	111211	29.9	12 + 19	15	1123221
				32.0	13 + 18	12M	1132212212221*
33.3X	14 + 17	11	11121111121*	34.2	13 + 18	13	112222223222*
				36.6	13 + 18	13	1122322133221*
				38.6	13 + 18	13	112322122222*

between the two species in counts of pterygiophores in anterior, successive interneural spaces, the two species can be separated well before the total complement is attained. A count of six pterygiophores in the 2d through 6th interneural spaces, characteristic of *S. japonicus*, was observed in bone-stained larvae as small as 11.7 mm and on radiographs at 20.2 mm; a count of six or seven pterygiophores in the 2d through 50th interneural spaces, characteristic of *S. scombrus*, was observed in bone-stained larvae as small as 18.2 mm and on radiographs at 20.1 mm.

In *S. japonicus* the first anal pterygiophore is anterior to the first haemal spine while in *S. scombrus* the first anal pterygiophore is posterior to the first haemal spine (Matsui 1967). This was observable in bone-stained *S. japonicus* at 11.7 mm and in *S. scombrus* at 32.0 mm, and on radiographs at 17.0 mm in *S. japonicus* and 32.0 mm in *S. scombrus*.

Body Proportions

Larvae of the two species differ noticeably in several body proportions. *Scomber japonicus* is deeper bodied and has a greater preanus length than *S. scombrus*. Measurements of body depth (BD) and preanus length (PAL) were converted to percentages of standard length (SL) and the results were graphed (Figure 2). Although the separation of the two species by these characters is not total, more than two-thirds of the larvae are separable by BD measurements at lengths of 4 to 11 mm and by PAL measurements at 3 to 15 mm long. Of these two characters the PAL difference is more useful, as it is present over a greater size range.

Other morphological differences between the two species have been reported by previous workers. These contrasts were not considered strong enough in the larvae from this study to warrant elaboration. Padoa (1956) noted a larger eye, shorter lower jaw, and shorter snout relative to eye diameter in *S. japonicus* than in *S. scombrus*. Dekhnik (1959) presented a brief and generalized comparison of larvae of the two species. She reported *S. japonicus* larvae are more advanced than *S. scombrus* of the same length. Thus *S. japonicus* are smaller than *S. scombrus* at hatching, at yolk and oil globule absorption, and at the initial formation of caudal fin rays. These differences were not as striking in my specimens. In our survey both species apparently hatched at about 3 mm long, and yolk and oil globules were absorbed in both by a length of 4 mm. Caudal ray development varied between species; in *S. japonicus* the

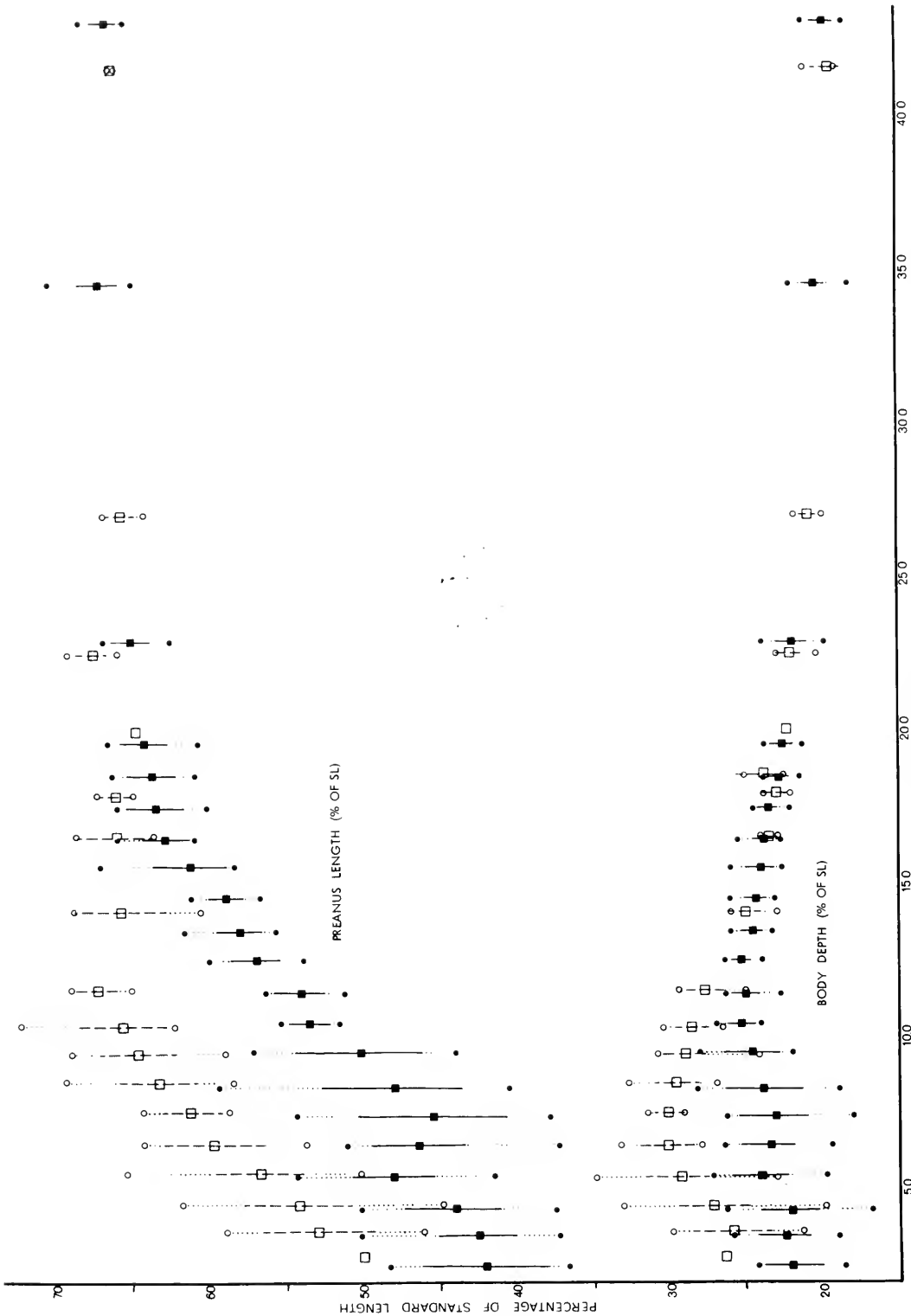


FIGURE 2.—Body proportions of two species of *Scomber* larvae; open symbols (squares, dashes, and circles) denote *S. japonicus*; solid symbols denote *S. scombrus*; squares denote means; bars denote $\pm\sigma$, dots and circles denote total range of observations.

rays were forming at a length of 5 mm and in *S. scombrus* at 7 mm.

Pigmentation

Differences in pigmentation were found between larvae of the two species. Pigmentation over the gut and midbrain and on the caudal region is not described in detail because it does not differ between the two species. A series of 210 *S. japonicus* specimens ranging from 2.8 to 49.0 mm long and 187 *S. scombrus*, 2.6 to 21.6 mm long, were used in the pigmentation comparison. Figure 3 illustrates the development of pigmentation and various body features.

Forebrain

Scomber scombrus larvae usually acquire melanophores on the forebrain at smaller sizes than *S. japonicus*. They were present on *S. scombrus* as small as 3.7 mm and were present on all larvae larger than 5.5 mm. The smallest *S. japonicus* with such pigment was 5.2 mm, and not until 8.7 mm was attained did all larvae have this pigment. Forebrain pigment should not be confused with that on the midbrain which larvae of both species possess at all sizes.

Hindbrain

Pigmentation on the hindbrain begins as a single melanophore then increases to three to five melanophores on the posterior and middle portion of the hindbrain. This pigmentation is increasingly obscured by overlying tissue after about 5 mm. All *S. scombrus* larvae examined had this pigment, but *S. japonicus* <3.5 mm did not.

Snout

Pigmentation on the snout refers to melanophores on, or within, epidermal tissue, not subsurface as on the forebrain. Melanophores appear first near the tip of the snout. *Scomber scombrus* generally develop snout pigmentation at smaller sizes than *S. japonicus*. The smallest *S. scombrus* with such pigmentation was 4.3 mm long and it was present in all that were 6.3 mm and greater. It was first observed in *S. japonicus* at 5.2 mm and was present in all specimens 10.5 mm and longer.

Cleithral Symphysis

Pigmentation at the symphysis of the cleithra, and on the isthmus immediately anterior to the symphysis, was lacking in all specimens of *S. japonicus*. However, in *S. scombrus* prominent melanophores were noted at this location in larvae as small as 3.7 mm and occurred in all larvae >8.0 mm (Figures 3, 4). Melanophores occurred on the isthmus of *S. scombrus* in: 13% of those 4.0 to 4.9 mm long; 41% of those 5.0 to 5.9 mm; 67% of those 6.0 to 6.9 mm; 95% of those 7.0 to 7.9 mm; and in all specimens 8.1 mm and longer. In larvae <8 mm the presence of melanophores at the cleithral symphysis indicates *S. scombrus*; however, the absence of this pigment at this size does not indicate either of the two species. At sizes >8 mm the presence of this pigment indicates *S. scombrus* and its absence indicates *S. japonicus*.

Lower Jaw

Melanophores on the lower jaw first appear at the mandibular symphysis, then spread laterally and posteriorly. *Scomber scombrus* acquire this pigment at a smaller size than *S. japonicus*. The smallest larval *S. scombrus* observed with lower jaw pigmentation was 4.6 mm long and it occurred in all specimens 6.2 mm and greater. The smallest *S. japonicus* with such pigment was 8.3 mm long and it occurred in all larvae of this species 11.7 mm and greater.

Ventrum of Gut

In his paper on the development of *S. japonicus*, Kramer (1960) referred to two or three characteristic, minute melanophores on the ventral surface of the gut, found after yolk absorption. During my study pigment in this location was observed in both *S. japonicus* and *S. scombrus*. The percent occurrence of melanophores on the ventrum of the gut in *S. japonicus* <12 mm long varied from 70% to 92% for each 1-mm size group, with an average of 88% occurrence. The occurrence for the same sizes of *S. scombrus* varied from 10% to 41%, with an average of 28%.

Dorsum of Trunk

There are substantial differences between the two species in pigmentation on the dorsum of the

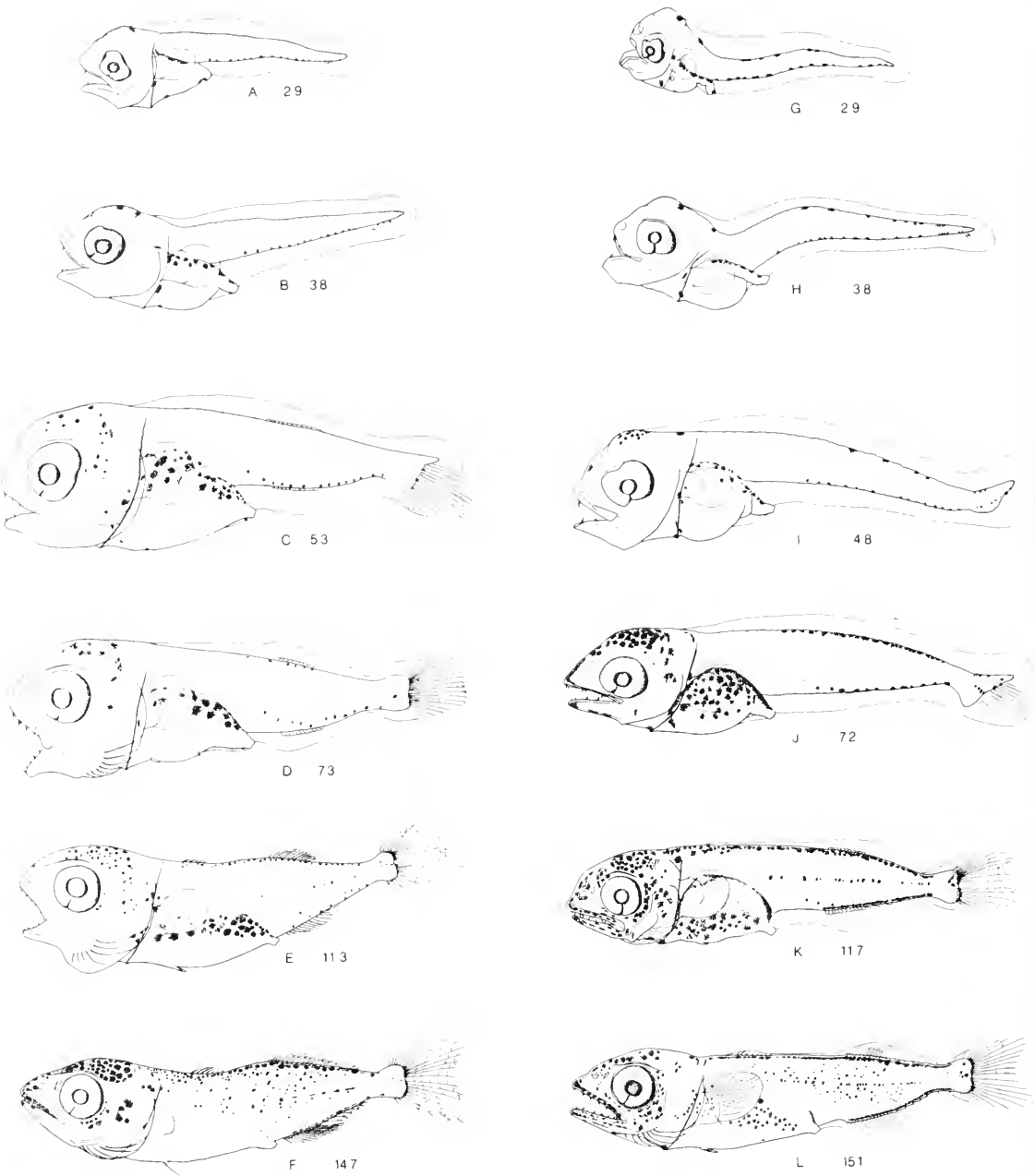


FIGURE 3.—*Scomber japonicus*, A to F; *S. scombrus*, G to L; lengths (SL) are given in millimeters.

trunk, posterior to the nape, particularly at lengths less than about 8 mm (Figures 3, 4). All *S. scombrus* specimens examined, 2.6 mm and larger, possessed dorsal melanophores. At lengths less than about 5 mm this pigmentation consists of a single median series of dendritic melanophores, initially 3 to 6 in number, increasing to 4 to 13, located between myomeres 13 and 28. In larvae greater than about 5 mm the median series becomes double, one row on each side of the developing dorsal fin base, and increases in number of melanophores and extent so that by a length of 9.5

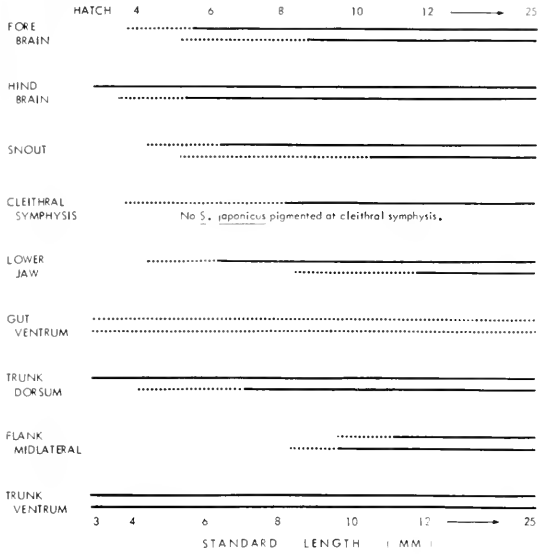


FIGURE 4.—Acquisition of pigmentation of larval *Scomber scombrus* and *S. japonicus*. Dashed lines indicate some specimens have pigmentation; solid lines indicate all specimens have pigmentation. The upper of each pair of lines refers to *S. scombrus*, the lower to *S. japonicus*.

mm the dorsal edge of the trunk is pigmented from nape to caudal fin. With further growth melanophores form on the flanks, and spread downward from the dorsal row; this happens first in the abdominal area, then posteriorly.

Scomber japonicus larvae develop this pigmentation at larger sizes than *S. scombrus*. Only one *S. japonicus* (4.1 mm) <5.2 mm long possessed dorsal melanophores. Subsequent percent occurrences of *S. japonicus* larvae possessing this pigmentation were: 24% at 5.0 to 5.9 mm, 59% at 6.0 to 6.9 mm, and 100% at 7.0 mm and greater. The largest *S. japonicus* lacking dorsal melanophores was 6.9 mm long. As in *S. scombrus* this pigmentation develops from a single median series into a double row and increases to extend from the nape to the caudal fin by a length of about 11.0 mm.

Thus at sizes smaller than about 11 or 12 mm there is a difference in dorsal pigmentation between the two species. While *S. scombrus* possess dorsal pigmentation many *S. japonicus* either lack melanophores in this location or have considerably less than comparably sized *S. scombrus*. This conclusion is in general agreement with earlier published statements. Padoa (1956) mentioned that postanal pigmentation of *S. japonicus* is less intense than that of *S. scombrus*, but he did not specify whether he was referring to dorsal or ventral postanal pigment. Dekhnik (1959) reported that, between yolk absorption and a length of 6.18 mm TL, larval *S. japonicus* lack melanophores on the dorsal edge of the trunk while larval *S. scombrus* have melanophores in this area.

Fry (1936a, figure 12G) illustrated a late yolk-sac stage *S. japonicus* with a small dorsal patch of melanophores near the 23d myomere, but did not comment in the text on the occurrence of this pigmentation. Uchida et al. (1958) and Kramer (1960) referred to a similar dorsal patch of melanophores in some of their late yolk-sac stage *S. japonicus*. Watanabe (1970) did not illustrate such dorsal pigment in his paper on this species. None of the *S. japonicus* larvae in my study had this dorsal patch; however, I identified only two larvae <3.0 mm long.

Flank

A longitudinal row of melanophores develops along the midline of the lateral trunk surface in *Scomber* larvae. This row begins forming in *S. japonicus* at 8.3 to 9.6 mm long and in *S. scombrus* at 9.6 to 11.1 mm long. The pigment in this row, first observable as a few distinct melanophores in the postanal region, increases to form a line flanked by scattered melanophores. These scattered melanophores tend to occur along the myosepta; this tendency is more pronounced in *S. scombrus* than in *S. japonicus*.

Postanus Ventral Pigmentation

Both species possess postanus ventral pigmentation, at all sizes examined. This pigmentation occurs in the smallest larvae as a median row of 15 to 20 melanophores. This series occurs first near the dermal surface and becomes internally situated along the median ventral septum as the anal fin develops. A second, double series of melanophores forms on the dermal surface, on either side of the developing anal fin base. This second series appears first at lengths of 7.0 to 7.9 mm in both species and increases in number of melanophores, so that by a length of about 15 mm there is a line of melanophores along either side of the anal fin, continuous with a median group of melanophores between the anal and caudal fin.

The initial median series of melanophores gradually becomes obscured by overlying tissue

and pigmentation, so that by a length of 15 mm only one to four melanophores of that series are still visible, and these only under favorable lighting conditions.

Summary of Contrasting Characters

The precaudal and caudal vertebral counts, 14 + 17 in *S. japonicus* and 13 + 18 (or 12 + 19) in *S. scombrus*, are distinguishable in *S. japonicus* as small as 7.6 mm and in *S. scombrus* at 8.6 mm. First dorsal fins, with 10 or 11 spines in *S. japonicus* and 12 to 17 spines in *S. scombrus*, attain their full complement by 13.0 and 17.0 mm in the two species, respectively. In *S. japonicus* a total complement of 13 or 14 first-dorsal-fin pterygiophores is attained by 20.2 mm while in *S. scombrus* a total complement of 22 to 25 is attained by 32.0 mm. Because anterior pterygiophores ossify before posterior ones, and the counts differ between the two species, counts of pterygiophores in the second through fifth or sixth interneural spaces serve to identify *S. japonicus* by 11.7 mm and in *S. scombrus* by 18.2 mm (Table 1).

The relative position of the first anal pterygiophore and the first haemal spine is first observable in *S. japonicus* at 11.7 mm and in *S. scombrus* at 32.0 mm. In *S. japonicus* the first anal pterygiophore is anterior to the first haemal spine while in *S. scombrus* it is posterior.

Scomber japonicus larvae are deeper bodied at 4 to 11 mm and have greater preanus lengths at 3 to 15 mm than comparably sized *S. scombrus* larvae.

Scomber scombrus larvae are more heavily pigmented and acquire pigmentation earlier than *S. japonicus* at lengths less than about 15 mm (Figure 4). Of the two species *S. scombrus* is earlier in developing melanophores on the snout and lower jaw. Some specimens of both species possess a few minute melanophores on the ventrum of the abdomen, but their occurrence is more frequent in *S. japonicus* larvae <4.2 mm. At given sizes up to 12 mm, where additional dorsal trunk pigmentation is developing in both species, the melanophores are more numerous and larger in *S. scombrus* than in *S. japonicus*. At lengths greater than about 12 mm this character is equally developed in both species. Melanophores are not found at the symphysis of the cleithra in any *S. japonicus* larvae, but are present in *S. scombrus* larvae as small as 3.7 mm, then in increasing frequency of occurrence so that all *S. scombrus* larvae >8 mm possess this pigmentation

DISTRIBUTIONS OF EGGS AND LARVAE

Scomber scombrus, Egg Distributions

During the May cruise, *S. scombrus* eggs were taken from Martha's Vineyard to below the mouth of Chesapeake Bay and were concentrated from Fire Island, N.Y., to Cape Henry, Va. (Figure 5). Spawning apparently extended northward in the inshore portion of shelf water in an area whose northeastern boundary roughly paralleled the surface isotherms. The egg distribution extended out to at least the edge of the continental shelf off Maryland to North Carolina on transects F, G, J, and K.

By the time of the June cruise, spawning of *S. scombrus* had shifted to the northeast. Eggs were taken only on the three northernmost transects, the majority occurring in the inner half of shelf waters (Figure 6).

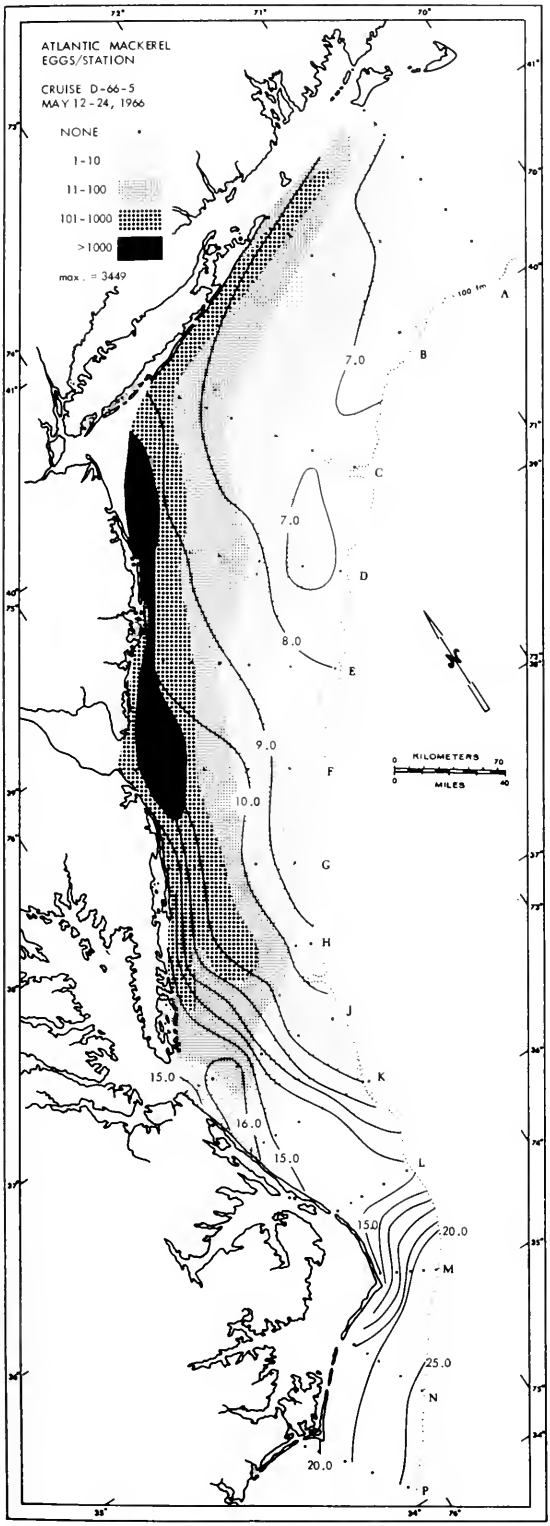
Scomber scombrus, Larva Distributions

During May, *S. scombrus* larvae were caught between Chesapeake Bay and Oregon Inlet, N.C., across the breadth of the continental shelf and south of the area where eggs were taken during this cruise (Figure 7). These larvae were small, ranging from 2.5 to 8.1 mm long with a mode of 3.0 to 3.9 mm.

During the June cruise we took *S. scombrus* young over a greater area than in May. Larvae occurred from the offing of Martha's Vineyard, which was probably not the northern limit of their distribution, south to the offing of Currituck Beach, N.C. (Figure 8). The distribution of larvae overlapped that of eggs on the three northernmost transects and extended across the entire breadth of the continental shelf between Martha's Vineyard and New Jersey. The largest numbers occurred off Montauk Point, N.Y. Most larvae taken in June were north of the area of larva occurrence in May.

A marked increase in lengths of young, progressing from north to south, is shown in length-frequency data for this cruise (Figure 9). This increase may be due to earlier spawning or higher temperatures to the south which may enable the larvae to grow faster.

The inordinately large increase in lengths between transects D and E and decrease in lengths south of transect E may have been caused by the



time sequence of sampling. We sampled transect E as much as 4 days after transects G, H, and K, and 8 or 9 days after transect D. If we had progressed southward over the whole cruise, the young taken on transect E probably would have been smaller by 8 or 9 mm and intermediate between the lengths of those found on transects D and G, assuming Sette's (1943) calculated growth rate of about 1.0 mm/day in 20- to 30-mm *S. scombrus* is correct.

During August we took *S. scombrus* larvae only on the two northernmost transects, off Martha's Vineyard and Montauk Point between about 10 and 90 km offshore. Relatively few larvae were caught, 76 in all. They were small, ranging from 2.6 to 7.7 mm with a mode of 3.0 to 3.9 mm long.

Because 1) no *S. scombrus* eggs were taken on the August cruise and 2) larvae occurred only near the northeastern extreme of sampling at a time when the adults are known to be migrating toward the north and east, it follows that these larvae may have resulted from the last spawning within our survey area for 1966. In fact, they may have been spawned northeast of the survey area, for Bumpus and Lauzier (1965) report a southwesterly drift in continental shelf waters off Rhode Island and Long Island, N.Y., in August.

Scomber scombrus, Catch Characteristics

Statistical tests were run on catch characteristics, in order to summarize the data. These tests included: 1) comparison of catch sizes by net 1 (0 to 15 m) versus those by net 2 (18 to 33 m) for eggs; 2) the same comparison for larvae; 3) comparison of larva lengths taken by net 1 versus net 2 during day; 4) the same comparison during night; and 5) comparison of larva lengths taken during day versus those taken during night. Because the samples were collected by open nets, net 2 catches were corrected for contamination.

Results of tests 1 and 2 showed significant differences in the catch between nets 1 and 2. Net 1 caught 2.3 times as many eggs (chi-square = 1,533.956, $P<0.005$, with 19 df) and 6.1 times as many larvae (chi-square = 1,360.618, $P<0.005$, with 26 df) as net 2. The larger catch in the 0- to 15-m (net 1) tow is probably related to the occurrence of most eggs and larvae of *S. scombrus*

FIGURE 5.—Distribution of *Scomber scombrus* eggs and selected surface isotherms (°C) during May 1966.

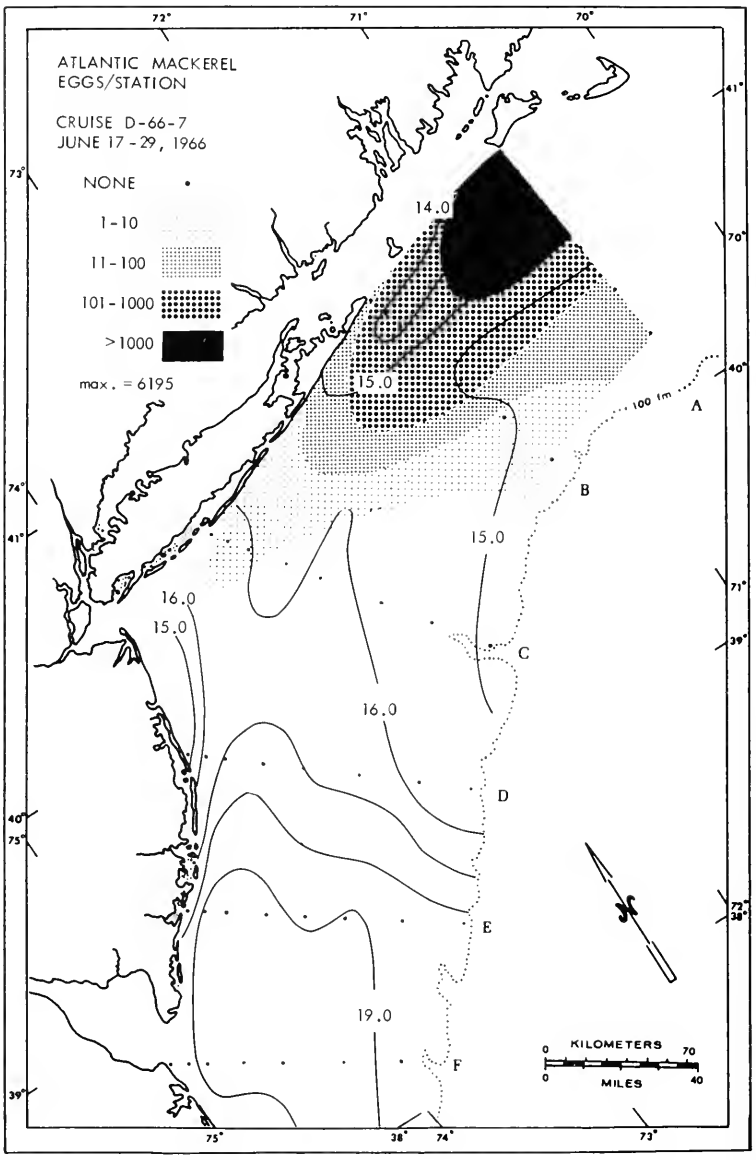


FIGURE 6.—Distribution of *Scomber scombrus* eggs and selected surface isotherms (°C) during June 1966.

above the thermocline as reported by Sette (1943). During Sette's study the thermocline occurred between 17 and 19 m. During this survey, at stations where *S. scombrus* eggs or larvae were caught, the thermocline was situated so that the surface mixed layer was sampled by net 1 and was rarely deep enough for the surface layer to be sampled by net 2.

I tested the two hypotheses that the mean lengths (SL) were equal in catches from net 1 and net 2 during both day and night tows, and found in both cases that the mean lengths were not significantly different between the paired catches. In another analysis I tested for differences in mean lengths between day and night tows. In this case the pairs tested were adjacent stations either on the same or adjacent transects. The result of the test was not significant, i.e., there was no significant difference between the means. I used analysis of variance in these tests for differences in mean lengths between the two nets and between light regimes because this procedure segregates the known differences in lengths observed over the geographical distribution.

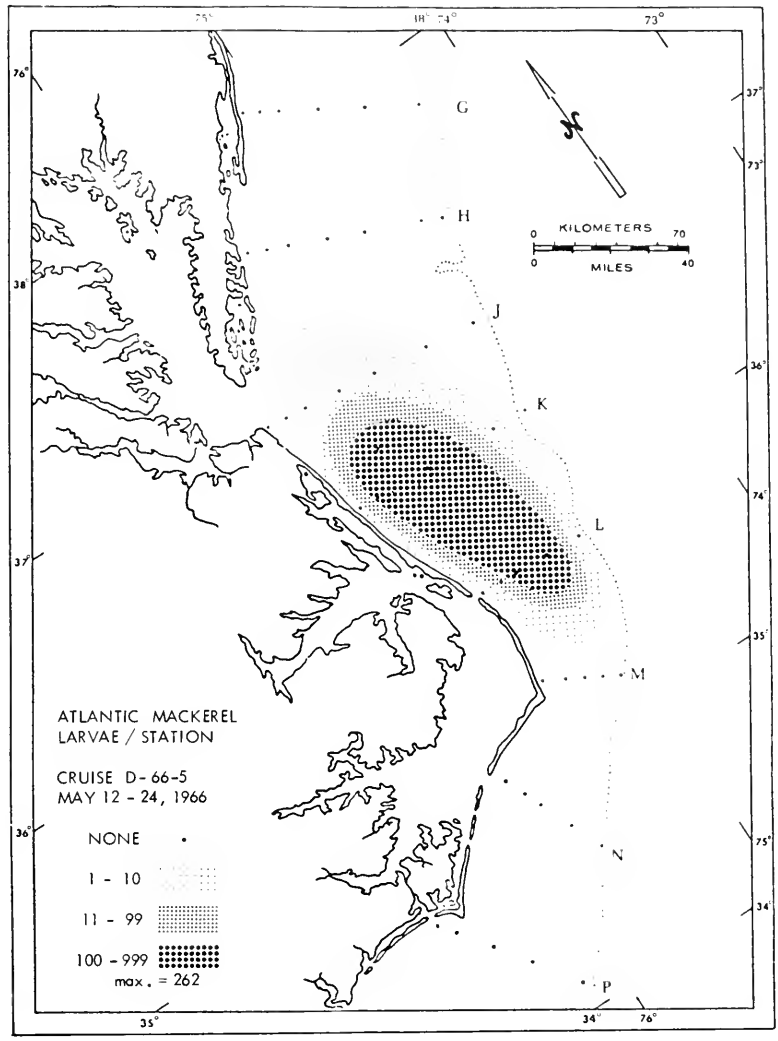


FIGURE 7.—Distribution of *Scomber scombrus* larvae during May 1966.

Scomber scombrus, Relationship of Temperature to Egg and Larva Occurrences

Temperature dependence of spawning is suggested by the parallel relationship of the surface isotherms and the northeastward edge of the egg abundance contours in May (Figure 5). This temperature dependence is also implied by the June cruise results, i.e., while shelf waters warmed, with consequent northward and eastward displacement of surface isotherms, the distribution of eggs moved accordingly (Figure 6). While the northern extent of the egg distribution was defined only during the May cruise, the southern extent was defined during both the May and June cruises, falling within the 16.0°- to 16.9°C-temperature interval despite the northerly displacement of temperatures between the two cruises. Along with even higher water temperatures prevailing during the August cruise, spawning had ceased entirely within the survey area by that time.

Sette (1943) related his egg catches to surface temperature and reported a weighted mean of 10.9°C for all eggs taken in 1932, with 98% occurring at 9.0°C to 13.5°C. During the May cruise of our survey, similar surface temperatures were associated with the eggs. The weighted mean surface temperatures for all eggs taken during May was 11.0°C, with 97% at 8.7° to 13.8°C and the temperature associated with all eggs in May ranged from 6.3° to 16.9°C.

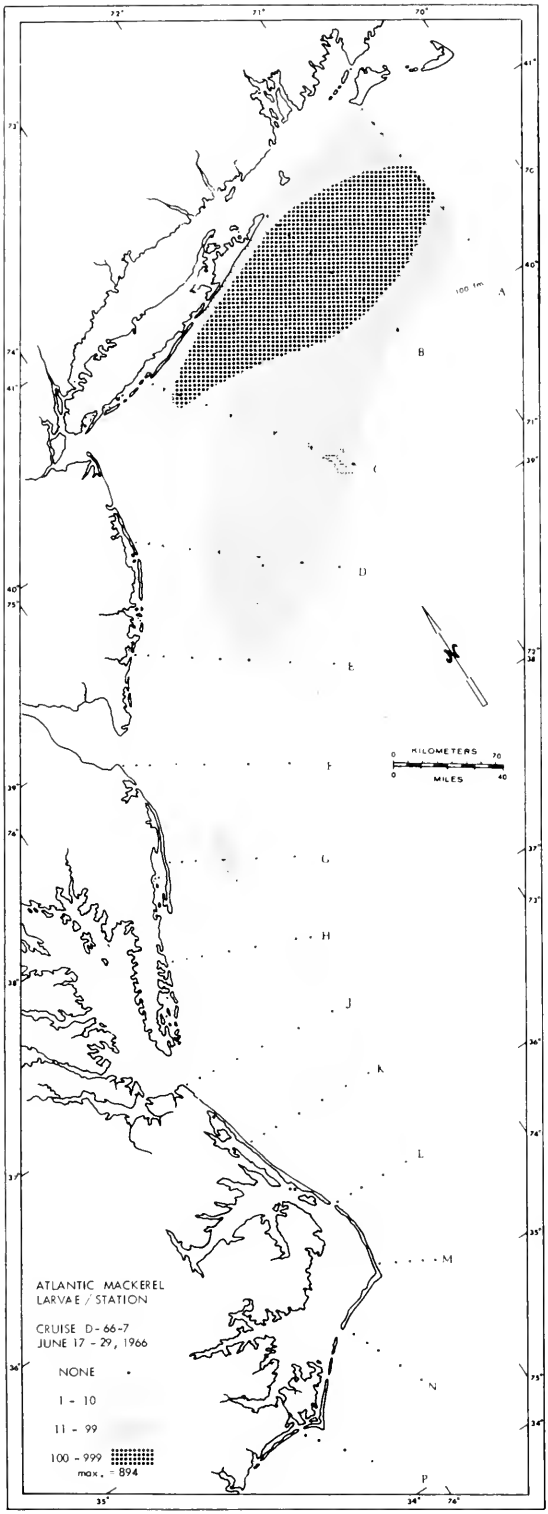


FIGURE 8.—Distribution of *Scomber scombrus* larvae during June 1966.

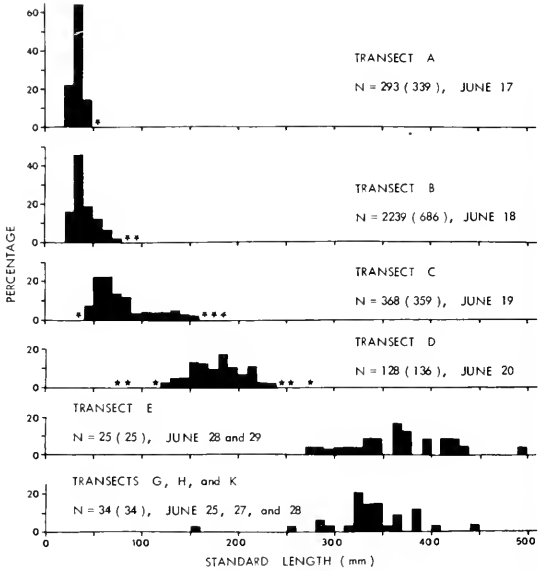


FIGURE 9.—Length-frequency distributions of *Scomber scombrus* larvae taken during June 1966. N indicates the adjusted total catch and, in parentheses, the number measured; a star indicates less than 1%.

Because larvae were inhabiting waters undergoing warming they were associated with slightly higher temperatures than were eggs. Surface temperatures associated with larvae caught during May, June, and August ranged from 12.3° to 20.7°C, with 96% occurring at 13.7° to 16.8°C.

Scomber japonicus, Egg Distributions

Eggs of *S. japonicus* were taken on two survey cruises conducted south of Cape Lookout. During the January-February 1968 cruise eggs occurred on seven transects, between Charleston, S.C. and St. Lucie Inlet, Fla. (Figure 10). During the May 1967 cruise they occurred more northerly, from New River, N.C., to Cape Canaveral, Fla. (Figure 11).

Most *S. japonicus* eggs were found over the outer half of the continental shelf. All were taken where the water was at least 32 m deep; the six largest catches (more than 10 eggs/station) were at locations where the water was at least 60 m deep. The fact that these eggs occurred at the offshore extremes of two-thirds of the transects

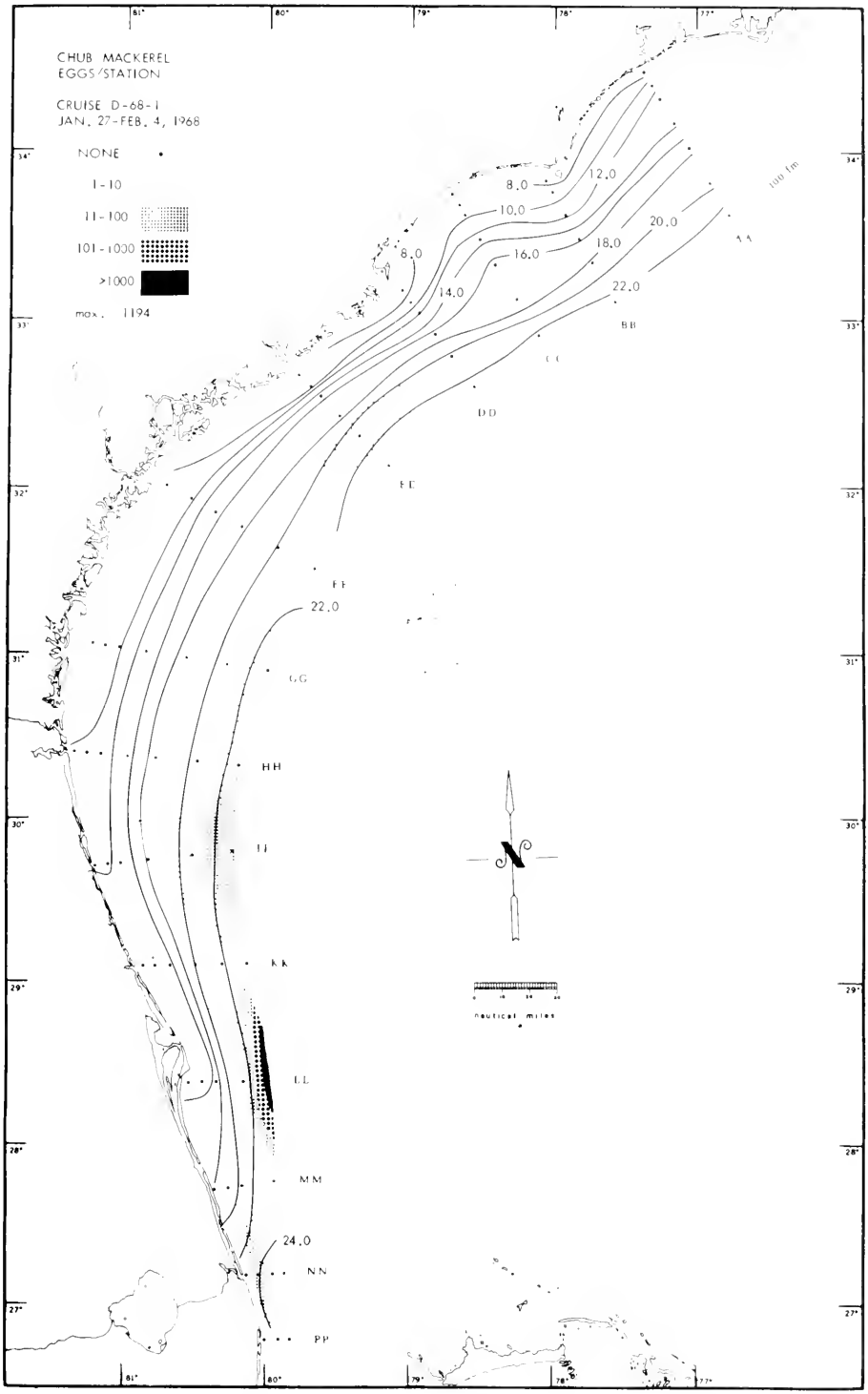


FIGURE 10.—Distribution of *Scomber japonicus* eggs and selected surface isotherms (°C) during January-February 1968.

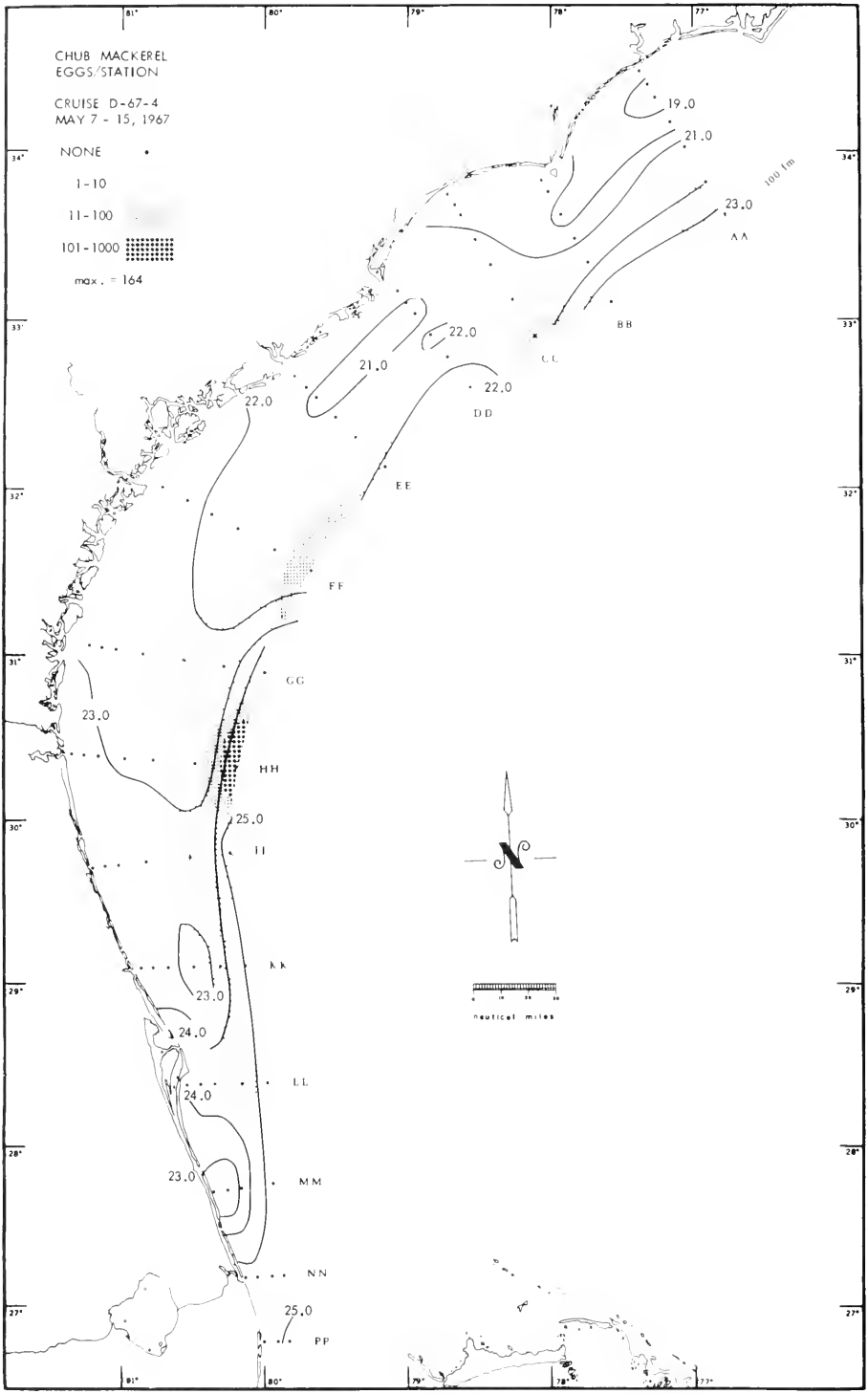


FIGURE 11.—Distribution of *Scomber japonicus* eggs and selected surface isotherms (°C) during May 1967.

where they were taken suggests that their distribution extended beyond the continental shelf.

Scomber japonicus, Larva Distributions

Larval *S. japonicus* were caught on five cruises, during January, February, April, May, and July. They were most abundant during the same two cruises on which eggs were taken (January-February 1968 and May 1967). During January-February 1968, larvae were caught from off New River to off Palm Beach (Figure 12). During May 1967, larvae were found from off New River to Ponce de Leon Inlet, Fla. (Figure 13). In addition to those plotted, there were single occurrences of *S. japonicus* larvae on three other crusies during: April 1966, off Currituck Beach; May 1966, off Cape Hatteras, N.C.; and July 1967, off St. Lucie Inlet.

Larvae were found slightly farther inshore than were the eggs, in waters as shallow as 25 m, but were generally over the outer half of the continental shelf. Larvae apparently occurred beyond shelf waters, for they were caught at the edge of the shelf on almost two-thirds of all the transects on which they were taken.

Scomber japonicus larvae taken during the January-February 1968 cruise ranged from 2.5 to 11.5 mm long. The modal length, 4.0 to 4.9 mm, for this cruise was made up of larvae from both areas of concentration, on the Brunswick, Ga., and Cape Canaveral transects. Larvae caught during May 1967 ranged from 2.8 to 20.5 mm long. There were two modal length intervals during this cruise; larvae composing the first, at 4.0 to 5.9 mm, were largely from the Cape Lookout transect while those of the second, at 8.0 to 8.9 mm, were from both the Cape Romaine, N.C., and Brunswick transects. No latitudinal size progression was observed in the data, as seen in *S. scombrus* data from June. Spawning appears to occur simultaneously from North Carolina to Florida, and to extend over at least 7 mo (January to July).

Scomber japonicus, Temperature vs. Egg and Larva Occurrences

During January-February the surface isotherms roughly paralleled the shoreline south of Cape Hatteras, with higher temperatures found offshore (Figure 10). Therefore, the generally offshore distributions of *S. japonicus* eggs and larvae mentioned previously were also correlated with the upper temperatures sampled on this cruise. Larvae were found over a greater range of surface temperature (18.5° to 24.7°C) Than were the eggs (20.4° to 23.2°C) in January-February.

Surface temperature conditions during May were different from those of the January-February cruise. During May many surface isotherms extended across the shelf (Figure 11), especially within the temperature range at which most eggs and larvae of this species were found (approximately 21° to 24°C). However, the distributions of eggs and larvae were similar on this cruise to those from the January-February cruise, i.e., restricted to the outer half of the shelf waters. Eggs were found within approximately the same surface temperature range as larvae during this cruise, 21.3° to 25.4°C for eggs and 21.3° to 24.2°C for larvae. Including all occurrences of *S. japonicus* eggs and larvae, on five cruises, the ranges of surface temperatures encountered were 20.4° to 25.4°C for eggs and 16.0° to 29.4°C for larvae.

DISCUSSION

Scomber scombrus spawns from Cape Hatteras to the Gulf of St. Lawrence. Spawning progresses northeastward along the coast as the adults migrate during spring and early summer. Within the survey area, most spawning takes place over the shoreward half of the continental shelf, with small numbers of eggs occurring out to and possibly beyond, the edge of the continental shelf. Surface temperatures associated with spawning (egg occurrences) range from about 7° to 16°C. In comparison, the majority of *S. japonicus* spawn south of Cape Hatteras; the southern extent of spawning is unknown, but it extends at least as far south as Key Biscayne, Fla. Spawning by this species may occur north of Cape Hatteras but farther offshore than sampling was conducted, possibly in Slope Water or the shoreward edge of the Gulf Stream. The spawning season extends at least from midwinter to early summer south of Cape Hatteras. Unlike *S. scombrus*, if *S. japonicus* undertakes a spawning migration it has not been described. Spawning occurs predominantly over the outer half of the continental shelf, and probably beyond. Surface temperatures associated with *S. japonicus* spawning in the western North Atlantic Ocean vary from about 20° to 25°C.

Scomber japonicus eggs were associated with generally higher temperatures (20° to 25°C)

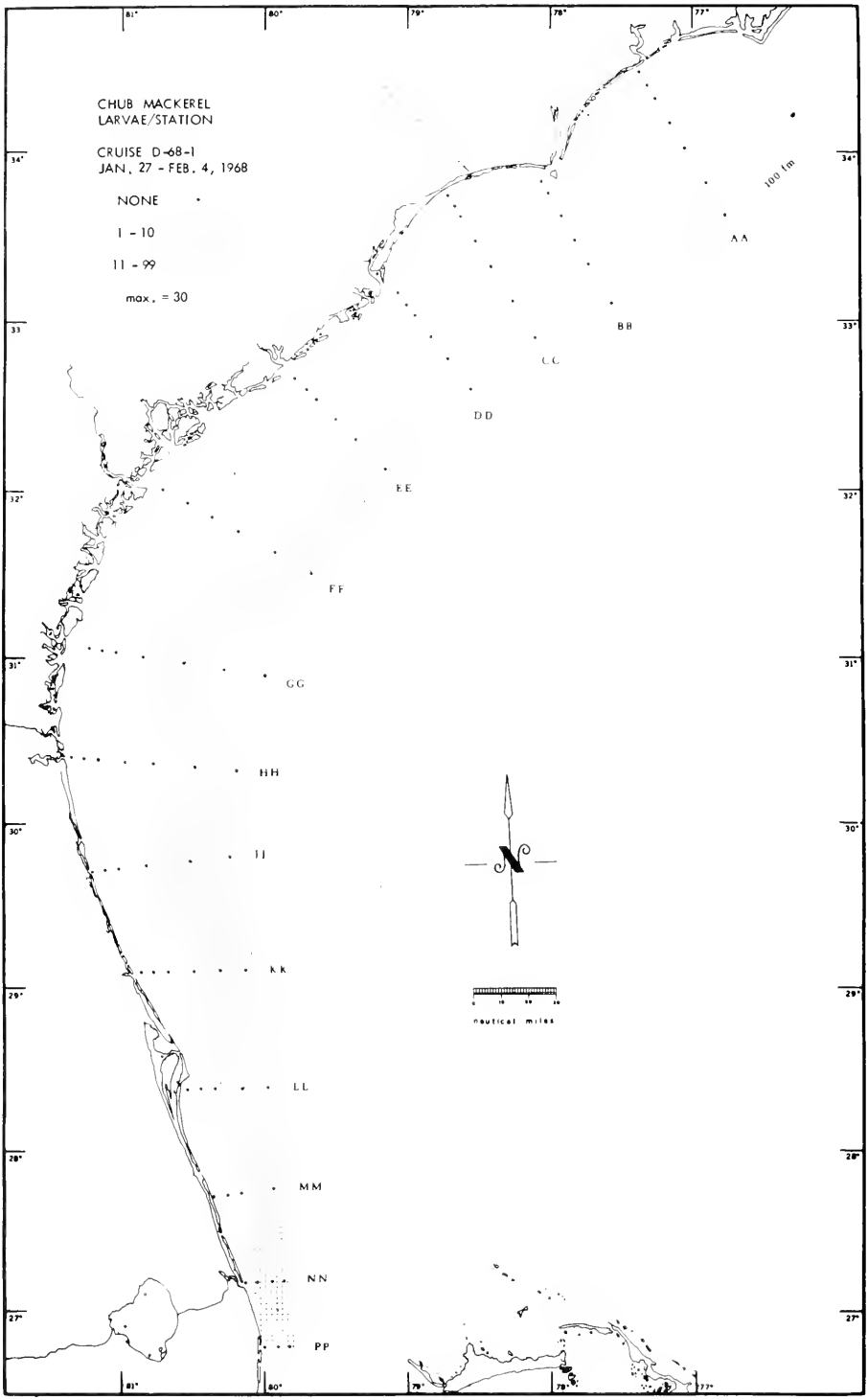


FIGURE 12.—Distribution of *Scomber japonicus* larvae during January-February 1968.

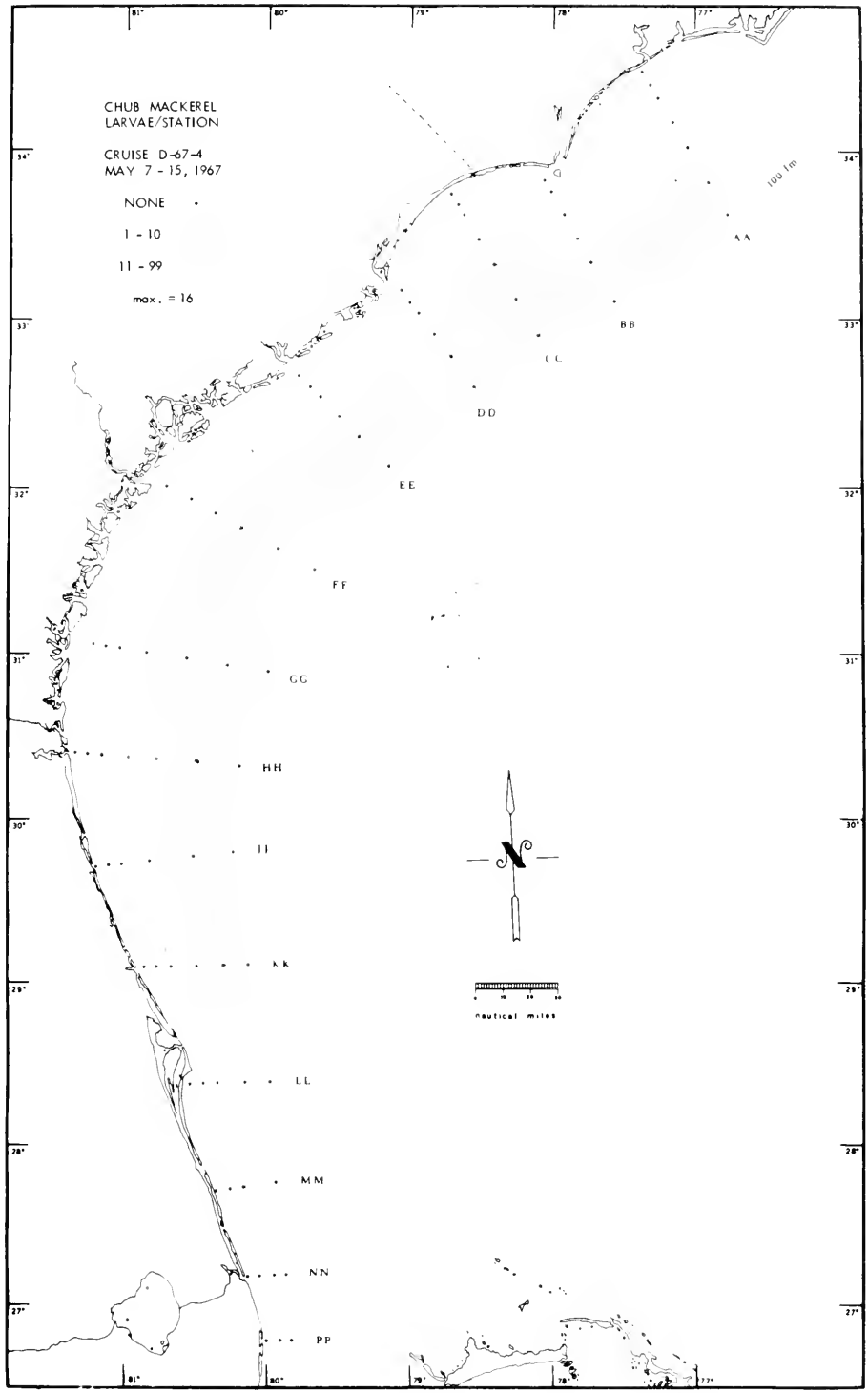


FIGURE 13.—Distribution of *Scomber japonicus* larvae during May 1967.

during this survey than in other studies on this species in the western North Pacific Ocean by Uchida et al. (1958), Dekhnik (1959), and Watanabe (1970) and in the eastern North Pacific Ocean by Fry (1936b). Although there was some variation between these studies, all reported surface temperatures within the range of 15° to 21°C associated with spawning or with the majority of eggs caught.

Scomber scombrus population estimates of 18 and 17 million spawners, based on our May and June 1966 cruises, respectively, were reported by Berrien and Anderson.[4] As discussed by the authors, these point estimates, calculated from egg catches, probably understated the true population size due to cruise timing and the area sampled. Apparently the May cruise occurred prior to peak spawning intensity resulting in many spawners being unaccounted for in the point estimate. During June, although the egg density was greater than in May, only a portion of the egg population was surveyed; therefore, the population was incompletely sampled.

Other plankton survey efforts within the Mid-Atlantic Bight have resulted in higher and probably more accurate, *S. scombrus* spawning population estimates. Sette (1943) reported a season-long, Mid-Atlantic Bight spawning population of 320 million spawners in 1932. Berrien and Anderson (see footnote 4) reported a point estimate of 392 million spawners within the New York Bight during May 1975.

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[4]Berrien, P. L., and E. D. Anderson. 1976. *Scomber scombrus* spawning stock estimates in ICNAF Subarea 5 and Statistical Area 6, based on egg catches during 1966, 1975 and 1976. ICNAF (Int. Comm. Northwest Atl. Fish.) Res. Doc. 76/XII/140, 10 p.

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DAILY AND SUMMER-WINTER VARIATION IN MASS SPAWNING OF THE STRIPED PARROTFISH, *SCARUS CROICENSIS*

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ABSTRACT

The "striped" phase of the striped parrotfish, *Scarus croicensis*, engaged in mass spawning during afternoon periods on a deep (24 m) coral pinnacle off Discovery Bay, Jamaica. During morning periods the fish occurred in a large foraging group on shallow reefs and moved to the spawning site in early afternoon. The occurrence of spawning rushes per day in June was about six times that during January. *Chromis cyanea* and *Clepticus parrai* fed on freshly released eggs of *S. croicensis*. Mass spawning by *S. croicensis* was similar to that of *Sparisoma rubripinne*.

The striped parrotfish, *Scarus croicensis* Bloch (Figure 1), is the smallest (reaching 25 cm SL, standard length) but the most common member of this genus in the tropical western North Atlantic (Randall 1968; Böhlke and Chaplin 1968). Like other scarids, *S. croicensis* is a benthic herbivore grazing on algal-covered rock and coral surfaces and is seldom found at depths below 30 m. The species possesses dimorphic color phases, termed the "striped" phase (male and female) and the "terminal" phase (male only), believed derived from striped phase females by protogynous sex reversal (Ogden and Buckman 1973).

Aspects of the general biology of this fish have been reported on by several authors. Ogden and Buckman (1973) followed movements of tagged individuals in Panama and found daily migrations between feeding and sleeping areas. Feeding was largely carried out in foraging groups of up to 500 individuals with a characteristic set of associate, but less numerous species. Buckman and Ogden (1973) described territoriality by striped phase females and terminal phase males. Barlow (1975) discussed the sociobiology of *S. croicensis* in comparison with three other species of parrotfishes and described their feeding pattern, group sizes, density, and color variation. He also added some notes on spawning behavior of *S. croicensis*.

Randall (1963) reported both mass spawning by the striped phase of *S. croicensis* and pair spawning by terminal phase males and striped phase females. Randall and Randall (1963) described pair spawning at St. John, V. I., during February, March, April, June, and August, and with their limited observations they felt that pair spawning accounted for most of the reproduction of the species. Buckman and Ogden (1973) commonly observed pair spawning at depths of 9-13 m, but also as shallow as 3 m, in Panama. Munro et al. (1973) found females of the striped parrotfish in ripe condition from March to May near Jamaica.

FIGURE 1.—Striped parrotfish, *Scarus croicensis*, with "contrast" color pattern approximately 100 mm standard length at Discovery Bay, Jamaica.

In August 1971 a large spawning group of striped parrotfish was encountered on a deep coral platform (24 m) offshore from the Discovery Bay Marine Laboratory on the north coast of Jamaica. This species is by far the most common parrotfish along this coast, which is heavily fished using Antillean fish pots. This spawning group consisted of several hundred individuals. Its reproductive activity was sufficiently regular and observable that investigation of diel patterning of spawning seemed feasible. Widely scattered observations from 1971 to 1975 indicated the continued presence of this group. During January and June

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1975 systematic observations of spawning behavior were conducted.

MATERIALS AND METHODS

For purposes of determining diel variation of spawning activity, the daylight period (from sunrise to sunset) was divided into 16 equal periods. As occasional checks during the morning indicated that the spawning population was not present at the spawning site and was not spawning elsewhere, only the latter eight periods of the day were included in this study. Since day length varied considerably between January and June observations, the length of each period also varied by the same factor. The change of day length during each of the two series of observations was only a few minutes.

During the winter observations (12-28 January), the day length was 11 h 10 min with 42 min for each period. During summer (19-29 June), the day length was 13 h 10 min with 50 min for each period, an increase of 17% in day length. Water temperature at the study site varied between 26° and 29°C seasonally.

The number of spawning rushes, the upward dash by groups of parrotfish culminating in the release of eggs and sperm, occurring during 15 min within the observation period was counted by an observer (wearing scuba equipment). This time was chosen as the minimum for measurements of spawning rush frequency due to the somewhat irregular occurrence of the rushes on a minute by minute basis. In the latter portion of the study, data were recorded minute by minute for the full 15-min period. The observers were tethered near the spawning site by lines attached to the bottom which caused them to float nearly motionless at 21 m depth, approximately 3 m above the substrate. This allowed observations to be made from a consistent location, minimized movement needed to stay in position, and decreased the depth of the observers slightly to allow more bottom time for observations with no or short decompression at the end of the dive. The presence of the observers did not seem to interrupt or affect the spawning behavior as the population did not move away or cease spawning after the observers' arrival.

Color motion pictures (16 mm) were made of spawning and feeding behavior of *S. croicensis*, including some at two times normal film speed for slow motion analysis of movement. Films were analyzed on a frame by frame basis.

GENERAL BEHAVIOR

A general profile of the area near the spawning site is presented in Figure 2. Sand channels run between fingers of reef directed seaward which gradually slope from a shallow reef crest to a zone dominated by the branched coral *Acropora cervicornis* at 10-13 m depth. At the seaward edge of this *A. cervicornis* zone, the reef slopes steeply to a sandy bottom at 24-25 m depth. Beyond this point the sand bottom either slopes rapidly downward to the near vertical dropoff or has an outer reef rising above it, often resembling a rounded pinnacle and somewhat trapping the sediment behind it. The pinnacle of "Dancing Lady Reef" was the location of the spawning observed in this study. On the

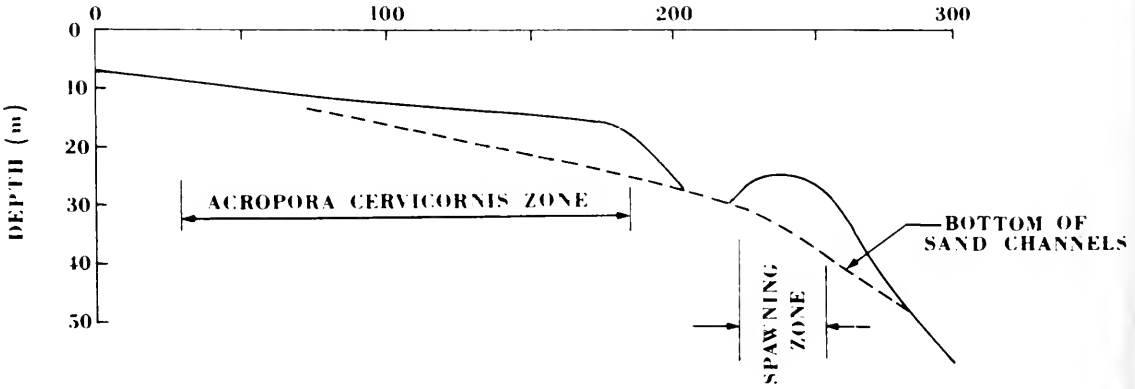

FIGURE 2.—Bottom profile of "Dancing Lady Reef" offshore from the Discovery Bay Marine Laboratory. Vertical exaggeration is 2×.

outer face of this pinnacle, the reef drops away steeply and at a depth of 50-70 m becomes nearly vertical in profile.

In Jamaica *S. croicensis* occurred in foraging groups similar to those described by Ogden and Buckman (1973) in Panama. In the vicinity of the spawning site only one sizeable foraging group occurred. Although no tagging experiments were carried out, this group almost surely constituted the major portion of the spawning population studied. During morning hours this group ranged as much as 300 m inshore from the spawning area onto the shallow reefs to depths of as little as 7 m. They also ranged only about 100 m in either direction parallel to shore along the reef.

These foraging groups consisted of several hundred *S. croicensis* (the exact number being impossible to determine in most cases) plus a few other fishes. In one instance at least 410 individuals of *S. croicensis* were visible in photos taken of the entire group. Only a few terminal phase males were seen in these groups. The group swam about 1 m above the substrate in the *A. cervicornis* zone and descended en masse at intervals to feed. Algae were scraped from rock surfaces of the reef, particularly from the dead lower portions of the branches of *A. cervicornis*.

Mixed foraging groups consisting largely of *S. croicensis* have been reported by Buckman and Ogden (1973) and Itzkowitz (1974). In the former two species of acanthurids (*Acanthurus chirurgus* and *A. coeruleus*); a hamlet, *Hypoplectrus puella*; a goatfish; and a few other parrotfishes were typically found associated with the foraging groups. Similar composition of associated species was observed in the present study. Only *A. coeruleus* among the surgeonfishes occurred with the foraging group. However, *A. chirurgus* is relatively rare in the study area. A different species of hamlet, *H. indigo*, also occurred with the foraging group rather than *H. puella*. Among fishes observed occasionally joining foraging groups and not mentioned by Buckman and Ogden (1973) was *Halichoeres maculipinna*.

The functionality of such schooling behavior has been commented on before. Various Indo-Pacific surgeonfishes form schooling groups which behave much like the foraging groups of *S. croicensis* (Jones 1968; Randall 1970; Barlow 1974). Randall (1970), Barlow (1974), and Vine (1974) believed this foraging herd was a method for the surgeonfishes to swamp the defenses of territorial food competitors, in the former instance an acanthurid and in the latter a pomacentrid. This also seems to be the case in the present study. When the foraging group entered the territory of *Eupomacentrus planifrons*, attacks were quickly directed at a few members causing an escape reaction in the few individuals near the center of attack. The group was largely undisturbed by the actions of the damselfish.

FIGURE 3.—Striped phase individuals of *Scarus croicensis* at Discovery Bay, Jamaica, in the "contrast" color form (A) and "gray" form (B). Standard length is approximately 100 mm.

Two color forms of striped phase *S. croicensis* were seen in both foraging and spawning groups. The first had two broad dark stripes separated by thinner pale stripes, the dorsal surface dark and the snout yellowish. This form is termed the "contrast" (Figures 1, 3). The second color form, termed the "gray" form does not have the sharp contrast between dark and pale stripes (Figure 3). The stripes are apparent on the head, but posteriorly they become much less distinct. The scales near the caudal peduncle, even in the center of the dark stripe, are pale-edged and resemble a checkerboard pattern. In foraging groups one-fourth to one-half of the indivuals had the gray color pattern and the remainder were of the contrast pattern. No functional role could be assigned to these color forms. The possibility does exist that they represent male and female, but this could not be established.

MASS SPAWNING BEHAVIOR

Spawning occurred on the deep coral pinnacle (Figure 2) of Dancing Lady Reef at 24 m depth. This pinnacle is the feature with the greatest re-

lief for a distance of several hundred meters along the outer face of the reef. Transects were swum along the sloping face for 200-300 m each direction from the study area while spawning was underway at that site and no other spawning aggregations were encountered. In one instance a group of several *S. croicensis* were observed spawning on the seaward face of a shallow reef immediately west of Dancing Lady Reef at 18 m depth.

The spawning population did not arrive en masse at the spawning site, but rather appeared in small groups over a lengthy period of time. Whether the foraging group breaks up on the shallow reef before the individuals move to the spawning site is not known. The behavior of the striped parrotfish after arrival at the spawning area consists of swimming in small groups around the area within a few meters of the bottom ("milling") and bouts of feeding (from the substrate).

The size of eight individuals speared from the spawning aggregations varied between 80 and 100 mm SL, relatively small for mature specimens. These are deposited in the University of Puerto Rico fish collection (UPR 3452). This sample is biased for small individuals since these were most easily approached and the mean size of specimens in the aggregation was certainly near or over 100 mm SL.

The numbers engaged in milling and the speed and frequency of turns gradually increased. Often groups of 20 or more individuals broke away from the main group and swam as a school farther above the substrate than the milling individuals (Figure 4A, B). The separated group swam increasingly rapidly making abrupt lateral turns ("weaving"). The entire group or a portion of it rushed upward extremely rapidly a distance of several meters (Figure 4C, D) releasing eggs and sperm at the peak of the "rush." They returned to the substrate nearly as rapidly (Figure 4E). Because of the large numbers of individuals present in the spawning aggregation, several separate weaving groups could be present and rush at near the same time. Rushes by some weaving groups began at the level of at least 3 m above the substrate as they were level with the observers' line of sight.

From analysis of motion pictures of spawning behavior the number of fish engaged in a rush varied between 5 and 30 with the mean number about 15 individuals. Generally only about one-half of the group engaged in weaving actually participated in the rush and often a few individuals starting the upward rush were left behind. The entire upward rush and return to the level of the weaving group took <1 s. Of seven rushes which were filmed in their entirety the time for the upward movement varied between 0.21 and 0.40 s and for the return 0.20 and 0.40 s. One rush with return occupied only 0.45 s total. Assuming a distance of 3 m was covered during the upward rush (probably a conservative estimate), the average speed from leaving the weaving group until turning at the point where the gametes are released was around 40 km/h.

The sexual composition of the rushing groups has not been determined. Randall and Randall (1963) believed that the spawning groups of *Sparisoma rubripinne* were predominantly males and that a single female participated in the spawning rush with 3 to 12 males.

A single terminal phase male *Scarus croicensis* was present at the spawning site. This fish vigorously defended a territory near the outer edge of the coral pinnacle and patrolled the area in the "bob-swim" manner with the caudal fin upturned as described by Barlow (1975). No attempts at pair spawning with striped phase females by this fish were observed. The only other parrotfish observed on the deep coral pinnacle was *Sparisoma viride* with only a few present.

SPAWNING FREQUENCY

The frequency of rushes during the daily periods for both January and June is presented in Figure 5. The summer spawning begins earlier in the day, continues later, and has a higher frequency of rushes than during the winter. It is impossible to determine the number of eggs released per rush and whether differences exist between summer and winter. No data are available concerning the number of fish participating in rushes during winter, but observations suggest this was also lower.

Considering an equal number of eggs are expelled on each rush, it appears that the production of eggs by this population of *Scarus croicensis* is about six times greater during a summer day than winter on the basis of the area beneath the curves derived from Figure 5. It is likely that *S. croicensis*, at least in the Caribbean, spawns year round, but the warm months are the most important period of egg production.

During the summer the occurrence of spawning rushes might be referred to as epidemic. When the

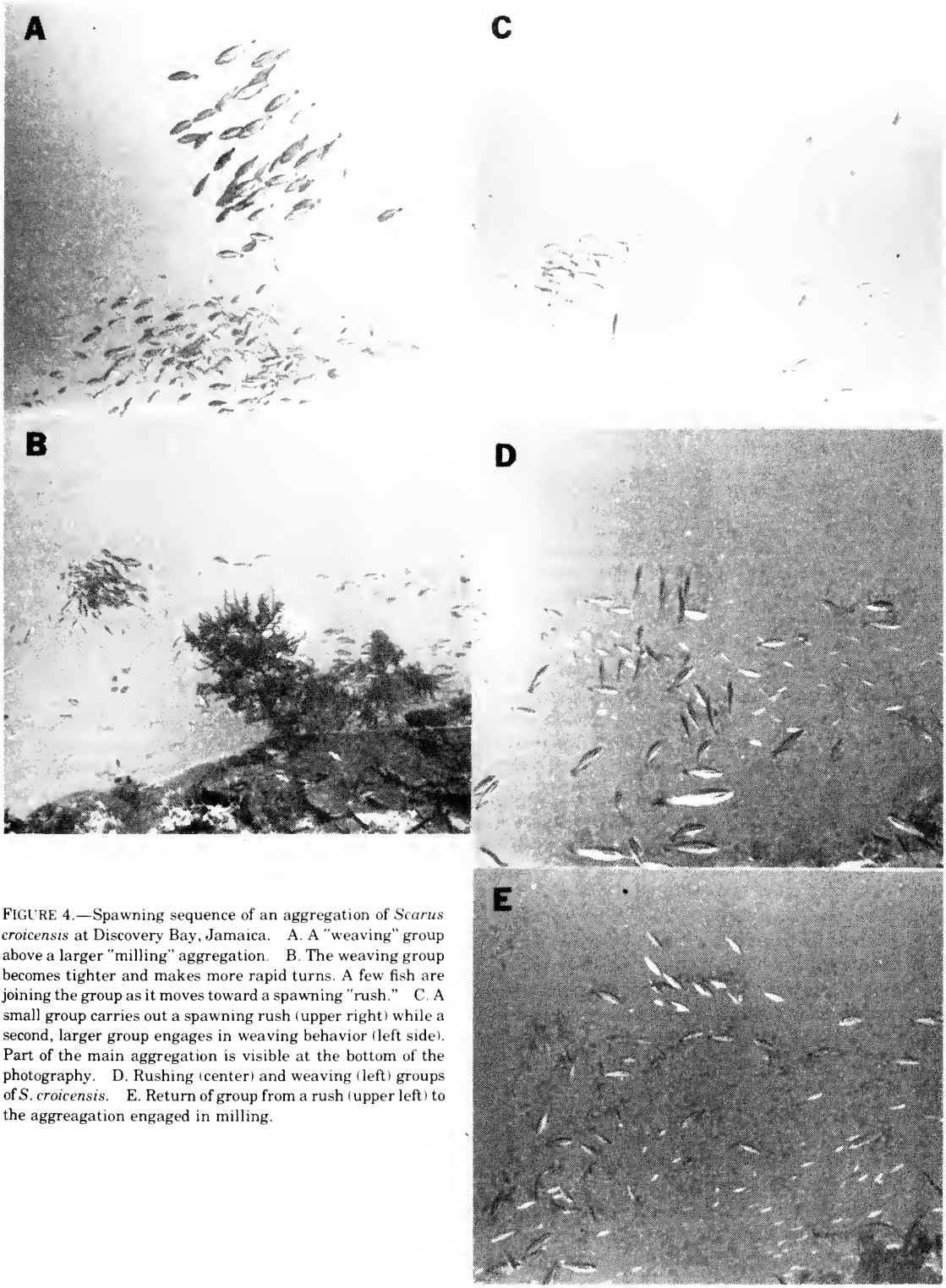

FIGURE 4.—Spawning sequence of an aggregation of *Scarus croicensis* at Discovery Bay, Jamaica. A. A "weaving" group above a larger "milling" aggregation. B. The weaving group becomes tighter and makes more rapid turns. A few fish are joining the group as it moves toward a spawning "rush." C. A small group carries out a spawning rush (upper right) while a second, larger group engages in weaving behavior (left side). Part of the main aggregation is visible at the bottom of the photography. D. Rushing (center) and weaving (left) groups of *S. croicensis*. E. Return of group from a rush (upper left) to the aggreagation engaged in milling.

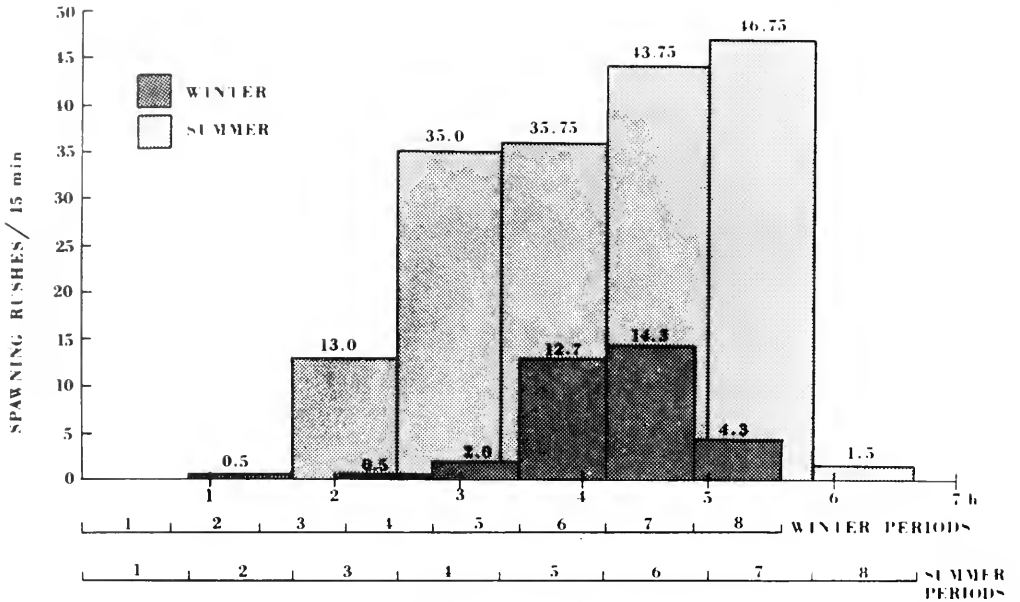

FIGURE 5.—Daily variation of spawning rushes during June (summer) and January (winter) by a population of striped parrotfish at Discovery Bay, Jamaica. The beginning of period 1 represents midpoint of the day and the end of period 8 sunset. Figures represent mean of two observations (periods 1-3) and four observations (periods 4-8).

data are analyzed on a minute by minute basis, over 90% of the spawning rushes observed occurred during only 33% of the 1-min periods. Since the group engaged in a spawning rush is considerably smaller than the total population at the spawning area, it is possible for several groups to carry out a spawning rush separately, but nearly simultaneously. The occurrence of the first rush by a group seems to trigger other groups to spawn. A flurry of rushes lasted a period of 1-4 min and in one case reached a frequency of 35 rushes in a 1-min period. This number may be underestimated due to the difficulty in observing and counting such rapid events. The period between groups of rushes was spent in milling about close to the substrate and feeding on exposed rock surface of the reef.

The time between episodes of epidemic rushing varied during the day in summer periods. During early periods when some spawning occurred (period 3 and to a lesser extent period 4) often 5-7 min would elapse without any rushes occurring. In one case there was 9 min between rushes. Later in the day, at times of peak spawning (periods 5-7), these nonspawning periods were reduced to 1, 2, and occasionally 3 min.

PREDATION

Mackerel (either cero, *Scomberomorus regalis*, or king mackerel, *S. cavalla*) twice attempted to prey on *Scarus croicensis* at the top of the spawning rush, once apparently successfully. These attacks interrupted the spawning behavior of the entire group. In one case only 1 rush occurred in the 10 min following the attack even though 67 rushes had occurred in the previous 15 min. On a third occasion, a lizardfish, *Synodus* sp., rushed upward from the substrate in an unsuccessful attempt to prey on *Scarus croicensis* and thus interrupted spawning for a short period.

Chromis cynaeus and *Clepticus parrai* were observed to feed actively on the freshly released eggs of *S. croicensis*. Within 5-10 s after completion of the spawning rush, numerous *Chromis cyaneus* converged on the area of egg release, followed shortly by a lesser number of *Clepticus parrai*, and while remaining in a tightly bunched group apparently picked individual eggs from the water. It was estimated that as many as 200 *Chromis cyaneus* and 20-30 *Clepticus parrai* composed one group picking eggs released in a single spawning rush. The group remained tightly bunched and fed

for about 1 min, moved slowly with the current (and presumably with the eggs), and dispersed quickly returning as individuals to a position closer to the substrate. Whether dispersion of the released eggs, depletion of the eggs by feeding, or some other factor caused cessation of the feeding by *Chromis cyaneus* and *Clepticus parrai* is not known. A few hundred predators, each ingesting at least one egg every few seconds for periods of nearly 1 min, could eliminate a significant portion of the eggs released in any given spawning rush.

These groups of egg predators form after only a small percentage of spawning rushes. During the "epidemic" rushes of summer periods, there are too many eggs released at several locations for these predators to significantly deplete the number released. During winter periods when rushes were few, there did not seem to be sufficient gamete release for the egg predators to wait for rushes to occur and consequently no predation on eggs was observed during these periods. The predation on newly released eggs of *S. croicensis* is obviously an intentional activity of the predators, not a chance occurrence, but probably serves only as a "bonus" for these fishes which normally spend lengthy portions of the day feeding on particulate zooplankton in the water column (Davis and Birdsong 1973).

DISCUSSION

The mass spawning behavior of *S. croicensis* is similar to that described for *Sparisoma rubripinne* by Randall and Randall (1963). The movement of the population to the deep-reef area in the early afternoon, its behavior before and during rushes, the epidemic rushes, and other behavior is nearly identical. This similarity in mass spawning between genera lines in parrotfishes is interesting.

It would be most informative to know the numbers needed before both foraging aggregations and striped phase spawning aggregations occur. Small groups of 15-20 *Scarus croicensis* have been seen moving together between bouts of feeding, but seem easily deterred by damselfishes defending territories.

At least on the north coast of Jamaica, mass spawning probably contributes most of the eggs produced by *S. croicensis*. Pair spawning was never observed in the vicinity of Discovery Bay although terminal phase males were present but never abundant. The summer season is certainly the most active reproductive period.

The occurrence of mass spawning by parrotfishes at specific locations on the reef is a relatively long-term phenomena. In the present case nearly 4 yr have elapsed since the initial encounter with the spawning group and the location of spawning has not varied. More interestingly, the spawning location of *Sparisoma rubripinne* at Reef Bay, St. John, investigated by Randall and Randall (1963), was visited in March 1977. Following the directions provided by those authors, a group of approximately 200 *S. rubripinne* were found engaged in spawning during the late afternoon. The presence of a spawning aggregation in what is believed the identical location on the reef after 17 yr in similar numbers to that previously reported indicates a stability and importance of spawning locations not previously documented. The occurrence of spawning by *S. rubripinne* on 3-4 March extends the period reported by Randall and Randall (1963) and supports their belief in year round spawning. Also the water temperature of 25.8°C was slightly lower than that previously reported.

The reasons for the abundance of *Scarus croicensis* compared with some other scarids (such as *Sparisoma rubripinne*) are difficult to determine. Randall (1967) reported three species of fishes (*Mycteroperca interstitialis, M. venenosa,* and *Caranx ruber*) which definitely preyed on *Scarus croicensis*; however, individuals of *Scarus* (not identifiable to species) were found in guts of several other predatory fishes. Ogden and Buckman (1973) added *Epinephelus striatus* and *Scomberomorus regalis* as predators of *Scarus croicensis*. Due to overfishing, few large predatory fishes are found on the outer reef at Discovery Bay. Indeed, few of the larger species of *Scarus* and *Sparisoma* occur there for the same reason. This may be an important factor allowing relatively high numbers of *Scarus croicensis* to occur there and schooling behavior to be effective in overwhelming the defenses of territorial herbivores.

Alevizon and Brooks (1975), in examining two coral-reef fish assemblages (Islas Las Aves, Venez. and Key Largo, Fla.), found *S. croicensis* to be only a minor component of one (Florida) and of no consequence at the other (Venezuela). Possibly they sampled areas where *S. croicensis* was not abundant. In other areas *S. croicensis* may be absent, even though the environment seems typical of that in which it normally occurs. At Isla Desecheo, a small (1 km^2) island 20 km west of Puerto Rico in the Mona Channel, extensive diving operations failed to reveal the presence of *S. croicensis* even

though we have specifically searched for it. Other scarids occur there, and there seems no simple reason for the nonoccurrence of *S. croicensis* at this island.

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FEEDING BEHAVIOR AND MAJOR PREY SPECIES OF THE SEA OTTER, *ENHYDRA LUTRIS*, IN MONTAGUE STRAIT, PRINCE WILLIAM SOUND, ALASKA

DONALD G. CALKINS[1]

ABSTRACT

Food habits and feeding behavior of sea otters were studied in Prince William Sound, Alaska, from May through August 1971. Otters fed primarily on clams, crabs, and sea stars: *Saxidomus gigantea*, *Telmessus cheiragonus*, and *Evasterias troschelii*, respectively, were the most important prey species identified in the major groups. Mean times for feeding dives were 67 s for females (mean water depth = 9.6 m) and 59 s for males (mean water depth = 11.9 m). Clams were dug from the bottom and opened with the aid of stones. Sea urchins and fishes were not identified as dietary components.

The sea otter, *Enhydra lutris*, hunted to near extinction by 1911 in Alaska, is steadily reoccupying its former range. Several areas are being repopulated naturally (Kenyon 1969), while others have been restocked with otters translocated from Amchitka Island in the Aleutians or from south central Alaska (Burris and McKnight 1973). In some areas of the Aleutian Islands, sea otters have become so abundant that an experimental harvest has been conducted by the Alaska Department of Fish and Game. Populations in Prince William Sound have become large enough to permit capture of a small number of animals for restocking areas of former abundance.

Large gaps still exist in our knowledge of the biology and life history of the sea otter. Past studies have dealt primarily with populations along the California coast and off Amchitka Island. No intensive study of sea otters in Prince William Sound has been completed, and the only available information from that area concerns restocking activities and population counts (Pitcher and Vania[2]). The lack of information on the biology of the sea otter in Prince William Sound and the impending development of oil reserves along the Alaska coast motivated this study.

STUDY AREA

This investigation took place in Montague Strait, Prince William Sound, Alaska (Figure 1). One week was spent in the field in September 1970. In May 1971, a camp was established at the northwestern end of Montague Island (lat. 60°15′54″N, long. 147°12′18″W). Observations were made from May through August 1971. The study area included the northwestern end of Montague Island, from Stockdale Harbor to a logging camp 19 km southwest. Green Island, Little Green Island, and the adjacent waters were also included (see Figure 1).

The area was selected as a location where sea otter populations have always existed. Although the population is still expanding, there has always been some sea otters in this area (Karl Schneider, Alaska Department of Fish and Game, pers. commun.).

The area is characterized by a rugged coastline with rocky shores. Two sand beaches occur in the area, one south of Port Chalmers and one on the south side of Green Island. Several streams empty into the Sound from Montague Island: mud flats and small estuaries are common. The mud flats support stands of eel grass, *Zostera* sp., and provide habitats for populations of clams—*Macoma* spp., *Saxidomus gigantea*, and *Protothaca staminea*.

Approximately 55 km of coastline was included in the study area. Kenyon (1969:57) stated that "generally sea otters favor waters adjacent to rocky coasts near points of land" and that "coasts adjacent to extensive areas of underwater reefs are particularly attractive." Using these criteria,

[1]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[2]Pitcher, K. W., and J. S. Vania. 1973. Distribution and abundance of sea otters, sea lions and harbor seals in Prince William Sound. Unpubl. manuscr., 18 p. Available Alaska Department of Fish and Game, Anchorage, Alaska.

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FIGURE 1.—Montague Strait sea otter study area located in Prince William Sound, Alaska.

at least 50 km of the coast within the study area seemed suitable for sea otters. The animals did not frequent the areas with sandy beaches or shallow estuaries.

Feeding habits were studied at three main locations at Montague Island: a small lagoon (Ookshilk Lagoon, see de Laguna 1956) on the south side of Stockdale Harbor, the area outside Ookshilk Lagoon to the north and west, and Port Chalmers south of Stockdale Harbor. Ookshilk Lagoon had water depths from 5 to 7 m and rock and mud beaches grading to subtidal sand which supported stands of eel grass, *Zostera* sp., and rockweed, *Fucus* sp. The area outside Ookshilk Lagoon was characterized by water depths of 5 to 16 m, rock beaches and sand with reef shoals subtidally, and *Fucus* sp. beach and subtidal flora. Port Chalmers had water depths of 14 to 26 m with rock beaches and subtidal sand with reefs and shoals. Beach and subtidal flora in the Port Chalmers area consisted of *Fucus* sp. and kelp, *Nereocystis lutkeana*.

METHODS

All observations on feeding habits were made from advantageous locations on land. Spotting telescopes with magnification of 15 to 60× were used to identify food organisms. Observation distances ranged from 20 to 500 m. The dimensions of the organisms were estimated relative to the otters paws, which were estimated to average 4 cm wide. Dimensions of octopuses were estimated across the tips of the tentacles, relative to the otter's body, and all sizes are reported in this manner. No identification of organisms was attempted beyond 100 m, but it was often possible to classify food items by categories such as clam, crab, sea star, etc., up to 500 m away. Dive and surface feeding times for a total of 14 feeding periods were measured with stopwatches. Timing of feeding periods began when other activities ceased and the otter dived for food and ended when the last bit of food was eaten and some other activity began.

Prey species were collected at low tide, and taken to the University of Alaska for identification. Clams were collected on a gravel beach in Ookshilk Lagoon where otters fed. Work was confined to 1 h before until 1 h after low tide (−0.86 m). Ten transects were dug 25 m apart with each transect running from the extreme high-tide mark to the water's edge. Sample holes of approximately 0.25 m^3 were dug at 5-m intervals along each transect. Sample holes were dug to a depth of 25 cm.

In areas where extensive observations were made, water depths were measured using a weighted line graduated at 25-cm intervals.

RESULTS

Types of Organisms Eaten

All food organisms were bottom-dwelling invertebrates from three major groups of organisms: molluscs, crustaceans, and echinoderms. The percentage occurrence of prey organisms in the diet is shown in Table 1. Five species of clams are found in this area (Table 1), and all were eaten. Empty shells and observations of feeding otters suggest that *Saxidomus gigantea* is the clam most commonly eaten by otters.

Several species were present in the area but never observed to be eaten by otters (Table 1). Each had been previously identified as food of sea otters (Barabash-Nikiforov 1947; Kenyon 1969).

TABLE 1.—Bottom-dwelling invertebrates of Montague Strait, Alaska, and the percent of occurrence in the diet of sea otters.

Food organism	No.of times consumed	Percent of occurrence in diet
Arthropoda:		
Crustacea:		
Telemessus cheiragonus	43	7
Mollusca		
Gastropoda:		
Nucella(=Thais) lamellosa	0	0
Pelecypoda		
Saxidomus gigantea[1]		
Protothaca staminea[1]		
Mya truncata[1]	481	81
Macoma inquinata[1]		
Macoma incongrua[1]		
Mytilus edulis, mussel[2]	2	0.3
Pododesmus macroschisma	0	0
Clinocardium nuttalli	0	0
Cephalopoda		
Octopus sp.	4	0.6
Echinodermata:		
Asteroidea:		
Evasterias troschelii	5	0.8
Echinoidea:		
Strongylocentrotus drobachiensis	0	0
Holothuroidea	2	0.3
Unidentified	60	10
Total	597	100

[1]Each of these pelecypods was identified as a dietary item one or more times, but the relative frequency of use was not determined

[2]Observations were made on two different occasions of otters feeding on mussels. The small mussels averaged around 2 to 3 cm each. This plus the fact that the observation distance was up to 100 m made it impossible to get an exact count.

Shells of the snail *Nucella (=Thais) lamellosa*; cockle, *Clinocardium nuttallii*; and the rock oyster or jingle, *Pododesmus macroschisma*, were abundant in the study area. Tests of sea urchins were rare.

Octopuses consumed by otters ranged from 30 cm to 1 m across the tips of the tentacles. Crabs (*Telmessus cheiragonus*) eaten ranged from 5 to 15 cm across the carapace. The clams consumed (*Mya truncata, Macoma inquinata,* and *M. incongrua*) were approximately 2 to 3 cm long, with *Protothaca staminea* and *S. gigantea* ranging from 2 to 10 cm long. Mussels (*Mytilus edulis*) were 2 to 3 cm long. Sea cucumbers measured 15 cm long and sea stars (*Evasterias troschelii*) 20 to 30 cm across the rays.

From the 30 stations occupied along the intertidal transects, a total of four clams (two *Macoma* spp., one *S. gigantea,* and one *P. staminea*) and 56 mussels were collected.

Feeding Behavior

Otters usually rose vertically so that the shoulders were above the water surface before diving (also see Limbaugh 1961). In water depths <4 or 5 m otters usually sank to shoulder level before rolling forward into a dive. In deeper water they ordinarily dove from the highest position of emergence, presumably to provide greater downward thrust. During the beginning of a dive, the forelimbs were kept close to the body. One otter often dove backward from a supine floating position by kicking its hind flippers and arching its back. The duration of feeding dives (average 66 s; Table 2) was approximately the same as that observed for sea otters in California (60-90 s; Limbaugh 1961).

Otters in Montague Strait ate crabs as described by Fisher (1939) for California otters and by Kenyon (1969) for Aleutian otters. Otters removed the legs with one paw while clasping the crab to the chest with the other paw. Kenyon (1969:116) reports that "in the Aleutians the carapace was not among the stomach contents," whereas Fisher (1939:28) noted for California otters "when the legs are finished, the body is eaten." While holding otters in captivity prior to translocation from the Montague Strait area during 1965 and 1966, the animals were fed commercially available crabs (*Cancer magister*) (Ed Klinkhart, Alaska Department of Fish and Game, pers. commun.). The otters consistently ate the chelipeds first and then the walking legs. Next the carapace was removed and the body eaten. Finally the carapace was generally licked prior to discarding. Unconfined sea otters occasionally bit the carapace but usually discarded it after finishing the legs. Two crabs were often taken during one dive.

Otters dug out clams with their forepaws while maintaining a head downward position (see Limbaugh 1961 for similar shallow-water feeding behavior of California otters). Holes or craters from 15 to 45 cm across and up to 50 cm deep, made by

TABLE 2.—Results of 673 timed feeding dives of sea otters in Montague Strait, Alaska, listed by depth.

	Sex	No. of dives observed	Mean diving time (s)	Approx. water depth (m)
1	F	20	3	4
2	M	80	47	4.8
	F	60	49	
3	M	3	108	10.6
	F	14	83	
4	M	14	83	13.3
	F	406	73	
5	M	6	118	13.3
6	F	26	83	16.3
7	M	44	69	17.6
Total F		526	67	[1]9.6
Total M		147	59	[1]11.9
Total both sexes		673	66	[1]11.9

[1]Average depths for combined observations.

the otters in this process, were abundant in intertidal and subtidal areas with gravel or sand bottoms.

A male otter was observed feeding on clams about 3 to 5 cm long; 38 clams were consumed in 35 min (1.08/min). A female and a large pup, observed at the same location, fed on clams of the same size range as those eaten by the male. Only the female successfully brought up clams although the pup dove with her. Together, they consumed 56 clams in 65 min (0.86/min). Both adults brought up as many as three clams per dive.

Generally, clams 3 to 5 cm long were eaten intact including the shell. The otter pushed each clam into its mouth, crushed the shell, and swallowed the entire clam immediately. Larger clams (5 to 10 cm long) were cracked with the cheek teeth, usually breaking one valve in half (see Miller et al. 1975). This has also been observed in Monterey Bay (H. Feder pers. commun.). Valves were then forced open by a rotating motion or were pulled apart with the paws, and the soft parts scooped or bitten out with the incisor teeth.

Large males were occassionally able to crack clams >10 cm with their cheek teeth and pull the valves apart with their paws. However, they typically opened larger clams by pounding them against each other or against a rock until the shell was fractured and the valves forced open. The size of the rocks ranged from 7 to 15 cm long but there was no preference for shape.

Otters often used stones as tools for opening hard shelled invertebrates such as clams (Fisher 1939; Limbaugh 1961; Hall and Schaller 1964). With the stone lying on the otter's chest, the clam was struck against it with several quick, hard blows until the shell or the hinge was broken. Otters were typically nonselective when striking the clam against a rock; however, one otter consistently struck the hinge area which usually separated after three or four blows. A rock was not used more than once. Each rock was always discarded immediately by allowing it to slip off the chest.

Otters obtained mussels by pulling up holdfasts of *Laminaria* sp. to which the bivalves were attached. The animal then floated with the algal frond across the body and picked individual mussels off with its forepaws and ate them whole. Otters never consumed algal material.

Octopuses were eaten completely. One female consumed an octopus (60 cm across the tips of the tentacles) in slightly more than 6 min. The otter held the body of the octopus in its paws and bit into an arm or the body while pulling away with its head and pushing away with its paws. This left a piece of octopus in the mouth, which was pushed in while the remainder was held in the otter's axilla or against the chest. This procedure was repeated until the entire octopus was eaten. Pieces dropped during the feeding process were retrieved.

Sea stars were not a preferred food. According to Kenyon (1969:119), "the otter usually tears off and eats one or two arms of a sea star . . . and discards the remainder." Otters in Montague Strait fed in a similar manner. Kenyon (1969) reported several species of sea stars are eaten by otters in the Aleutians. Only one sea-star species (*Evasterias troschelii*) was taken by otters in the present study, although others were available (*Dermasterias imbricata* and *Pycnopodia helianthoides*).

Sea cucumbers were rarely eaten and were also apparently of minor importance to Aleutian otters (Kenyon 1969). Sea cucumbers were torn open, a portion of the viscera and part of the body wall eaten, and the remainder discarded.

Feeding periods ranged from 25 to 147 min, averaging 84.5 min. Elapsed times for eating at the surface during the 14 feeding periods ranged from 17 s for a clam to 6 min for an octopus, with a mean value of 38 s for all foods (see Table 2 for diving times and Table 3 for average consumption times of each food item).

TABLE 3.—Range and mean of feeding times for individual food items measured in seconds for sea otters in Montague Strait, Alaska.

Food item	No. of observations	Surface feeding time	
		Range	Mean
Clam	81	17-64	38.6
Crab	2	30-39	34.5
Sea star	4	25-41	30
Octopus	1	—	380
Unidentified	5	17-53	34
No food brought up	52	10-54	24.5

DISCUSSION

The sea otter is an opportunistic feeder throughout its range. It generally feeds on bottom-dwelling invertebrates, but may select fishes if the invertebrate supply is depleted (Kenyon 1969 in Table 4). Mollusks were the most important food of otters in California and Montague Strait, echinoderms are apparently most important in the Commander Islands, and fishes most important in the Aleutians (Table 5). Crustaceans were second in importance at Pico Creek, Calif.,

TABLE 4.—Qualitative comparison of food of sea otters in Montague Strait, Alaska.

Location and reference	Method of analysis	Major food items consumed			
		Molluscs	Crustaceans	Echinoderms	Fishes
Amchitka Island, Aleutian Islands, Alaska (Kenyon 1969)	Stomach and fecal analyses and direct observation	Chiton *Cryptochiton stelleri* Snails *Buccinum* sp. *Argobuccinium oregonensis* Mussels *Musculus vernicosa* *Volsella volsella* Octopus *Octopus* sp. Rock oyster *Pododesmus macroschisma*	Crabs *Cancer* sp. *Placetron wosnessenski*	Green sea urchin, *Strongylocentrotus drobachiensis*,	Globe fish, *Cyclopterichthys glaber*, Red Irish lord, *Hemilepidotus hemilepidotus*,
Pico Creek, Calif. (Ebert 1968)	Direct observation	Red abalone, *Haliotis rufescens*, Gaper clam, *Tresus nuttalli*,	Rock crab, *Cancer antennarius*,		
Monterey Bay, Calif (Limbaugh 1961)	Direct observation	Red abalone, *Haliotis rufescens*, Purple hinged scallop, *Hinites gigantea*, California mussel, *Mytilus californianus*,		Sea urchin *Strongylocentrotus franciscanus*	
Point Lobos, Calif. (Hall and Schaller 1964)	Direct observation	Mussel *Mytilus californianus* Red abalone, *Haliotis rufescens*,	Crab *Cancer* sp.	Purple urchin, *Strongylocentrotus purpuratus*,	
Commander Islands, USSR (Barabash-Nikikforov 1947)	Direct observation and fecal analysis	Clam *Mya truncata* Mussel *Mytilus edulis*	Crab *Telmessus cheiragonus*	Sea urchin *Strongylocentrotus drobachiensis*	Hexigrammidae
Montague Strait, Alaska (this study)	Direct observation	Clams *Saxidomus gigantea* *Protothaca staminea* Mussel *Mytilus edulis*	Crab *Telmessus cheiragonus*	Sea star *Evasterias troschelii*	

and Montague Strait with molluscs second in the Aleutians and echinoderms second at Point Lobos, Calif.

Sea urchins seem to be a relatively minor part of the diet in Montague Strait. No living sea urchins were found in the intertidal zone and only an occasional test was found. Kenyon (1969:111) indicated that "the bones of those sea otters utilizing sea urchins . . . are stained purple by the biochrome polyhydroxynaphthoquinone (Scott *in* Fox 1953)." Of the six different sets of skeletal remains found on the beaches of Montague Strait during this study, none showed this diagnostic purple stain. Schneider (Alaska Department of Fish and Game, pers. commun.) reports that of the several skulls he obtained from Prince William Sound, none show purple pigmentation.

Fishes are an important food source in the Aleutians when invertebrates become depleted. Kenyon (1969:110) reported that "At Amchitka it appears that the otters fall into two groups—those eating mostly fish and those eating mostly invertebrates." Otters were not observed eating fishes in Montague Strait and fishes are probably not important here. During the latter part of this study pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, became abundant. Vania[3] found that otters captured in Montague Strait and held for translocation refused to eat chum and pink salmon for a period of 24 h.

[3]Vania, J. 1967. Sea otter. *In* Marine mammal investigations. Alaska Dep. Fish Game, Vol. 7 Annual Project Segment Rep., Fed. Aid Wildl. Restoration, Proj. W-14-R-1 and -2, work plan G, p. 6-13.

TABLE 5.—Frequency of occurrence of major food items in the diet of sea otters in Montague Strait, Alaska, compared with other locations. Organisms from the Commander Islands study are shown according to relative abundance as indicated by plus signs, increasing plus signs indicate increasing abundance.

Location and reference	Amchitka Island, Aleutian Islands, Alaska (Kenyon 1969)	Pico Creek, Calif. (Ebert 1968)	Point Lobos, Calif. (Hall and Schaller 1964)	Commander Islands, USSR (Barabash-Nikiforov 1947)	Montague Strait, Alaska (this study)
Method of analysis	Stomach and fecal analyses and direct observation	Direct observation	Direct observation	Direct observation and fecal analysis	Direct observation
Food item	Percent	Percent	Percent	Abundance	Percent
Mollusks					
Clams		2.5		++	81
Mussels		0.8	40	++	0.3
Snails					
Chiton		0.4	0.8		
Octopods			0.4		0.6
Abalone		63.4	9.9		
Rock scallop		2.1			
Total	37	69.2	51.1		81.9
Crustaceans					
Crabs	Present	25.9	14.5	++	7
Spiny lobster			0.6		
Total		25.9	15.1		7
Echinoderms					
Sea urchins	Present		32.8	+++	
Sea stars	Present		0.6		0.9
Sea cucumbers	Present				0.3
Total			33.4		1.2
Fishes	50		0.4	++	
Others	13	4.9			9.9
Grand total	100	100	100		100

Prior to this study, little use of rocks as tools for opening clams had been observed in Alaska. Kenyon (1969) did not observe this phenomenon in the wild, but saw a captive Alaskan otter pound a clam against the side of its cement pool. Schneider (pers. commun.) observed otters using rocks near Amchitka, but considers this behavior uncommon. Kenyon (1969) compared rock-pounding behavior in the sea otter to the use of gravity by gulls (*Larus* sp.) and ravens (*Corvus corax*). He also suggested that tool-using behavior is derived from "chest pounding, frustration behavior" (Kenyon 1969). Otters will often pound clams on their chest when the clams are particularly difficult to open (also see Hall and Schaller 1964).

Limbaugh (1961) noted that otters used the same rocks on successive dives in California. This was not observed in Montague Strait.

Although Kenyon (1969:123) felt that "clams which are buried are not dug from the bottom" and that only those exposed to view or with exposed parts are taken by the otters, otters in Montague Strait frequently and successfully dug clams. *Saxidomus gigantea* and *Protothaca staminea* are found at depths of 8 to 45 cm along the North Pacific coast (Fitch 1953; Quale and Bourne 1972; Paul and Feder[4]). Miller et al. (1975) presented evidence which suggests California otters have dug pismo clams, although no direct observations have been made.

When otters dig in soft sediments characteristic of clam habitats, they undoubtedly locate clams by touch due to obscured vision and, in fact, Kenyon (1969) has shown that otters can locate food by tactile sense alone. One blind captive otter located food successfully and another normal individual used only forepaws in the selection of a preferred food (*Mytilus edulis*) from a bucket of turbid water that also contained small crabs (*Pachygrapsus*), and pebbles of various sizes.

It is apparent that sea otters are able to subsist on a wide variety of bottom-dwelling invertebrates and some fishes. Although they seem to have local preferences, they tend to exploit whatever is available. As otter populations increase they can effect drastic changes in bottom communities.

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[4]Paul, A. J., and H. M. Feder. 1976. Clam, mussel and oyster resources of Alaska. Univ. Alaska I.M.S. Rep. 76-4. Sea Grant Rep. 76-6, 41 p.

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TROPHIC RELATIONSHIPS AMONG FISHES AND PLANKTON IN THE LAGOON AT ENEWETAK ATOLL, MARSHALL ISLANDS

EDMUND S. HOBSON AND JAMES R. CHESS[1]

ABSTRACT

Trophic relationships among fishes and zooplankters in the nearshore lagoon at Enewetak differ sharply between day and night, and are strongly influenced by current patterns. Adults of most diurnal planktivorous fishes are numerous in certain places where tidal currents are strong, but few where such currents are consistently weak. Thus, the sea bass, *Mirolabrichthys pascalus;* the snapper *Pterocaesio tile;* and the damselfishes (*Chromis agilis, C. caerulea, C. lepidolepis, C. margaritifer,* and *Pomacentrus coelestus*) are numerous in strong-current areas near interisland passes, but relatively few or absent in weak-current areas close in the lee of islands or interisland reefs. The former areas are rich, the latter poor, in the major prey of these fishes—copepods, larvaceans, and fish eggs. On the other hand, the zooplankton-poor waters close in the lee of islands and interisland reefs are rich in debris from the reefs, and fishes that can subsist on these materials are abundant. *Dascyllus reticulatus* is numerous here, although less so than where currents are strong, and takes algal fragments as an important, if secondary, part of its diet; *Pomacentrus vaiuli,* equally abundant in both strong- and weak-current areas, feeds largely on algal fragments, as does *P. pavo,* which is more numerous here than where currents are strong.

In contrast, the major nocturnal planktivores are concentrated where currents are weak, but relatively sparse where these currents are strong. Included are: the soldier fishes *Myripristis pralinus* and *M. violaceus,* and the cardinalfishes *Apogon gracilis* (young also feed by day), *A. novaeguinae,* and *A. savayensis.* They are strictly carnivores that prey mostly on larger zooplankters—including large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—absent (except for the mysids) in the nearshore water column by day. These prey organisms generally find conditions unfavorable where strong currents flow. Most of them are sheltered on or near specific nearshore substrata during the day and enter the water column only at night; but others are in deeper water offshore by day and move inshore at night after rising toward the surface.

Limited evidence indicates that planktivorous juvenile and larval fishes, as well as the tiny plankters on which they feed, follow patterns different from those followed by larger individuals.

Many nearshore fishes find most of their food among the plankton. Clearly, the water column is a rich feeding ground. Nevertheless, fishes that would take plankters face problems perhaps not immediately apparent. Consider, for example, the feeding-related morphologies of planktivorous fishes, which obviously are products of strong selection pressures. Fishes that take plankters by day are characterized by modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively consume tiny organisms in midwater, whereas fishes that take plankters at night tend to be large-mouthed species with specialized means to detect, and capture, the larger organisms that are in the nearshore water column only after dark. Awareness of these facts evolved from studies in tropical seas (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966; Davis and Birdsong 1973) and was emphasized in more detailed study in warm temperate waters of southern California (Hobson and Chess 1976). Additional study has shown that many fishes which take plankters by day accentuate fusiform bodies and deeply incised caudal fins—features that promote rapid swimming, and which, significantly, are undeveloped among their nocturnal counterparts. Increased speed, it was suggested (Hobson 1974, 1975; Hobson and Chess 1976), has given diurnal planktivores that swim in the water column quicker access to shelter in response to severe pressures from piscivorous predators; that these speed-inducing features are comparatively undeveloped among the nocturnal species, the suggestion continued, reflects a sharply reduced threat from piscivorous predators in the water column after dark.

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The present paper considers these aspects of the interactions among the plankton and adult planktivorous fishes as expressed in the lagoon of a coral atoll. It is based on a study over 21 days at Enewetak, Marshall Islands, during April 1976.

STUDY AREA

Enewetak Atoll (lat. 11°26′N, long. 162°22′E) is a ring of shallow coral reefs and low islands encircling a lagoon about 37 km north to south and 56 km east to west. It sits amid the westward flowing North Equatorial Current and was buffeted throughout our visit (as during most of the year) by trade winds from the east. So with surface waters generally moving to the west, it was not surprising that tidal currents in passes between the open ocean and the lagoon on the windward side of the atoll were strong on the flood, but weak on the ebb. Furthermore, water over the windward interisland reefs, driven by the incessant trade winds and seas breaking over the outer reef, flowed in just one direction—into the lagoon. Presumably the situation was reversed on the leeward side of the atoll, as described for Bikini and Rongelap, two other Marshallese atolls (von Arx 1948).

From most islands, and interisland reefs, a narrow shelf of sand and isolated patch reefs extend several hundred meters into the lagoon. At the outer edge of this shelf, where the water in most places is about 20 m deep, the sea floor drops sharply to about 50 m, which is the approximate water depth over much of the lagoon. Our study centered on the lagoon's nearshore shelf along the eastern (windward) side of the atoll, where the waters are sheltered from the trade winds and prevailing seas. Initially, we made observations from Aoman Island in the north, to Enewetak Island in the south—a distance of about 32 km. Underwater visibility ranged from about 5 to over 30 m, and so at all times was suitable for observing activity. From these observations we gained a general impression of how the planktivorous fishes were distributed, as well as something of their activities.

It was soon apparent that the distribution of the planktivorous fishes was strongly influenced by nearshore current patterns. This knowledge permitted us to select fruitful locations for more intensive work, including sampling the plankton and gut contents of planktivorous fishes. Because time was short, we limited intensive study to two sites that represented opposing extremes in prevailing current velocities, weak and strong—a variance that proved to identify certain major influences on fish-plankton interactions.

Currents were weak or nonexistent at our site in 7 m of water among coral heads on level sand about 100 m from Walt Island, close in the lee of the interisland reef (Figure 1, site A). These weak currents were most evident when water covered the reef, and always flowed from the reef. We made observations here at all hours of day and night during both spring and neap tides, and our collections sampled the full range of currents encountered, from no perceptible water movement to a velocity of 9 cm/s.

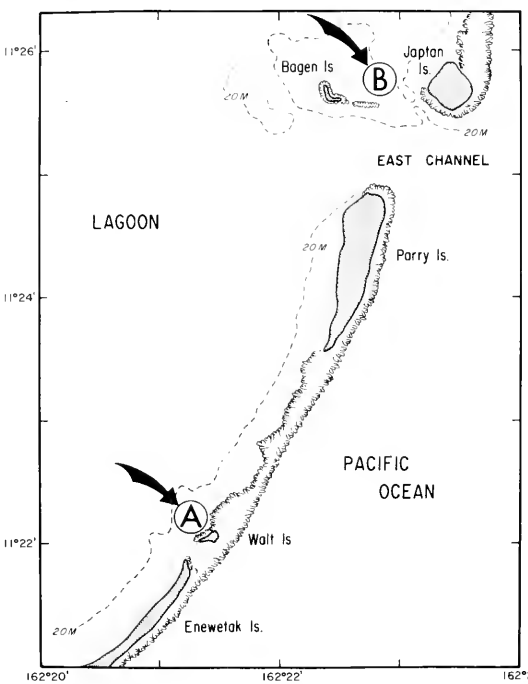

FIGURE 1.—The study area, Enewetak Atoll, Marshall Islands.

Strong tidal currents fed by water entering the lagoon through East Channel periodically swept through our site in 13 m of water among coral heads on gently sloping sand about 600 m windward of Bogen Island (Figure 1, site B). During our sampling here, currents ranged from 15 to 90, $\bar{x}$ = 51, cm/s, always on flood tide. Observations (but no sampling) were also made at this station at slack water and during ebb tide when there was little perceptible current. Although there was scant evidence of an ebb current at the collection

site, a slow outflow from the lagoon was evident in East Channel itself. Even though strong currents at this site were limited essentially to flooding spring tides, their impact was clearly visible on the substrate at all times. Most notable, the sand, which swirled about in the stronger currents, was piled high in the lee of the patch reefs.

METHODS

Plankton

The methods used to collect plankton differed between the two primary sites owing to the contrast in prevailing current velocities. Nevertheless, all collections employed the same 0.333-mm mesh net and produced comparable assessments of the plankton at the two places, particularly between day and night.

Collecting Where Currents Were Weak

When sampling at the Walt Island site, we pushed the net through the water around one patch reef (Figure 2), a circuit that always took 5 min. The procedure was similar to that used at Santa Catalina Island, Calif. (Hobson and Chess 1976). When swimming with the net by day, we could watch organisms in its path, and this gave us insight into which of them might be evading the net. Mysids, for example, could do so, and often did. But these organisms reacted to us less than expected, perhaps because the meter net's opening was large, and its approach was slow and quiet. Certainly our collections would have sampled these large mobile forms less effectively if the net had been preceded by the harness and tow line used when operating from a boat.

Three series of collections were made during midday (between 1000 and 1400 h), and three series were made at night (1 h after last evening light, at midnight, and 1 h before first morning light). We spaced the noctunal collections over the night because earlier work had suggested that certain organisms are in the water column only briefly during specific periods of the night, a phenomenon we did not find among the diurnal plankters (Hobson and Chess 1976). Of the three collections in each series, one was made within 1 m of the bottom, one midway between bottom and surface, and one with the net breaking the surface. At night, ambient light in this clear water over white sand permitted us to collect without diving lights. Our stay at Enewetak spanned the period from full to new moon, so that we sampled both spring and neap tides, but generally there was no moonlight during the collections owing to cloud cover or time of night.

Net speed was 28 cm/s, as calculated from readings of a current meter calibrated by the speed at which the smallest fragments of algae visible to us drifted along a measured course. We decided it was necessary to determine net speed only once at this station, because all collections were made by the same two swimmers who each time exerted about the same effort, and covered the same distance.

FIGURE 2.—Collecting plankton at Walt Island, Enewetak Atoll, site of weak currents. The square frame permitted more accurate assessments at the surface and close to the sea floor.

Collecting Where Currents Were Strong

All collections at Bogen Island were made at the height of flood tide, when currents often were too strong to swim with the net, so here we worked from a boat anchored fore and aft above the study site. The net was secured to a line that passed from the boat, through a block anchored on the reef below, and returned to the boat. It was positioned at the three collecting depths—bottom, middepths, and surface—by pulling the line one way or the other through the block (Figure 3). The collections were extended to 15 min (compared with 5 min at the other station) to reduce error introduced by organisms taken during the few seconds it took to raise and lower the net. In presenting these data, however, we make the values equivalent to a 5-min collection. These collections depended on the current (which was measured with every collection) to carry plankton into the net, and the weakest current sampled, 15 cm/s, was judged close to the minimum necessary. Two series of collections were made during the day—at midday and in midafternoon—and two series were made at night—1 h after last evening light and at midnight.

There are problems in comparing data collected by these different methods at the two stations, but we had the advantage of sampling precisely defined positions—a critical requirement when relating the plankton to food habits of specific fishes.

The volume of water filtered by this stationary net varied with the different current velocities, which strongly influenced the numbers of plankters taken. Nevertheless, these numbers accurately reflect the relative numbers of plankters available to fishes feeding in these currents. On the other hand, differences in volumes of water sampled must be considered when comparing estimates of the plankton in the water column from one time or place to another. Therefore, plankton volumes from the strong-current site are presented two ways: volumes actually sampled and volumes adjusted for current differences. In adjusting for current, the volumes in all collections were made equivalent to those taken in a net moving at the same relative speed that we pushed the net at the Walt Island site—28 cm/s. These adjustments also permit rough comparisons with data from California (Hobson and Chess 1976), where plankton were collected in the same way and by the same swimmers.

Fishes

A total of 154 fish specimens of 16 species were speared immediately after the plankton collections. Species names are those used by Schultz et al. (1953, 1960), except where more recent taxonomic study has indicated change.

The specimens were preserved in 10% Formalin[2] immediately after collection. Later, food items in the gut were identified and their positions in the gut noted. The following data were recorded for

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

FIGURE 3.—Collecting plankton at Bogen Island, Enewetak Atoll, site of strong currents.

items of each food type: 1) number, 2) size range, 3) state of digestion (subjectively assessed on a scale of 5, from fresh to well-digested), and 4) an estimate of their representation among the gut contents as percent of the total volume.

RESULTS

Our widespread observations along the sandy shelf which rims the lagoon established that the planktivorous fishes were centered about the isolated patch reefs. At least a few planktivores foraged in the water column above virtually every reef, but more of them were above some reefs than others and there were clear patterns to their distributions. For example, during the day there tended to be more planktivores above reefs at the outer edge of the shelf than above similar reefs at comparable depths, and shallower, shoreward on the shelf. But diurnal planktivores were most numerous where strong tidal currents flowed through passes from the open sea, and least numerous where reefs or islands blocked the flow of water into the lagoon. On the other hand, the reverse was true of the nocturnal planktivores. Because the distributions and activities of these fishes proved to be closely related to current patterns, we judged that the contributing influences are best isolated by concentrating on the more extreme current situations. This was true even though in most places over the range of our observations currents were variably moderate, and prevailing conditions intermediate between the two extremes.

Where Currents Were Weak

General Observations

There is relatively little water movement near the lee shores of the islands and close behind the interisland reefs that block entry of water into the lagoon from the open sea. In some of these locations there is enough circulation to permit rich coral growth and underwater visibility that exceeds 15 m, but in other places the circulation is more limited, and living corals exist as small heads or encrustations on otherwise dead reefs, while underwater visibility often is <5 m. The lagoon floor in these regions generally is of relatively undisturbed, fine-grained sand. (A sample of sediment from the Walt Island site proved to be 75% foraminiferans, with a density of 1.32 g/ml. Grain size in over 80% of this sample was <1 mm.)

PLANKTON.—Usually we made no effort to detect the smaller plankters during our general diurnal observations, even though many of the copepods and others were visible with close inspection. Dense swarms of mysids, however, were outstanding features of the daytime scene in many places where currents were weak, especially above sand close to the patch reefs. With increasing distance from the bottom, their swarms were smaller and less numerous, though swarm-members always were closely spaced. Juveniles predominated at the lower levels, adults were more numerous above. The swarms dispersed at night, when both adults and juveniles scattered near the bottom and at middepth, but only adults were near the surface.

Although mysids were the only plankters routinely noted during the day, others were prominent after dark. Most conspicuous were large calanoid copepods—larger than any copepods present in daylight—that for a few hours after last evening light swarmed around us in dense numbers whenever we turned on our diving lights. Highly motile epitokous nereids, as well as an opheliid, *Polyophthalmus* sp., were numerous polychaetes, with other forms including hyperid and gammarid amphipods, stomatopod larvae, reptantian zoea, and brachyuran megalops. None of these forms were seen in daylight.

FISHES.—Adult diurnal planktivorous fishes were relatively few in these surroundings compared with their numbers elsewhere. Nevertheless, this seemed a favored habitat for at least one species, *Pomacentrus pavo,* which was widespread in groups of four to six individuals 2 to 5 cm above low coral-rock outcroppings in the sand, usually in the vicinity of patch reefs. *Pomacentrus vaiuli,* another abundant species, was present only as solitary individuals that rarely moved more than a few centimeters from the larger patch reefs, yet most of its food was small organisms swimming or drifting free in the water immediately adjacent to the substrate. *Dascyllus reticulatus* was numerous by day in feeding aggregations up into the midwaters, usually above large heads of branching corals, while at the same time *Amblyglyphidodon curacao,* which usually fed in groups of <10, often ranged up to the water's surface. Of the diurnal planktivores considered here that ranged into the

water column, *D. reticulatus* and *A. curacao* were the only deep-bodied forms. Other diurnal planktivores were more sparse. The more prominent of these were species of *Chromis* that usually stayed within 2 m of the reef. *Chromis caerulea*,[3] mostly juveniles, generally hovered in small aggregations above heads of the coral *Pocillopora*, but *C. agilis* and *C. margaritifer* more often were solitary or in groups of just a few. At night all of these fishes were under reef shelter, and we saw no evidence of them feeding at that time.

Despite the relative paucity of adult diurnal planktivores in this habitat, planktivorous juveniles and larvae of at least several fish species frequently were numerous and fed by day. An outstanding example was the juveniles of *Apogon gracilis*, well under 50 mm long, which hovered in large, umbrella-shaped aggregations above coral heads in open sand (Figure 4). Dense schools of larval fishes, 7 to 10 mm long, (often taken on first glance as mysid swarms) were sometimes prominent, but so close to the reefs that our net sampled only an occasional outlier.

Although adult diurnal planktivores were comparatively sparse in this habitat, their nocturnal counterparts tended to be especially numerous. During daylight, dense, inactive concentrations of *Myripristis* spp. abounded at openings of reef crevices. Prominent as these concentrations were, they represented only a small part of the tremendous numbers of their species packed into the reef interstices. We became fully aware of the immensity of these populations when, about 30 min after sunset, they abruptly streamed into the open and entered the water column. Shortly after emerging, most individuals of one species, *M. murdjan*, apparently moved elsewhere, because though they were numerous initially, relatively few were seen during the night, and their numbers did not in-

[3]At the distances that most of our observations were made, we were unable to consistently distinguish *Chromis caerulea* from the very similar *C. atripectoralis*, and so referred all observations to the former. Significantly, however, the behavior attributed to this species is consistent with that in all individuals observed.

FIGURE 4.—Juvenile cardinal fish, *Apogon gracilis*, approximately 25 to 30 mm long, feeding on plankton by day where currents are weak.

crease again until just before dawn. In contrast, large numbers of *M. pralinus* and *M. violaceus* remained concentrated in the waters above the nearshore patch reefs throughout the night.

Also prominent in daylight were *Apogon* spp., which concentrated close to reef cover. These included adults of *A. gracilis*, which schooled quietly at the bases of the same coral heads above which juveniles of the species (see above) actively fed; nevertheless, the true numbers of apogonids were fully appreciated only after nightfall, when many large species unseen during the day emerged from reef shelters. The most prominent of the larger apogonids entering the water column was *A. savayensis*, although some of the smaller species, notably *A. gracilis* and *A. novaeguinae*, were more numerous. Larger apogonids were solitary at night, but smaller ones often were loosely aggregated, including *A. gracilis*, of which the adults joined the juveniles in the water column after dark.

TABLE 1.—Composition of plankton at Walt Island, Enewetak Atoll, site of weak currents.

Materials	Day (n = 9)		Night (n = 9)	
	Mean vol (ml)	Mean % of total vol	Mean vol (ml)	Mean % of total vol
Zooplankters	3.4	38.3	10.7	79.0
Algae fragments	3.6	51.8	3.1	21.0
Crustacean molts	0.5	9.9	0.0	0.0
Totals	7.7	100.0	13.8	100.0

Samples From Walt Island

PLANKTON.—Major materials (zooplankters, algae fragements, and crustacean molts) taken in the plankton net during day and night at the Walt Island site of weak currents are listed in Table 1. Zooplankters, grouped by major taxonomic categories and with data pooled from the three sampled depths (surface, middepth, and near bottom), are listed in Table 2. Additional data for calanoid copepods are presented in Table 3 to support certain points developed in the Discussion.

TABLE 3.—Size distribution of calanoid copepods, day and night, at Walt Island, Enewetak Atoll, site of weak currents.

Size (mm)	Midday (n = 9)		Night: 1 h after last light (n = 3)		Night: Midnight and later (n = 6)	
	Percent	Mean no.	Percent	Mean no.	Percent	Mean no.
>3-5	0	0	0	0	24	[1]138.7
>2-3	0	0	0	0	31	[2]180.5
>1-2	48	[3]10.9	43	[4]40.1	31	[5]179.0
<1	52	11.8	57	53.2	14	81.3

[1]Including *Euchaeta marina*, *Pleurommama xiphias*, and *Undinula vulgaris*.
[2]Including *Candacia* sp., *E. marina*, *Neocalanus* sp., *Pleurommama xiphias*, and *U. vulgaris*.
[3]Including *Acartia* sp., *Metridia* sp., *Pleurommama* sp., and *Scolothricella* sp.
[4]Including *Acartia* sp., *Candacia* sp., *E. marina*, and *U. vulgaris*
[5]Including *Acartia* sp., *Candacia* sp., and *Euchaeta* sp.

TABLE 2.—Occurrence, number, and size of zooplankters collected day and night at Walt Island, Enewetak Atoll, site of weak currents.

Plankton categories present	Day (n = 9)			Night (n = 9)		
	Size (mm)	Percent occurrence	Mean number	Size (mm)	Percent occurrence	Mean number
Foraminiferans[1]	0.4-1.0	100	36.7	0.4-2.0	100	337.0
Siphonophores	4.0-6.0	11	0.4	4.0-8.0	38	2.6
Polychaetes	—	0	0.0	3.0-25.0	33	28.3
Mollusk larvae	0.3-1.0	78	21.0	0.5-2.0	89	55.2
Pteropods	—	0	0.0	2.0-5.0	33	2.0
Squid	—	0	0.0	3.0-12.0	22	0.3
Ostracods	0.5-1.0	67	5.4	0.6-2.0	100	26.4
Calanoid copepods	0.5-2.0	89	22.7	0.5-5.0	100	579.5
Cyclopoid copepods	0.5-1.5	56	8.0	0.5-2.0	100	39.0
Harpacticoid copepods	0.5-1.0	22	0.3	0.5-2.0	89	9.3
Stomatopod larvae	—	0	0.0	18.0-26.0	11	1.0
Mysids	2.0-8.0	89	[2]1,398.7	1.0-8.0	100	[3]3,031.8
Cumaceans	—	0	0.0	1.0-1.5	56	12.4
Isopods	—	—	0.0	1.0-12.0	67	5.3
Hyperiid amphipods	0.6-2.0	33	5.0	1.0-4.0	100	17.8
Gammarid amphipods	—	0	0.0	1.0-5.0	100	23.2
Caridean larvae	2.0-3.0	89	6.0	1.0-12.0	100	504.2
Caridean adults and juveniles	—	0	0.0	4.0-15.0	100	20.0
Reptantian zoea	0.5-2.0	78	20.0	0.5-4.0	100	629.8
Brachyuran megalops	2.0-3.0	22	0.2	2.0-8.0	100	60.3
Chaetognaths	4.0-10.0	44	1.0	3.0-12.0	100	92.4
Larvaceans	—	0	0.0	2.0	11	0.4
Apendicularian larvae	2.0	11	0.1	2.0	11	0.4
Fish eggs	1.0-2.0	100	40.0	0.5-3.0	100	273.6
Fish larvae	2.0-13.0	44	11.3	2.0-25.0	100	51.2

[1]Most of them planktonic stage of *Tretomphalus*.
[2]All appeared to be *Mysinae* sp. Mysids constituted 52.8% of the volume of daytime collections.
[3]Included *Mysinae* sp. and *Siriella* sp., the latter unseen in daylight. Mysids constituted 44.8% of the volume of nighttime collections.

GUT CONTENTS OF THE PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 4, and those from the nocturnal species, which were collected between midnight and first morning light on nights when the plankton were sampled, are listed in Table 5.

Where Currents Were Strong

General Observations

Currents were periodically strong near the passes from the open sea, and here, where patch reefs and other hard substrata typically are covered with living corals, underwater visibility consistently exceeded 20 m.[4] The lagoon floor in these areas generally is coarse, well-sorted sand (a sample of the sediment at the Bogen Island site proved to be about 60% fragments of calcareous algae, *Halimeda* spp., with a density of 1.25 g/ml; grain size in over 80% of this sample was greater than 1 mm).

PLANKTON.—Plankters were noted infrequently during casual diurnal observations where currents were strong. Nevertheless, the mysids so prominent where currents were weak occurred here only in small, inconspicuous swarms that concentrated close in the lee of patch reefs when currents were running. The larger zooplankters, frequently so prominent after dark in weak-current areas, were not noted here in any abundance, although nocturnal observations underwater in this habitat were limited.

FISHES.—During the day planktivorous fishes were especially numerous in these surroundings. Many diurnal species were concentrated here, the more prominent being: the serranid *Mirolabrichthus pascalus,* the lutjanid *Pterocaesio tile,* and the damselfishes *Chromis agilis, C. caerulea, C. lepidolepis, C. margaritifer, Pomacentrus coelestus,* and *Dascyllus reticulatus. Pomacentrus*

[4]Our concept of strong-current locations does not include those breaks in the interisland reefs where the lagoonward flow of water crossing the reef concentrated and spilled into the lagoon at sometimes exceptionally high velocities. These currents were localized and relatively shallow. Planktivorous fishes present were essentially those of nearby weak-current locations in the lee of these reefs, and although no collections were made here we would not have expected such currents to be rich in zooplankters, for reasons developed in the Discussion.

TABLE 4.—Food habits of diurnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. The value outside the parentheses is the rank of the item as food of that fish species (based on incidence and volume in diet); of the two values in parentheses, the first is the percent of fish of that species containing the item, the second is the mean percent of the total diet of that fish species represented by the item.

1. *Apogon gracilis* (juveniles) n = 10; 17-37, $\bar{x}$ = 27 mm SL
2. *Pomacentrus pavo* n = 6; 46-65, $\bar{x}$ = 57.2 mm SL
3. *P. vaiuli* n = 6; 40-51, $\bar{x}$ = 50 mm SL
4. *Dascyllus reticulata* n = 5; 50-74, $\bar{x}$ = 63.7 mm SL
5. *Amblyglyphidodon curacao* n = 5; 67-82, $\bar{x}$ = 74.2 mm SL
6. *Chromis agilis* n = 2; 50-54, $\bar{x}$ = 52 mm SL
7. *C. caerulea* n = 5; 44-73, $\bar{x}$ =58.6 mm SL
8. *C. margaritifer* n = 3; 43-50, $\bar{x}$ = 46 mm SL

Categories present	Mean no.[1]	1	2	3	4	5	6	7	8
Plankton:									
Foraminiferans	36.7	—	—	—	—	—	—	—	—
Siphonophores	0.4	—	—	—	—	—	—	—	—
Mollusk larvae	21.0	—	—	—	—	—	—	—	—
Ostracods	5.4	—	—	—	—	—	—	—	—
Calanoids and cyclopoids	[2]30.7	1(100:90)	2(100:16.2)	4(17:2.5)	1(100:62.7)	2(100:23)	1(100:75)	1(100:85.8)	2(100:41.7)
Harpacticoids	0.3	4(20:0.4)	6(17:0.3)	—	—	—	—	—	
Mysids	1,398.7	—	4(17:0.8)	—	5(33:1.0)	—	4(50:6.0)	4(20:1.4)	—
Hyperids	5.0	—	—	—	—	—	—	—	—
Caridean larvae	6.0	—	5(17:0.5)	—	4(67:2.3)	—	—	5(20:1)	—
Reptantian zoea	20.0	—	—	—	—	—	—	—	—
Brachyuran megalops	0.2	—	—	—	—	—	—	—	—
Chaetognaths	1.0	3(40:3.6)	—	—	—	—	—	—	—
Larvaceans	([3])	—	—	—	—	—	—	2(20:8)	4(33:3.3)
Apendicularian larvae	0.1	—	—	6(17:0.5)	—	—	—	—	—
Fish eggs	40.0	2(40:60)	3(67:5.0)	2(50:5.3)	3(67:7.3)	3(40:5.0)	2(100:8.5)	3(60:1.8)	3(67:8.3)
Fish larvae	11.3	—	—	—	—	—	—	—	—
Algal fragments		—	1(100:77.2)	1(100:85)	2(67.15)	1(100:65)	3(50:10.5)	—	1(100:46.7)
Crustacean fragments		—	—	—	(33:17)	—	—	—	—
Gurry		—	—	—	(33:10.0)	(60:7.0)	—	(20:2.0)	—
Benthic:									
Cephalaspidean mollusks		—	—	5(17:1.7)	—	—	—	—	—
Compound ascidians		—	—	3(33:5.0)	—	—	—	—	—

[1]Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.
[2]Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species but calanoids predominated.
[3]Larvaceans not present in plankton collections but in two fish guts.

TABLE 5.—Food habits of nocturnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. See Table 4 legend for explanation of listed values.

1. *Myripristis pralinus* n = 10; 82-124, $\bar{x}$ = 100 mm SL
2. *M. violaceus* n =11; 120-168, $\bar{x}$ =149 mm SL
3. *Apogon savayensis* n = 9; 50-71, $\bar{x}$ = 60.7 mm SL
4. *A. novaeguinae* n = 10; 20-42, $\bar{x}$ = 32.1 mm SL

Plankton categories present	Mean no.[1]	1	2	3	4
Foraminiferans	337.0	—	—	—	—
Siphonophores	2.6	—	—	—	—
Polychaetes[2]	28.3	6(20:5.3)	1(91:45.4)	5(11:5.6)	7(10:5.5)
Mollusk larvae	55.2	—	—	—	—
Pteropods	2.0	—	—	—	—
Squid	0.3	—	10(9:0.5)	—	—
Ostracods	26.4	11(10:0.2)	—	—	—
Calanoids	579.5	[3]1(100:37.0)	[3]5(36:1.4)	[3]6(11:2.2)	1(70:38.3)
Cyclopoids	39.0	—	—	—	—
Harpacticoids	9.3	—	—	—	—
Stomatopod larvae	1.0	—	4(18:4)	7(11:1.7)	—
Mysids	3,031.8	2(80:17.5)	3(56:9.7)	2(67:26.1)	5(30:4)
Cumaceans	12.4	—	—	—	—
Isopods	5.3	7(20:1.5)	—	8(11:1.1)	—
Tanaids	([4])	10(10:0.5)	—	—	9(10:1)
Hyperids	17.8	—	—	—	—
Gammarids	23.2	8(20:1)	11(9:0.2)	—	10(10:0.3)
Caridean larvae	504.2	—	—	9(11:0.6)	2(70:18.2)
Caridean adults and juveniles	20.0	5(50:7.0)	8(9:3.7)	4(44:7 8)	3(30:16.0)
Reptantian zoea	629.8	—	—	—	11(10:0.2)
Brachyuran megalops	60.3	3(50:17.3)	2(82:23.1)	1(100:28.3)	6(20:3)
Chaetognaths	92.4	9(10:1)	—	—	—
Larvaceans	0.4	—	—	—	—
Apendicularian larvae	0.4	—	—	—	—
Fish eggs	273.6	—	—	—	8(10:2)
Fish larvae	51.2	4(30:8.2)	6(18:2.7)	3(56:20.6)	4(30:11.5)
Fish adults and juveniles	0.3	—	7(9:4.7)	—	—
Insects	([4])	—	9(27:0.9)	—	—
Algal fragments		—	—	—	—
Crustacean fragments		—	(9:2.3)	(33:6.0)	—
Unidentified fragments		—	(18:1.4)	—	—

[1]Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.
[2]Most polychaetes in guts of fishes were nereid epitokes.
[3]Predominant calanoids in the three larger fish species were *Pleurommama xiphias* and *Euchaeta marina*, which were relatively large (3 to 5 mm).
[4]Tanaids and insects were not present in plankton collections but were in several fish guts. Both are known from plankton collections elsewhere (e.g., Hobson and Chess 1973, 1976).

vaiuli was numerous, but perhaps no more so than where currents were weak (see above), and here too it confined itself to the immediate proximity of the reef.

The nature of the substrate can be important. *Chromis caerulea* and *Dascyllus reticulatus*, for example, swam in tight well-defined aggregations above specific growths of branching coral—particularly large heads of *Pocillopora* spp. (Figure 5A). *Pomacentrus coelestus* generally stationed itself low in the water column above outcroppings of coral rock and rubble, its relation to the substrate much like that of the similarly hued, but deeper-bodied, *P. pavo*. *Chromis agilis*, *C. lepidolepis*, and *C. margaritifer* generally swam in small widespread groups over patch reefs. Compared with their congener *C. caerulea*, they showed less affinity to specific substrata or locations on the reef. Thus *C. caerulea* invariably responded to a human intruder by sheltering among the branches of a large coral head directly below its feeding station (Figure 5B), whereas *C. agilis*, *C. lepidolepis*, and *C. margaritifer* frequently responded to the same stimulus by moving away, and taking shelter in a variety of places only when the stimulus was intensified.

In places where many of these diurnal planktivores were concentrated, a relation was evident between their morphologies and the distances they swam from the reef: those with feeding stations farther from the reef tended more toward cylindrical bodies and deeply incised caudal fins (Figure 6). This generalization proved valid despite exceptions among such deep-bodied forms as *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao*, in which the effect of their deeper bodies is even further enhanced by longer fin spines. Thus, for example, 7 *D. reticulatus*, 47

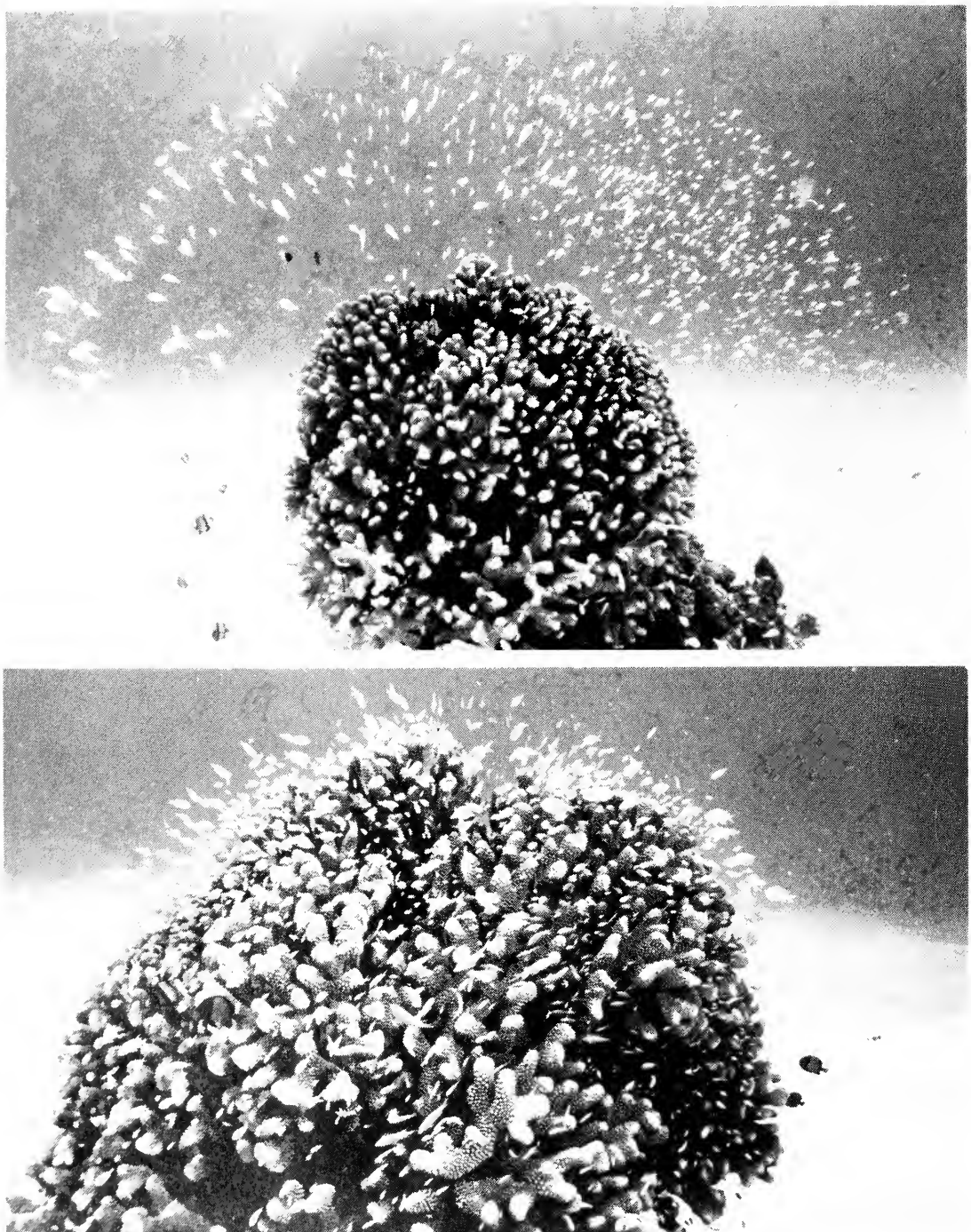

FIGURE 5.—A. *Chromis caerulea*, and a few *Dascyllus reticulatus* (lower left), feeding on plankton above a head of *Pocillopora* at the Bogen Island site. The largest fish are about 70 mm SL; the coral head is about 1.5 m in diameter. B. Upon being threatened, the fish shown in 5A dive to shelter in the interstices of the coral head.

FIGURE 6.—Planktivorous fishes where currents are strong. Major species in each of the zones identified in the photo by roman numerals are illustrated in the appropriate column below the photo (placement based on observations made at the scene). I. *Pomacentrus vaiuli;* II. a, *Chromis agilis,* b, *C. margaritifer;* III. a, *C. caerulea,* b, *C. lepidolepis;* IV. *Mirolabrichthys pascalus;* V. *Pterocaesio tile.*

to 60 mm SL, $\bar{x} = 55.9$, had longest dorsal fin spines that were 20.3 to 23.4%, $\bar{x} = 21.0\%$, of their standard length, whereas these values for 13 individuals of *Chromis* spp. (4 *C. agilis*, 4 *C. caerulea*, and 5 *C. lepidolepis*), 52 to 70 mm SL, $\bar{x} = 59.4$, were 12.3 to 16.1%, $\bar{x} = 15.3\%$. The significance of these data becomes clear when possible selective values of both fusiform and deep-bodied morphologies in planktivorous fishes are treated in the Discussion.

Although most diurnal planktivorous fishes favored conditions associated with current, the strongest currents observed at this site, approximately 1 m/s, clearly exceeded optimum velocities. When such currents flowed, most of the smaller planktivores were close to the reef, many of them concentrated in the lee, and their feeding rates had noticeably declined.

In comparison to the great numbers of adult diurnal planktivores in these surroundings, the nocturnal planktivores were sparse. Although observations underwater in this habitat at night were limited, only a relatively few individuals of

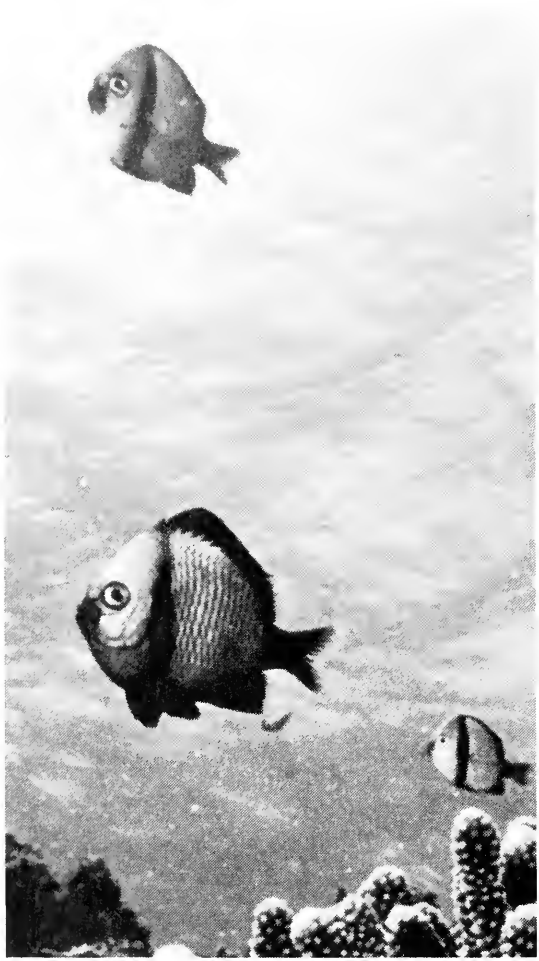

FIGURE 7.—*Dascyllus reticulatus* illustrates the tendency toward a deep body in certain diurnal planktivores that is in contrast to the tendency toward a more cylindrical body in many others.

Myripristis spp. and *Apogon* spp. were seen. Furthermore, during extensive daytime observations here we failed to note the dense concentrations of these and other nocturnal fishes in diurnal shelters that were widespread and obvious where currents were weak.

Samples From Bogen Island

PLANKTON.—The major materials taken in the net at the Bogen Island site of strong tidal currents were zooplankters and algae fragments (Table 6). To facilitate comparisons with collections from the weak-current site, all volumes are standardized to a 5-min collection. The table lists volumes of plankters actually collected, as well as volumes adjusted to the standard relative net speed of 28 cm/s (the net speed at the weak-current site).

TABLE 6.—Composition of plankton in 6 day and 6 night collections at Bogen Island, Enewetak Atoll, site of strong currents.[1]

Items	Zooplankters	Algae fragments	Totals
Day collections:			
Mean vol (ml):			
Collected	2.8	5.7	8.5
Adjusted	1.2	2.7	3.9
Mean % of total vol	32.3	67.7	100.0
Night collections:			
Mean vol (ml):			
Collected	7.3	1.9	9.2
Adjusted	3.9	1.0	4.9
Mean % of total vol	78.8	21.2	100.0

[1]Currents during diurnal collections: 32 to 90 cm/s, $\bar{x}$ = 57; currents during nocturnal collections: 15 to 83 cm/s, $\bar{x}$ = 45.

The zooplankters collected at Bogen Island, grouped by major taxonomic categories and with data pooled from the three collection depths (surface, middepths, and near bottom), are listed in Table 7. For the reasons given above concerning volumes, the table lists numbers of plankters actually collected and numbers adjusted to the standard relative net speed. Additional data on calanoid copepods (Table 8) are presented to support certain points developed in the Discussion.

Possibly zooplankters attempting to hold station above precise points on the sea floor would be sampled less effectively by the stationary net during the slower currents sampled at Bogen Island than by the moving net used at Walt Island. We discount this possibility as a significant source of error, however, because we did not see such organisms during our underwater observations of the operation, or when examining collections that sampled a wide range of current velocities.

GUT CONTENTS OF THE DIURNAL PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 9. Only a relatively few nocturnal planktivores (all of them *Myripristis* spp. and *Apogon* spp.) were seen during the limited observations in this habitat after dark, and none were sampled.

DISCUSSION

We were unable to intensively sample more than two stations in the limited time available to us at Enewetak. Nevertheless, data collected at these two sites under a variety of conditions,

TABLE 7.—Occurrence, number (actual and adjusted for current velocity), and size of zooplankters collected day and night at Bogen Island, Enewetak Atoll, site of strong currents.

	Day (n = 6)				Night (n = 6)			
Plankton categories present	Size (mm)	Percent occurrence	Mean no. (collected)	Mean no. (adjusted)	Size (mm)	Percent occurrence	Mean no. (collected)	Mean no. (adjusted)
Foraminiferans[1]	0.3-1.0	100	56.3	27.7	0.3-2	100	558.7	346.4
Siphonophores	4.0	17	0.6	0.3	4-8	50	5.7	3.5
Polychaetes	3.0	17	0.6	0.3	3-20	100	6.9	4.3
Mollusk larvae	0.5-2.0	100	11.1	5.4	0.5-2	100	31.1	19.3
Pteropods	0.5-6.0	100	6.3	3.1	2-12	83	33.7	20.9
Squid	—	0	0.0	0.0	3-4	50	1.8	1.1
Cladocerons	0.7-1.0	33	0.9	0.4	—	0	0	0
Ostracods	0.5-2.0	100	14.1	6.9	0.5-2	83	107.6	66.7
Calanoid copepods	0.5-4.0	100	1,726.7	846.4	0.5-5.0	100	7,751.1	4,820.1
Cyclopoid copepods	0.5-2.0	100	840.0	411.7	0.5-2.0	100	303.6	188.6
Harpaticoid copepods	0.5-2.0	100	23.0	11.3	0.8-2	67	6.2	3.8
Mysids	2.0	83	6.2	3.0	0.5-7	67	16.2	10.0
Stomatopod larvae	—	0	0	0	20-25	17	0.2	0.1
Cumaceans	—	0	0	0	2	17	0.1	<0.1
Tanaids	2.0	17	0.6	0.3	—	0	0	0
Isopods	—	0	0.0	0.0	1-3	100	57.3	35.5
Hyperid amphipods	0.4-2.0	50	32.2	15.8	0.5-6	100	76.0	47.1
Gammarid amphipods	1.0	17	0.6	0.3	3-4	100	38.4	23.8
Euphausid larvae	0.5-7.0	50	5.0	2.5	0.8-1	33	9.1	5.6
Caridean larvae	1.0-4.0	100	81.2	39.8	1-10	100	386.1	239.4
Caridean adults and juveniles	2.0-6.0	33	2.8	1.4	5-15	83	13.1	8.1
Reptantian zoea	0.5-2.0	100	252.8	123.9	0.5-4	100	509.7	316.0
Brachyuran megalops	1.5	17	0.6	0.3	1-6	100	115.4	71.6
Ophiuroid larvae	2.0	17	0.5	0.3	—	0	0	0
Chaetognaths	2.0-15.0	100	75.3	36.9	3-55	100	440.0	272.8
Larvaceans	1.0-3.0	100	25.3	12.4	2-4	100	87.4	54.2
Salps	—	0	0	0	(?)	17	1.1	0.7
Fish eggs	0.5-2.0	100	732.2	358.8	1-2	100	3,785.6	2,347.1
Fish larvae	2.0-6.0	50	6.6	3.2	[2]3-90	100	46.6	28.9

[1]Most of them planktonic stage of *Tretomphalus*.
[2]A 90-mm leptocephalus larva.

TABLE 8.—Size distribution of calanoid copepods, day and night, at Bogen Island, Enewetak Atoll, site of strong currents.

Size (mm)	Midday (n = 6)		Night (n = 6)	
	Percent	Mean no.[1]	Percent	Mean no.[1]
>3-4	0	0	5	[2]246.7
>2-3	3	[3]26.2	25	[4]1,203.6
>1-2	54	[5]453.7	60	[6]2,888.6
<1	43	366.5	10	481.4

[1]Numbers from collections in varying currents adjusted for equivalence to collections from the Walt Island site.
[2]Including *Euchaeta marina*.
[3]Including *Candacia* sp. and *E. marina*.
[4]Including *Candacia* sp., *E. marina*, *Neocalanus* sp., and *Undinula vulgaris*.
[5]Including *Acartia* sp. and *Euchaeta* sp.
[6]Including *Acartia* sp., *E. marina*, and *Metridia* sp.

supplemented by widespread observations elsewhere, permit a synthesis that we hope stimulates needed additional study. The following discussion pertains to adults of the planktivorous fishes and to plankters collected by our 0.333-mm mesh meter net. All food items found in the fish guts occurred in these plankton collections, so the combined assemblage can be considered a trophic unit. The situation described from these data, however, may not apply to smaller individuals. Limited data, including that from *Apogon gracilis*, the only planktivore studied as an early juvenile, suggest that the smaller plankters which passed through our net, and their predators among juvenile and larval fishes, may follow significantly different patterns (see Miscellaneous Considerations below).

Diurnal Relationships

Probably diurnal planktivores concentrated where strong tidal currents flowed into the lagoon through the passes because these waters were rich in zooplankters, particularly calanoid copepods (Table 7). We presume that at least many of these were oceanic zooplankters carried to within reach of inflowing tidal currents on the eastern side of the atoll by the westward flowing North Equatorial Current—a phenomenon amplified by the trade winds. In addition, some of the materials carried from the lagoon on the preceding ebb tide probably return. Although this outflow is minimal on the windward side of the atoll, at least during the trade-wind season (see von Arx 1948), it probably contains significant amounts of certain kinds of organisms. Gerber and Marshall (1974) noted that the waters of the Enewetak lagoon are much richer in zooplankton than the surrounding ocean. Describing the same condition at Bikini, Johnson (1949) stated: "Much of the oceanic plankton

TABLE 9.—Food habits of diurnal planktivorous fishes from Bogen Island, Enewetak Atoll, site of strong currents. See Table 4 legend for explanation of listed values.

1. *Mirolabrichthys pascalus* n = 10, 62-98, $\bar{x}$ = 79 mm SL
2. *Pterocaesio tile* n = 5; 160-195, $\bar{x}$ = 174 4 mm SL
3 *Dascyllus reticulatus* n = 10, 50-68, $\bar{x}$ = 59 6 mm SL
4 *Chromis agilis* n = 10, 54-67, $\bar{x}$ = 62 1 mm SL
5 *C carulea* n = 9, 60-77, $\bar{x}$ = 67 7 mm SL
6. *Chromis lepidolepis* n = 9, 45-67, $\bar{x}$ = 55.1 mm SL
7. *C. margaritifer* n = 10; 47-55, $\bar{x}$ = 50.7 mm SL
8. *Pomacentrus coelestus* n = 8; 37-63, $\bar{x}$ = 50 6 mm SL
9 *P. vaiuli* n = 5; 45-56, $\bar{x}$ = 52 6 mm SL

Plankton categories present	Mean no (from Table 2)[1]	1	2	3	4	5	6	7	8	9
Foraminiferans	27 7	—	—	9(10:0.1)	—	—	—	—	—	—
Siphonophores	0.3	—	—	—	—	—	—	—	—	—
Polychaetes	0.3	—	—	—	—	—	—	—	5(25:1.1)	—
Mollusk larvae	5.4	—	—	—	—	—	—	—	—	—
Pteropods	3.1	—	—	—	—	—	—	—	—	—
Cladocerans	0 4	—	—	10(10:0 1)	—	—	—	—	—	—
Ostracods	6 9	—	—	—	—	—	—	—	—	—
Calanoids and cyclopoids[2]	419 5	1(100:70.4)	1(100:80.7)	3(100:18.9)	2(100:33.6)	1(100:61.1)	1(100:43)	3(100:11.8)	1(88:33.5)	2(80:6.2)
Harpacticoids	11.3	8(10:0.8)	—	8(20:0.6)	5(20.0.2)	5(11:0 6)	5(11:0 6)	—	7(13:0.3)	—
Mysids	3.0	—	—	—	—	—	—	—	—	—
Tanaids	0.3	—	—	—	—	—	—	—	—	—
Hyperids	15.8	9(10:0.2)	—	—	—	—	—	—	—	—
Gammarids	0.3	—	—	—	—	—	—	—	—	—
Euphausid larvae	2.5	—	—	—	—	—	—	—	—	—
Caridean larvae	39 8	2(50:20.4)	2(80:6.0)	5(20:1.3)	4(30:0.7)	5(11.1.1)	4(22:2.6)	4(40:1.2)	4(50:4.3)	—
Caridean adults and juveniles	1.4	—	—	—	—	—	—	—	—	—
Reptantian zoea	123.9	3(50:2)	3(20:0.8)	7(20:0.7)	—	4(11.1.3)	—	—	—	—
Brachyuran megalops	0.3	—	—	—	—	—	—	—	—	—
Ophiuroid larvae	0.3	—	—	—	—	—	—	—	—	—
Chaetognaths	36.9	7(20:0.7)	4(20:0.4)	—	—	—	—	—	—	—
Larvaceans	12.4	6(20:1.2)	—	1(100:40.9)	1(100:49 6)	2(67 17.8)	3(67:20 4)	1(100:61 2)	—	—
Apendicularian larvae[3]	0.0	—	—	6(10:2)	—	—	—	5(10:0 5)	—	—
Fish eggs	732.2	4(30:2.5)	5(20.0.2)	4(90:7.7)	3(100 8)	3(78:12.6)	2(89:20)	2(100:24 1)	2(100:26.3)	3(80:5)
Fish larvae	6 6	5(20:1.5)	—	—	—	—	6(11:0.6)	—	6(13:0.4)	—
Fecal pellets			—	—	7(10:0 3)	—	—	—	—	—
Algal fragments			—	2(90:21 2)	6(20:0.2)	—	—	6(10:0 2)	3(75:23.9)	1(100:84.8)
Crustacean fragments		—	—	(30:0.8)	—	—	—	—	(13:0.6)	—
Unidentified fragments		—	(40:5.0)	(20:5.7)	—	—	—	—	(33:8.3)	—
Gurry		—	—	—	(50:7.4)	(33:5.5)	(44:12.8)	(20:1.0)	(13:1.3)	(20:4.0)

[1]Numbers of plankters (adjusted values from Table 7) provided only for rough measure of relative abundance.
[2]Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species, but calanoids predominated.
[3]Apendicularian larvae not present in plankton collection, but in two fish guts.

swept into the lagoon thrives there and becomes concentrated so that the average concentration per cubic meter of the eleven most common animal groups is about four times higher than outside." In addition, by the time the incoming current passed our Bogen Island station it presumably had picked up lagoon materials upstream, so its contents probably were of diverse origin.

Of course, currents in themselves enhance the planktivorous habit because planktivores holding station above a reef receive more plankters in currents than in equally rich waters without currents. Most of these fishes, however, take shelter by the time a current reaches 1 m/s, so that optimal velocities are somewhat below this. As the current increases, the advantage of receiving more plankters is progressively outweighed by the difficulty of holding station (as was pointed out for *Chromis punctipinnis* in California by Hobson and Chess 1976).

The relatively few adult diurnal planktivores that foraged where currents were weak probably owed their low numbers to the lack there during the day of calanoids and other zooplankters suitable as prey (Table 2). The many zooplankters that tidal currents carried to planktivores elsewhere were unavailable to fishes here, and those taken as prey or otherwise lost were not quickly replaced. Although the volume of zooplankters collected at the weak-current site by day (Table 1) actually exceeded the volume at the strong-current site (Table 6), it consisted largely of swarming mysids (Table 2) which are local residents seemingly unavailable as prey to diurnal planktivores (possibly for reasons discussed below under Miscellaneous Considerations). The strong-current site was in fact much richer in copepods, caridean larvae, larvaceans, and fish eggs—the major prey of the diurnal planktivores (compare Tables 2 and 7).

Locations in the lee of reefs, however, can be rich in drifting debris from these reefs (Gerber and Marshall 1974). This situation existed at the Walt Island site, where *Pomacentrus pavo* and *P. vaiuli*, the most numerous diurnal planktivores there, subsisted largely on algal fragments. Furthermore, the only other diurnal planktivores numerous in weak-current areas, *Amblyglyphidodon curacao* and *Dascyllus reticulatus*, demonstrated a capacity to utilize algae even though both species are largely carnivorous. Gerber and Marshall (1974), too, found that *D. reticulatus* fed on algal fragments when zooplankters were sparse. Obviously, the capacity to utilize algae as food is highly adaptive for planktivorous fishes that would live where drift from a reef is rich in algal fragments, though relatively poor in zooplankters (Table 1).

Despite the adaptiveness of herbivory to planktivores under these circumstances, most of the fishes studied by us were strictly, or predominantly, carnivores. Drifting algal fragments were plentiful in nearly all nearshore habitats, but where zooplankters were also numerous the algae were insignificant in the diets of most planktivores. To be sure, certain species capitalized on drifting algae even where zooplankters were numerous. For example, *P. vaiuli*, which we frequently observed plucking items from the water column, was herbivorous and numerous at the zooplankton-rich Bogen Island site, just as it was at the zooplankton-poor Walt Island site. And *P. coelestus*, which may have replaced *P. pavo* where currents were strong, fed heavily on algal fragments where zooplankters were readily accessible. Yet the pattern is clear—zooplankters were favored by most. Generally *Chromis* spp. have been reported as strictly carnivores even where other planktivorous pomacentrids fed substantially on drifting algae (e.g., in the Marshall Islands by Hiatt and Strasburg 1960; in the West Indies by Randall 1967; and in Hawaii by Hobson 1974). Nevertheless, species of *Chromis* display some capacity to accept algal fragments, as we found in *C. margaritifer* and Gerber and Marshall (1974) found in *C. caerulea*. Thus, where waters are rich in reef debris but poor in zooplankters, we should expect to find *Chromis* spp. in relatively low numbers, just as we did at Walt Island. On the other hand, *Mirolabrichthys pascalus* (a serranid) and *Pterocaesio tile* (a lutjanid) are members of strictly carnivorous families, a fact that probably limits them to places adequately supplied with zooplankters. This view finds support from Gerber and Marshall (1974), who reported that *M. pascales* (as *M. tuka*) and *P. tile* fed entirely on zooplankters. They noted the same for *A. curacao*, *C. agilis*, and *C. lepidolepis* but did not indicate where any of these fishes had been collected, nor whether anything but zooplankters had been available to them. This may be important because one of their major stations was in East Channel, where their plankton collections were without algae, and though they found *A. curacao* strictly carnivorous, we found that it fed heavily on algal fragments where zooplankters were in short supply (Table 4). Gerber and Marshall also noted that *P. vaiuli* fed mainly on algal fragments while

coocurring pomacentrids concentrated on zooplankters, but concluded from this that the species is a benthic grazer.

Nocturnal Relationships

Nocturnal planktivores probably concentrated where currents were weak because their prey—including polychaetes, large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—were most numerous there (Table 2). With the probable exception of at least most of the calanoids (see below), most of these zooplankters were local residents that rose into the water column at night after spending the daytime sheltered on or near the sea floor. This pattern has been adequately documented among these groups of organisms from both Atlantic and Pacific Oceans (Emery 1968; Williams and Bynum 1972; Alldredge and King 1977), and its importance in shaping the activities of nocturnal planktivorous fishes has been stressed (Hobson 1968, 1972, 1974; Hobson and Chess 1976). Food-habit studies have shown that these groups include the major prey of apogonids, holocentrids, and other tropical nocturnal planktivores (Atlantic Ocean: Randall 1967; Indian Ocean: Vivien 1973, 1975; and Pacific Ocean: Hobson 1974).

Only a relatively few nocturnal planktivorous fishes occurred where currents were strong, probably because prey suitable to them were relatively scarce there (Table 7). Many of the organisms on which these fishes feed most likely find conditions in places with strong currents adverse. For example, those nocturnal zooplankters that return each morning to shelter in specific habitats would likely be transported to foreign surroundings should they encounter strong currents while in the water column. The mysids, which include some of the strongest swimmers, probably cannot hold station in currents much over 15 cm/s (based on the maximum swimming speeds of several species: Steven 1961; Clutter 1969) and currents at the Bogen Island station regularly exceeded this sixfold. Organisms that need to spend only a few hours in the water column each night might time their emergence to avoid currents, as pointed out by Alldredge and King (1977), but probably even these would find it advantageous to live without this complex timing problem. Furthermore, many of these nocturnal forms rest in sediments by day (Hobson and Chess 1976; Alldredge and King 1977) and might find the coarse, unstable sand characteristic of strong-current areas unfavorable.

Only part of the increased numbers of zooplankters at night were suitable prey of the nocturnal planktivores. These were individuals more than about 2 mm long, which predominated among the nocturnal visitors at the weak-current site but which were a much smaller segment of the zooplankters that appeared after dark at the strong-current site. Among calanoids, for example, only individuals longer than 2 mm (mostly *Euchaeta marina, Pleurommama xiphias,* and *Undinula vulgaris*) were important prey of such larger nocturnal planktivores as *Myripristis* spp., and while these larger calanoids were never seen or collected by us at the weak-current site during the day, they were more numerous than the smaller ones at that station after dark (Table 3). On the other hand, most of the dramatic increase in calanoids at the strong-current site involved only slightly larger individuals of essentially the same species that were there by day, including *Acartia* sp., *Candacia* sp., and *E. marina* (Table 8), and these were largely unexploited by nocturnal planktivores. At 3 mm or less, the majority may be too small to be taken by the relatively large mouths of most of the nocturnal fishes considered here (see Hobson and Chess 1976), although they were important prey of some of the smaller species, such as *Apogon novaeguinae.*

The daytime location of the many calanoids which appear above the reefs at night remains in question. Our nearshore plankton collections in southern California (Hobson and Chess 1976) showed far less increase in calanoids after dark, and we concluded they were in the nearshore water column day and night. But the dramatic increase in calanoids nearshore after dark at Enewetak suggests a different situation. We recognize one or a combination of two possibilities: 1) that some calanoids reside under shelter on the sea floor by day, and join the plankton at night, or 2) that some calanoids reside elsewhere by day, and migrate, or are transported, to the nearshore waters only after dark. There is evidence for both possibilities. The large calanoids that swarmed around our lights shortly after last evening light (but not taken in our collections) could not have traveled far. Alldredge and King (1977) reported calanoids emerging at night from nearshore benthic substrata on the Great Barrier Reef in numbers that could readily account for the increase in calanoids we observed after dark at

Enewetak; but there may be a problem with Alldredge and King's sampling technique. Their samples were taken with Plexiglas traps that rested on the bottom and collected zooplankters that rose into the water column at night; however, there were gaps between the rigid lower edges of these traps and irregularities on the sea floor. Conceivably, as Alldredge and King themselves recognized, the samples could have included swimming organisms from the base of the surrounding water column that entered the traps through these gaps. These collections need to be repeated with this possibility for error eliminated. While it would be surprising if the numbers of calanoids they collected had actually entered the traps through these gaps, we are concerned that the only calanoid identified in their samples, *Acartia* spp. (listed as cyclopoids), are of a genus known to include species that are exceedingly numerous in the water column during both day and night (e.g., Emery 1968; Hobson and Chess 1976). 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. So although there may have been nearshore residents among the calanoids whose numbers sharply increased after dark at Enewetak, we believe that at least most of them, especially the larger ones, appeared following regular movements from deeper water.

The calanoids that visited the nearshore waters after dark seemed to be part of a nocturnal move shoreward made by many zooplankters, including chaetognaths and larval fishes. Because each of our primary collecting sites probably received nocturnal visitors from different sources, the two are discussed separately.

Walt Island

Perhaps some of the nocturnal plankters that visited the weak-current site were carried from the open sea by the turbulent flow of water that crossed the interisland reef at higher tides, but this would have been a hazardous transit for most zooplankters, and we doubt that significant numbers came this way. If many had come by this incidental route, at least some would still have been there at daybreak—probably somewhat disoriented in these foreign surroundings. But they were always gone by early morning twilight, suggesting they followed a well-established pattern with consistent and predictable arrivals and departures.

Probably most of the nocturnal plankters that visited Walt Island came from the deeper waters of the lagoon, moving over the lagoon's shallow periphery as part of a regular nocturnal rise into the surface waters. The general rise of zooplankters at night in lagoons of the Marshall Islands has been documented (at Bikini by Johnson 1949; and at Majuro by Hobson and Chess 1973). It has also been noted that by day the midlagoon is much richer in zooplankters than is the shallow periphery (Gerber and Marshall 1974), but a shoreward movement among zooplankters at night would reduce this difference between the two regions. Probably it is widespread that zooplankters rising from the depths at night spread out over shallow water near shore. At Kona, Hawaii, where great depths lie adjacent to a coastal shelf (see Hobson 1974), one of us (E. Hobson) often observed myctophids (lanternfishes), and other deep-water forms, in <5 m of water close to shore after dark (unpubl. obs.).

Swimming to the Walt Island site from the deeper water of the lagoon would usually entail moving against the drift from the reef. Although comparatively weak, this current would nevertheless obstruct small or weak-swimming forms. The nocturnal shoreward movement of zooplankters at this location, then, would favor the larger, stronger swimming components of the plankton—forms like chaetognaths, larval fishes, and the larger calanoids. Likely for this reason most of the calanoids among the increased numbers of zooplankters at Walt Island were >2 mm (Table 3), whereas at Bogen Island, where zooplankters were carried by currents, most of a much greater number were 1 to 2 mm long (Table 8). Distinction between the two locations is important because it is the larger zooplankters that were important prey of the nocturnal planktivores. Of course, the upcurrent swim from deeper water would take even the most mobile zooplankters some time. Thus, it is significant that larger calanoids were absent in the plankton collections made at Walt Island 1 h after last evening light, but were numerous in the collections made here at midnight and later (Table 3).

Bogen Island

We presume that most of the zooplankton collected in the flooding tidal currents at Bogen Is-

land had been carried in through East Channel from outside the lagoon—just as during the day. The greatly increased numbers at night probably followed a general rise of zooplankton toward the surface waters in the open sea. Some of these zooplankters were larger than any that were present by day, but such forms represented a lesser proportion of the nocturnal plankton here than they did at the weak-current site. Presumably the collections also included lagoon organisms from upstream, but we would expect these to be relatively few because the entrance to East Channel is only about 1.2 km away (Figure 1). Although the incoming tidal currents probably carried materials that had been transported from the lagoon on earlier ebb tides, we would not expect many of the larger mobile organisms to be among them. Most large mobile forms, it would seem, could avoid being transported from the lagoon by the comparatively weak outgoing currents. But certainly the incoming tide could be returning substantial numbers of passive drifters, like fish eggs and algal fragments, in addition to forms like the smaller calanoids. In any event, we can understand the relative scarcity in the flooding tidal currents of the relatively large nearshore residents (e.g., polychaetes, mysids, and postlarval carideans) that are so important in the diets of nocturnal planktivores.

Probably at least some zooplankters from the deeper waters of the lagoon visited the Bogen Island site at night during periods between flooding tides, but we made no collections at these times. Nevertheless, it would seem that the impact of such forms on the area would be limited, considering how long it takes them to travel without benefit of transport by current, and the fact that a flooding tide sweeps through here during much of most nights.

Miscellaneous Topics

The Nocturnal Increase in Fish Eggs

Planktonic fish eggs represent a special case. Unlike most other zooplankters, which are mobile forms that strongly influence their own distributions, fish eggs are passive drifters that are quickly carried from where they are released if there is any current. Presumably their relative numbers in the water column closely follow the incidence of their release by fishes on the reefs below, and certainly the circumstances of this release have been strongly influenced by the threat from predators that abound over the nearshore reefs. Planktonic fish eggs were a major food of diurnal planktivores (Tables 4, 9) but, despite an almost sevenfold increase in numbers at night (Tables 2, 7), they were insignificant in the diets of nocturnal planktivores (Table 5). Clearly these largely transparent eggs are relatively safe from predatory fishes after dark, probably because they are then invisible. Thus, it would be highly adaptive for reef fishes to release planktonic eggs late in the day, or early in the night, when the eggs have maximum time for dispersing in the dark, relatively free of threat from planktivorous reef fishes.

Possible Influences of Water Depth and Size

Among the promising topics we lacked time to pursue during our short stay at Enewetak were ways that water depths, and the sizes of interacting fishes and zooplankters, may influence trophic relationships.

We believe that the difference in water depth between our primary collecting sites (7 vs. 13 m) did not significantly influence our findings, especially as the deeper station was well away from the deep part of the lagoon (Figure 1)—farther, in fact, than the shallower station. It was apparent to us, nevertheless, that water depth in the lagoon can, directly or indirectly, influence fish-zooplankton interactions. Obviously both fishes and zooplankters are physically limited in extreme shallows, especially in turbulent waters above shallow reefs. But probably the major depth-related influence stems from the general tendency of lagoon zooplankters to seek deeper water during the day (e.g., Johnson 1949; Hobson and Chess 1973)—a tendency that apparently increases with size. We suggest above that many of the larger zooplankters active above the nearshore shelf at night were in the deeper lagoon waters by day, when the water column of the nearshore shelf was largely without such forms. Perhaps the concentrations of planktivores along the outer edge of the nearshore shelf during the day were in contact with the fringe of these deep zooplankton populations.

This leads to a possible influence related to size. Very small zooplankters (those passing through the mesh of our net, and so unrepresented in the collections), and their predators among juvenile and larval fishes, may follow patterns sig-

nificantly different from patterns followed by the larger forms studied here. The zooplankters descending into the depths by day tend to be the larger individuals, so we wonder where the very small ones are located. In sharp contrast to the relatively few adult planktivores active in weak-current areas of the nearshore shelf by day, large numbers of juvenile and larval fishes (Figure 4) clearly found planktonic food abundant. It may be that very small zooplankters, unsampled by our net and too small to be taken by most adult planktivores, remain numerous in shallow weak-current areas during the day.

Mysids as Prey During the Day

It is striking that when mysids swarm in dense numbers near many reefs during the day they are relatively unimportant as prey of the major planktivorous fishes. They seem to escape the interest not only of diurnal planktivores, but also of the many nocturnal planktivores (e.g., *Myripristis* spp.) that hover within easy reach close among the coral.

To be sure, a number of the fishes we studied took some of these mysids by day. *Chromis caerulea, C. agilis, Dascyllus reticulatus,* and *Pomacentrus pavo* included mysids as minor components of their diet at the weak-current site. Furthermore, Hiatt and Strasburg (1960) reported that *C. atripectoralis* preyed significantly on mysids. But considering the preponderance of mysids in the water column at so many places during the day, these fishes took only token numbers.

Probably the relatively large size of the mysids is important in this context. The evolution of feeding morphologies in diurnal planktivores appears to have been determined by strong selective pressures to take tiny prey (Davis and Birdsong 1973; Hobson and Chess 1976). Significantly, most of the zooplankters taken by these fishes (e.g., copepods, larvaceans, and fish eggs) were <2 mm long, and the size range of mysids that swarmed around these reefs in daylight was 2 to 8 mm (Tables 2, 7). In reporting a similar situation in the tropical Atlantic Ocean, Emery (1968) speculated that planktivorous pomacentrids fail to prey on swarming mysids because normally these fishes feed on smaller prey.

The failure of *Myripristis* spp. and other large-mouthed nocturnal planktivores to exploit this diurnal resource cannot be attributed to the size of the mysids, however, because these fishes find the same mysids major prey at night. Apparently the nocturnal fishes simply do not react to these readily accessible mysids as prey during daylight. In warm-temperature waters of southern California the large juvenile olive rockfish, *Sebastes serranoides,* feeds primarily on zooplankters after dark, but during the day sometimes preys on mysids that are within reach of the rockfish where it hovers in relatively inactive diurnal schools (Hobson and Chess 1976). However, predominantly nocturnal habits seem to be characteristic of the olive rockfish only during its large juvenile stage—both before and after this stage it feeds mainly by day (Hobson and Chess 1976). Therefore, even at that time of its life when the olive rockfish feeds primarily at night, we should not expect it to be as strongly nocturnal as *Myripristis* spp. and the other more specialized nocturnal forms that ignore mysids by day at Enewetak.

Possibly swarming mysids are protected from predators by the nature of their aggregations. Emery (1968) noted that mysid swarms respond to predators just as fish schools do. The analogy can be expanded. Like these nocturnal mysids, many nocturnal fishes congregate in dense numbers above the reef during the day, and at this time they too are relatively undisturbed by the many predators at large in the same area (Hobson 1965, 1968). It is widely believed that fishes are less vulnerable to predators when they aggregate (e.g., Bowen 1931; Springer 1957; Brock and Riffenburgh 1960; Manteifel and Radakov 1961; Williams 1964). Of the many theories that would explain this circumstance, we favor the existence of a confusion effect, as advocated by Allen (1920) and others. This theory suggests that visually orienting predators which select individual prey have trouble singling out a target among the many alternatives they confront in an aggregation. That mysids achieve some safety from predators by aggregating is further supported by the experiments of Welty (1934), who found that goldfish, *Carassius auratus*, consumed fewer daphnia when these prey were concentrated. (These comments apply as well to the relative lack of diurnal predation on larval fishes, which, in their dense schools close to the reef, resembled swarming mysids.)

Planktivore Morphology and Their Distance From the Reef

It was suggested earlier (Hobson 1974) that in

their tendencies toward more fusiform bodies and deeply incised caudal fins, diurnal planktivores have acquired added speed that is adaptive in quickening their return to reef shelter when threatened. Expanding this suggestion, these features are more developed in planktivores that swim farther from the reef because threats from predators probably increase in more exposed locations. Although morphology that permits faster swimming would also enhance holding station in a current, we believe the major selection pressures shaping these features in planktivores have come from predators.

Despite the obvious adaptiveness of fusiform bodies and of deeply incised caudal fins in many planktivores, the morphologies of certain other highly successful diurnal planktivores have taken the opposite course. For example, among the fishes we studied, *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao* are among the deepest bodied of pomacentrids, and yet they range farther into the water column than the species of *Chromis* or *Pomacentrus*. Similarly, the many planktivorous chaetodontids in Hawaii (e.g., species of *Chaetodon* and *Hemitaurichthys*), all deep-bodied forms with truncate caudal fins, are highly successful planktivores that range widely in the water column (Hobson 1974).

We suggest that whereas fusiform bodies increase the chance of eluding predators, deep bodies increase the chance of discouraging predators. The basis of this second suggestion is the fact that piscivores live with the danger of choking on spiny-rayed prey lodged in their pharynx or esophagus. Over the years we have seen many predators in this predicament—often fatally. Piscivores generally swallow their prey head-first, frequently after manipulation to ensure proper orientation. Reasons for not swallowing a spiny-rayed fish tail-first are obvious. Assuming, then, that a prey fish is swallowed head-first, the danger of it becoming lodged in the pharynx or esophagus increases with its depth or width. Thus, predators equipped to take prey from among the variety of planktivores in the water column (where those at a given level tend to be about the same length) would find greater risk ingesting deeper bodied forms, especially those with prominent fin spines. Of course, this advantage of a deep body and prominent spines in thwarting predators extends beyond planktivores; the entire family Chaetodontidae, for example, would benefit (Hobson and Chave 1972).

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SPAWNING CYCLE, FECUNDITY, AND RECRUITMENT IN A POPULATION OF SOFT-SHELL CLAM, *MYA ARENARIA*, FROM CAPE ANN, MASSACHUSETTS

DIANE J. BROUSSEAU[1]

ABSTRACT

A population of *Mya arenaria* in the Annisquam River system, Gloucester, Mass., was studied for 3 yr to determine spawning frequency, fecundity, and recruitment rates under natural conditions. This population was observed to spawn twice each year, in March-April and June-July. Temperature appeared to be a more critical factor in the timing of gonad maturation than in triggering the release of gametes. Female body sizes and oocyte production were positively correlated (1973, $r = 0.95$; 1974, $r = 0.90$). Regression lines were compared by analysis of covariance. Slopes of the lines did not differ significantly between years or between spawning cycles within years ($P \geq 0.05$). Elevations of the lines differed significantly from one another ($P \leq 0.05$) indicating annual and seasonal variability in fecundity. Sex ratios of *M. arenaria* 25-95 mm shell length did not differ significantly from 1:1 over the 3-yr study period. In smaller individuals, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry was observed. Recruitment rates of juveniles fluctuated widely between spawning cycles as well as between years.

Although the literature contains widely scattered references to the reproductive cycle of *Mya arenaria* in New England, there is no combined account of egg production (= fecundity), spawning, and recruitment of this species under natural conditions. Inferences about the time and frequency of spawning by *M. arenartia* have been made from observations on larvae in the plankton (Stevenson 1907; Stafford 1912; Sullivan 1948; Landers 1954; Pfitzenmeyer 1962); from first appearances of newly settled juveniles (Belding 1930; Warwick and Price 1975); and from the presence of ripe gametes in the gonads (Battle 1932; Coe and Turner 1938; Shaw 1962; Stickney 1963; Ropes and Stickney 1965; Munch-Peterson 1973; Porter 1974). Observations on larvae and recently metamorphosed clams, however, are useful only as indirect measures of the frequency and duration of spawning, since larval abundance and juvenile recruitment are controlled by factors other than spawning alone. Conversely, evidence concerning gonad maturation and gamete release obtained by means of histological methods defines the spawning period without contributing to knowledge about recruitment.

Most shallow-water marine animals reproduce in a cyclic manner, the time of spawning ultimately depending on environmental factors (Orton 1920; Giese 1959; Kinne 1963). As with most other commonly studied bivalves, the timing of spawning by *M. arenaria* has been linked to water temperatures (Nelson 1928; Belding 1930; Battle 1932). Nevertheless, it remains unclear whether gametogenesis, spawning, or both occur at a specific temperature or in a specific temperature range in *M. arenaria*.

Reliable information on fecundity of *M. arenaria* is also unavailable. Laboratory methods for stripping eggs or inducing spawning in oysters and hard-shell clams (Brooks 1880; Churchill 1920; Galtsoff 1930; Belding 1930; Davis and Chanley 1956; Loosanoff and Davis 1963) are generally unsuccessful with *M. arenaria*. Consequently, the only information on egg production by *M. arenaria* is an unsupported statement by Belding (1930) that a 2.5-in clam (63 mm) produces about 3 million eggs per breeding season.

In an effort to clarify the breeding habits of *M. arenaria*, this study was designed to determine 1) the reproductive cycle in a natural population, 2) the temperature at which gametogenesis and spawning begin in this locale, and 3) the total numbers of eggs produced by individuals of different sizes.

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MATERIALS AND METHODS

The Annisquam River is a natural waterway approximately 3 mi long connecting Ipswich Bay on the north side of Cape Ann peninsula with Gloucester Harbor on the south (Figure 1). The river consists of a dredged channel with extensive tidal mud flats or shallow water on both sides. The mean tidal amplitude at Gloucester Harbor is 3 m. The Annisquam River receives limited freshwater drainage, resulting in salinities of 28-33.5‰. Water movement is largely dependent on the tides. Average monthly surface water temperatures (1 m depth) for the years 1973 and 1974 obtained from the University of Massachusetts Marine Station at Hodgkins Cove (Figure 1) indicate that monthly temperature fluctuations are great (Figure 2). Temperature data for 1975 were not available.

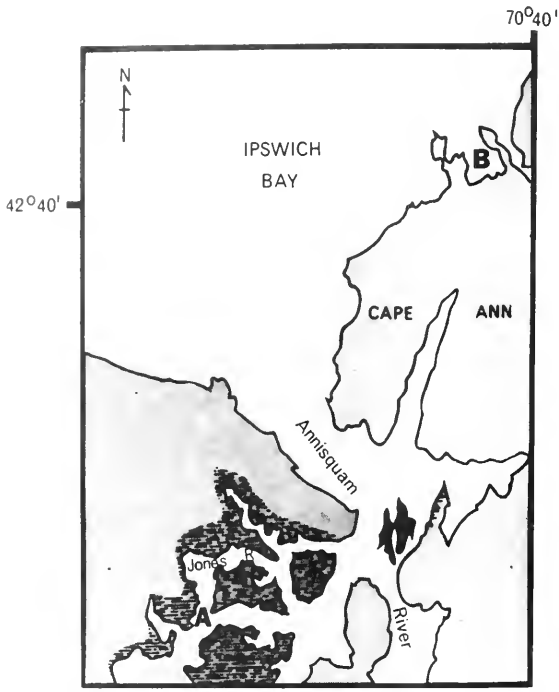

FIGURE 1.—Map showing locations of the Jones River study site (A) and the University of Massachusetts Marine Station, Hodgkins Cove (B).

The site for this study was located on a mudflat along the west bank of the Jones River, a small tributary opening at the northern end of the Annisquam River (Figure 1). Historically, this area has been the site of a productive shellfish bed and is known to sustain numerous clams of differing age classes (Mass. Dep. Resour., Div. Mar. Fish. pers. commun.).

The study began in February 1973 and was completed in October 1975. Clams were collected from the middle of the intertidal zone (+1 m tidal level) once a month from October 1973 through February 1974 and October 1974 through October 1975, and twice a month from March through September 1973 and April through August 1974. No samples were taken in September 1974 or in May, June, July, and September 1975. Sample sizes varied greatly. Samples collected during the spring and summer months consisted of 30 to 127 clams, 21-90 mm shell length. Those collected during the winter months consisted of 15 to 30 clams each in a similar size range. Large numbers of clams were

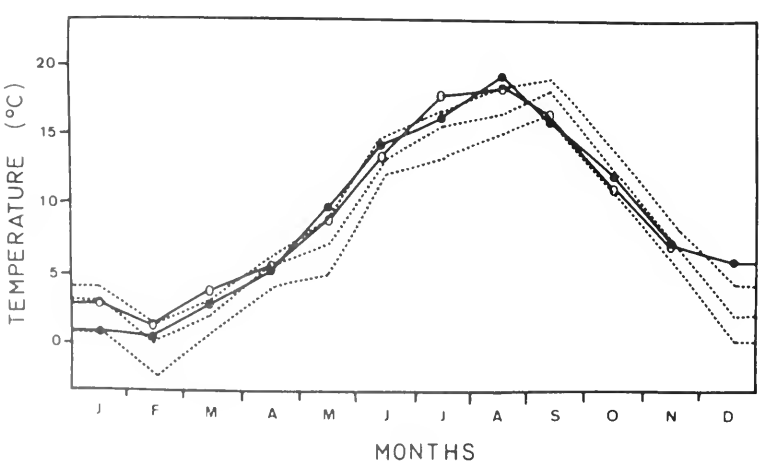

FIGURE 2.—Sea-surface (1 m depth) temperatures for Hodgkins Cove, Gloucester, Mass. Monthly means for 1973 (●●) and 1974 (○ ○) are plotted. The dashed lines represent 8-yr average maxima, means, and minima for the period 1963-71, based on temperatures for the Portland Lightship (Chase 1965-1973) corrected for Hodgkins Cove.

collected during the spawning season in order to insure sufficient numbers of "ripe" females for fecundity studies. A total of 2,480 clams were examined of which 11% were immature, leaving 2,206 mature clams that were used in the analysis of the reproductive cycle.

The samples were returned to the laboratory where they were kept at 0°C for not more than 3 days before being dissected. Each clam was numbered and its maximum length (±0.1 mm) determined. The visceral mass (gonad, liver, and gastrointestinal tract) was taken out and fixed in 10% buffered Formalin[2] (Humason 1967). The displacement volume of each visceral mass was taken to determine its size. The amount of gonadal tissue present was determined after sectioning by the planimetry method described below. The fixed mass was then dehydrated in alcohol, embedded in paraffin, sectioned at 8 μm, and stained in Harris' hematoxylin and eosin. Each clam was classified with respect to gonad development and the number in each developmental stage was recorded for both sexes.

Previous studies on the gonadal cycles of *Mya arenaria* have divided the developmental sequence into five morphologically distinct phases: inactive, active ripe, spawning, and spent (Ropes and Stickney 1965; Porter 1974). Since semantic problems arise with this usage, several terms are redefined for use here. The term "indifferent" is preferred to "inactive" to describe low levels of oogenic and spermiogenic activity. As pointed out by Keck et al. (1975) in work on hard clam gonadal cycles, the term "inactive" is biologically inaccurate since it implies a "static condition where absolutely no morphological or biochemical activity is proceeding." The term "developing" is used when describing the onset of gametogenesis since it can be argued that ripe and partially spawned gonads are active in the sense that gametogenic activity continues at a reduced level. Developing, ripe, and partially spawned stages are collectively termed "active," whereas spent and indifferent stages are termed "inactive." This distinction aids in defining peaks of spawning within the annual cycle.

Recognition of the five phases of gonadal condition was based on the same characteristics as those used by other investigators (Ropes and Stickney 1965; Porter 1974).

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

The number of oocytes present in each female gonad was determined in the following manner. Using an ocular grid, triplicate counts were made of the number of oocytes present per 0.49 mm² of gonad for each female reported in a ripe condition. This area was then multiplied by the mean oocyte diameter (0.65 mm) in order to determine oocyte densities on a cubic basis. An estimate of the total number of oocytes in the gonad could then be calculated on the basis of gonad size. Analysis of variance confirmed that the number of oocytes per unit volume was constant throughout the ripened gonad ($P \leq 0.05$).

Mean oocyte diameter was determined for a representative sample of ripe females, selected at random from each of the reported spawning periods. Twenty oocytes per clam were measured using an ocular micrometer. Only those oocytes which were spherical in shape and ready for release were selected for measurement.

The relationship between the size of the ripe female gonads and the volume of the total visceral mass was determined as follows. Entire viscera from 17 ripe females (53-76 mm shell length) were sectioned at 12 μm. Next, 18 sections from each individual were chosen at random, mounted on a Plexiglas base and fitted into a 35-mm slide projector and the projected tissue outlines were traced. A planimeter was used to estimate the percentage of gonad tissue present. A correction factor representing the proportion of gonad in the total visceral mass was used in estimating the total number of oocytes per individual (0.763±0.21, 95% C.I.).

Photographs of representative stages of the female reproductive cycle were taken with a light microscope at 160× and 100× magnification using a 35-mm camera. High contrast, Panatomic X ASA32 film was used.

Densities of juvenile *M. arenaria* were tabulated from the monthly samplings of the tidal flat during October 1973, from May to November 1974, and in November 1975. At each sampling period, 12 random samples (0.11 m², 20 cm deep) were taken along a 90-m transect from mean low water shoreward to the marsh scarp. Samples were wet seived in the field (2-mm mesh) and the size-frequency distribution of the clams was determined. Cohorts in the population were isolated by the probability paper method (Harding 1949; Cassie 1954).

RESULTS

Reproductive Cycle

Reproductively active individuals were encountered throughout the 3-yr study period, the largest numbers occurred in April and July of 1973, March and early July of 1974, and mid-March of 1975 (Figure 3). Due to the limited sampling undertaken during the summer of 1975, the summer spawning peak cannot be determined with certainty.

In February 1974, gametogenesis had begun in both sexes (Figure 4). Ripe and partially spawned clams were observed in mid-March. By late April,

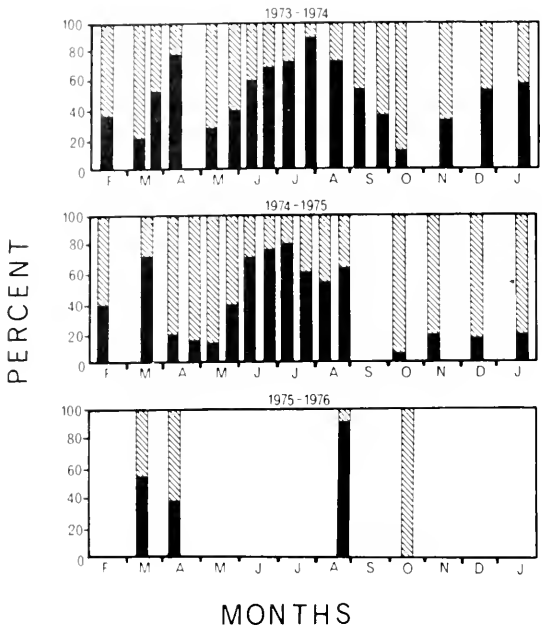

FIGURE 3.—Proportions of *Mya arenaria* population with active or inactive gonads during 1973-74, 1974-75, and 1975-76. Cross-hatched portions of each bar represent inactive gonads (indifferent, no gamteogenesis, or spent); solid portions represent active gonads (developing, ripe gametes, or partially spent). Observations on males and females were combined.

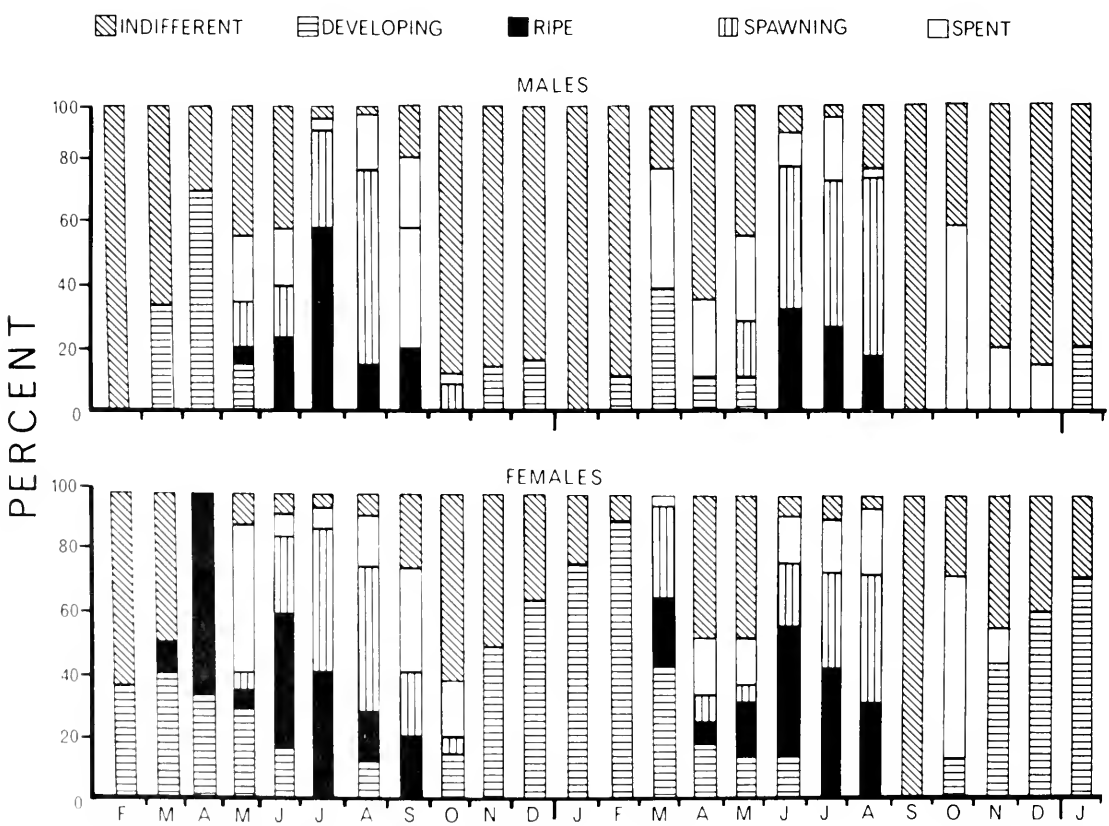

FIGURE 4.—Proportions of male and female *Mya arenaria* with gonads in each developmental phase during 1973-74 and 1974-75.

about 75% had completely spawned and returned to the indifferent condition. Gametogenesis usually resumed after spawning, and by early June about one-quarter of the clams were again ripe and partially spawned. The presence of cytolyzed unspawned gametes in the summer samples suggested that the same individuals had also been ripe earlier in the year. Thus the observed spawning pattern was due to repeated spawning by the same individuals rather than asynchronous spawning of individuals within the population.

A similar spawning pattern was observed in 1973, except that gametogenesis did not begin until April (Figure 4) and the summer spawning peak occurred in July rather than late June-early July. The data for both years indicate a more or less consistent recovery period between reproductive cycles. The data for the 1975 season indicate that spring spawning occurred in March as it did in 1974, but the summer sampling intervals were too irregular to describe details of the summer spawning. Nevertheless, occurrence of a summer spawning is confirmed by the gonad condition of the clams in the August sample.

Photomicrographs of representative female stages in the spring and summer peaks of the annual cycle are shown in Figure 5. The pattern of development in the clams during the spring cycle differs from that of the later summer one. In the female, the spring cycle is characterized by rapid gametogenesis, resulting in smaller oocyte size and fewer numbers of oocytes produced per unit of gonad tissue (Table 1), so different density values were used for calculations of fecundity (gonad volume $\times$ density) in different seasons. A significant seasonal difference in the diameter of ripe oocytes of female *M. arenaria* was detected using one-way analysis of variance ($P \leq 0.05$). Similarly, male clams appear to undergo rapid maturation and produce fewer gametes than during the summer spawning. Fully ripe males were not encountered in any of the spring samples, however, spent males were numerous, indicating that spawning had taken place. Spring spawning may be a facultative event, characterized by rapid maturation and the subsequent utilization of the abundant food supply that is available during the major phytoplankton "bloom" that occurs nearshore during this period.

Temperature is an important factor influencing the gonadal cycle in a variety of marine bivalves (Loosanoff 1937a, b; Landers 1954; Giese 1959; Carriker 1961; Ansell et al. 1964; Galtsoff 1964; Calabrese 1970). If temperature is indeed a factor in the onset of reproduction in *M. arenaria* as previously believed (Nelson 1928; Belding 1930), short-term temperature patterns in winter and early spring should correlate with the annual timing of gametogenesis (Figure 4). In fact, temperatures during January-March 1974 averaged about 2° higher than during the same period of the previous year (Figure 2) and gametogenesis began a month earlier than in 1973.

The actual role of temperature in the timing of gamete release remains unclear. Spring spawning peaks occurred at surface water temperatures of 4°-6°C and summer spawnings at 15°-18°C. Although the interstitial water of exposed tidal flats warms up considerably during midday spring lows (Johnson 1965), it is unlikely that interstitial temperatures would be high enough to account for these differences. If these is a critical minimum temperature for spawning it is at or above 4°-6°C. No maximum limit can be discerned from these data. The role of rapid temperature change in triggering spawning as suggested by other authors (Battle 1932; Stickney 1963) has not been assessed here.

Sex Ratios and Fecundity

The reproductive potential of a population depends, in large part, on the number of fertile females and the number of young produced per female. The proportion of females in all size-classes in three large samples from the Jones River in 1973 (n = 1,266), 1974 (n = 859), and 1975 (n = 150) did not differ significantly from one-half. In size-classes <25 mm, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry was observed.

The number oocytes produced was found to increase exponentially with increasing female body size. The regression equations for oocyte numbers (O) versus female shell length (S) are:

$$\text{Spring 1973: } \log_{10}O = -1.45 + 3.29 \log_{10}S$$
$$\text{Summer 1973: } \log_{10}O = -1.29 + 3.28 \log_{10}S$$
$$\text{Spring 1973: } \log_{10}O = -0.90 + 2.91 \log_{10}S$$
$$\text{Summer 1974: } \log_{10}O = -1.42 + 3.32 \log_{10}S$$

Comparison of the regression lines by analysis of covariance indicated that the lines were parallel ($P \geq 0.05$) but the elevations of the lines were significantly different ($P \leq 0.05$). Total oocyte production during 1973 was greater than during 1974.

b
d
a
c

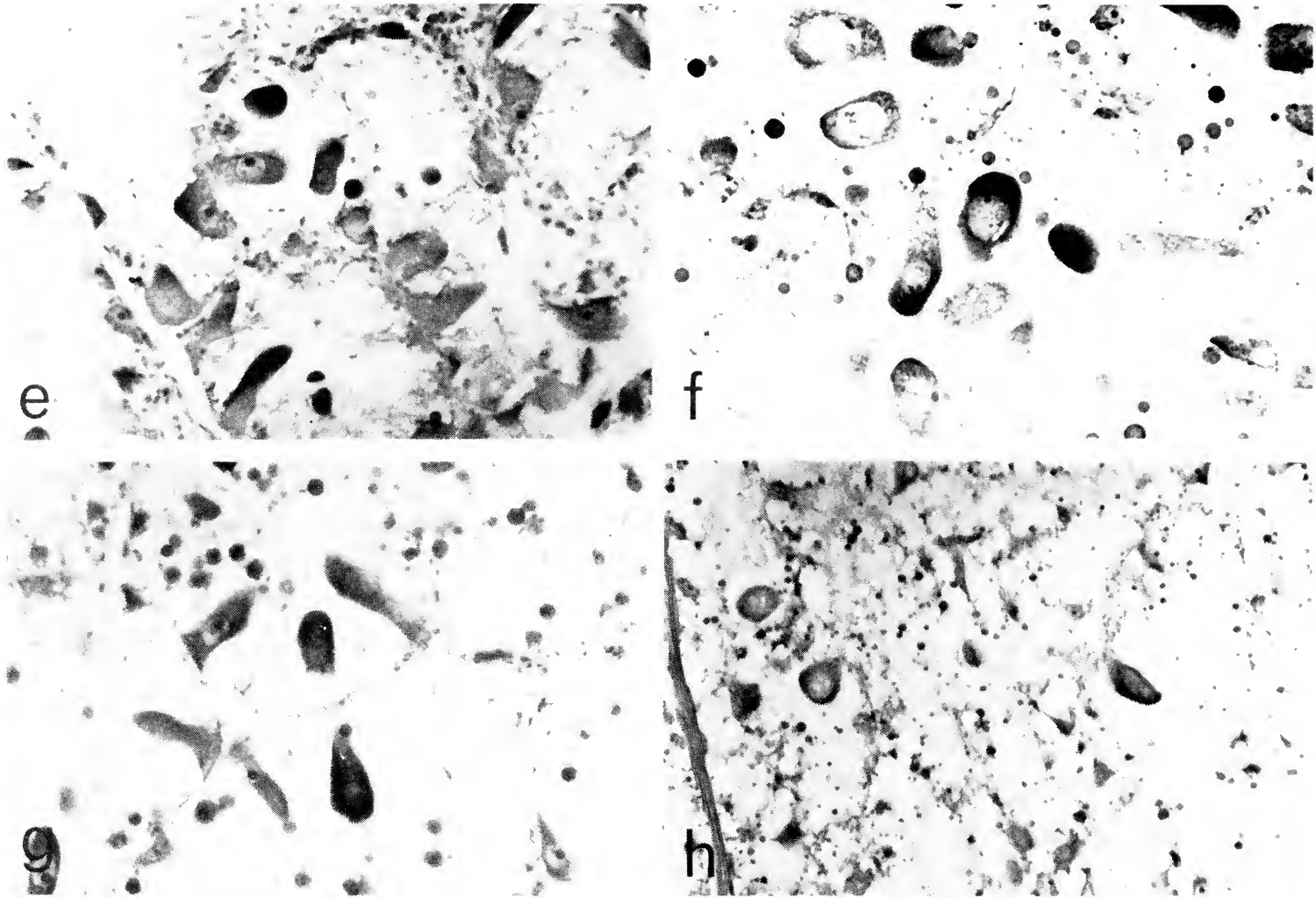

FIGURE 5.—Photomicrographs of gonadal stages of the soft-shell clam, *Mya arenaria*. a) Developing female (100X), 7 April 1973; b) Developing female (100X), 21 May 1973; c) Ripe female (100X), 24 March 1973; d) Ripe female (100X), 1 July 1973; 3) Partially spawned female (160X), 16 March 1974; f) Partially spawned female (160X), 1 July 1973; g) Spent female (160X), 5 May 1973; and h) Spent female (100X), 1 July 1973.

TABLE 1.—Oocyte diameter (microns) of "ripe" female *Mya arenaria* from each of the spawning periods of the annual reproductive cycles of 1973-75. Values represent the means of measurements on 20 individual oocytes per clam. The number of individuals sampled (n) and the overall means ($\bar{x}$) are given.

Spring 1973	Summer 1973	Spring 1974	Summer 1974	Spring 1975
48.3	57.9	41.0	59.0	39.3
42.4	66.9	40.4	58.0	45.2
43.1	62.8	40.7	56.9	41.0
44.5	62.4	40.0	73.8	44.2
43.5	43.5	41.0	60.4	39.9
41.4	61.1	42.1	63.1	43.8
43.8	61.8	33.3	68.0	42.4
45.2	64.2	40.4	63.1	41.0
51.4	64.5		58.6	36.2
	64.9		59.7	42.1
	61.8		58.6	36.2
	64.9		55.2	40.7
	63.1		68.0	37.3
	62.8		65.2	41.0
	61.1		61.1	40.4
	63.1		62.8	46.2
	62.8		58.3	
	64.2		64.9	
	61.1		64.9	
	50.0		65.9	
	52.8		71.1	
	58.3		71.8	
	58.0			
n 9	23	8	22	16
$\bar{x}$ 44.7	60.6	39.9	63.1	41.2

The limited data available for 1975 were not analyzed. In addition, fecundity differed between spawning seasons within a single year. Oocyte production was larger during the summer spawning cycle than during the spring one in 1973 and 1974. Females <40 mm in length were never gravid.

Recruitment

In sedentary bivalves, such as *M. arenaria*, settlement of recently metamorphosed larvae from the plankton is the only significant source of recruitment. Spat were most abundant in May and September of 1974 (Figure 6). Allowing approximately 5 wk for planktonic life, metamorphosis, and growth to 2 mm, these peaks correlate with and probably result from the spawnings described above. This timetable for metamorphosis corresponds with similar estimates made for *M. arenaria* under natural (Kellogg 1905) and laboratory (Stickney 1964) conditions.

Large fluctuations in yearly recruitment are characteristic of many bivalve populations (Hughes 1970). Therefore, recruitment of young, when it occurs, may represent a large proportion of the population. A comparison of the size-frequency distributions in samples taken in October 1973 and October 1974 reveals that this is also true for *M. arenaria*. A substantial settlement occurred in May of 1974, but by the fall, this cohort had nearly disappeared. Similarly, the fall set (Figure 6, 1B) quickly vanished. In contrast, survival of individuals from the spring and summer sets in the previous year was good, as evidenced by the numbers of these size-classes persisting in the October samples. The spring and fall sets of 1975 were extremely poor (Robert Knowles pers. commun.) and nearly 100% juvenile mortality had occurred by November of that year (Figure 6).

DISCUSSION

The results of the gonad examinations indicate that *M. arenaria* from Gloucester, Mass., spawn twice each year (Figure 3). This spawning pattern is similar to that reported for populations south of Cape Cod (Mead and Barnes 1903; Landers 1954; Pfitzenmeyer 1962), although isolated instances of single spawnings have been documented (Shaw 1962). Previous investigators have reported that clams from northern Massachusetts began spawning in July and completed spawning by late September. There is strong evidence to indicate that populations from Plum Island Sound studied by Belding (1930) and Ropes and Stickney (1965), spawn only once annually. Proof of annual spawning in populations south of Plum Island Sound to Cape Cod, however, is less convincing. Based on the presence of larval *M. arenaria* in plankton samples, Stevenson (1907) reported that clams from Ipswich and Plymouth spawn in the late summer. It is not clear from his report whether sampling was conducted year-round or only during the summer months. If the latter is true, then early spring spawning activity may have been overlooked and the later summer peak (Figure 3) incorrectly interpreted as evidence for a single late spawning season for clams of this area. It is possible that the biannual spawning observed in Gloucester is a local phenomenon. Nevertheless, more work is needed before any generalizations concerning the frequency of spawning of clams in northern Massachusetts can be made.

Indirect evidence also gives clear indication of a biannual spawning cycle. First, recruitment patterns both corroborated the evidence from gonad examinations and indicated other populations in the area spawned at the same times. Owing to pelagic larval dispersal in *M. arenaria*, bursts of recruitment (Figure 6) would be obscured if spawning were not synchronous in nearby populations. Secondly, sea-surface temperatures for 1973

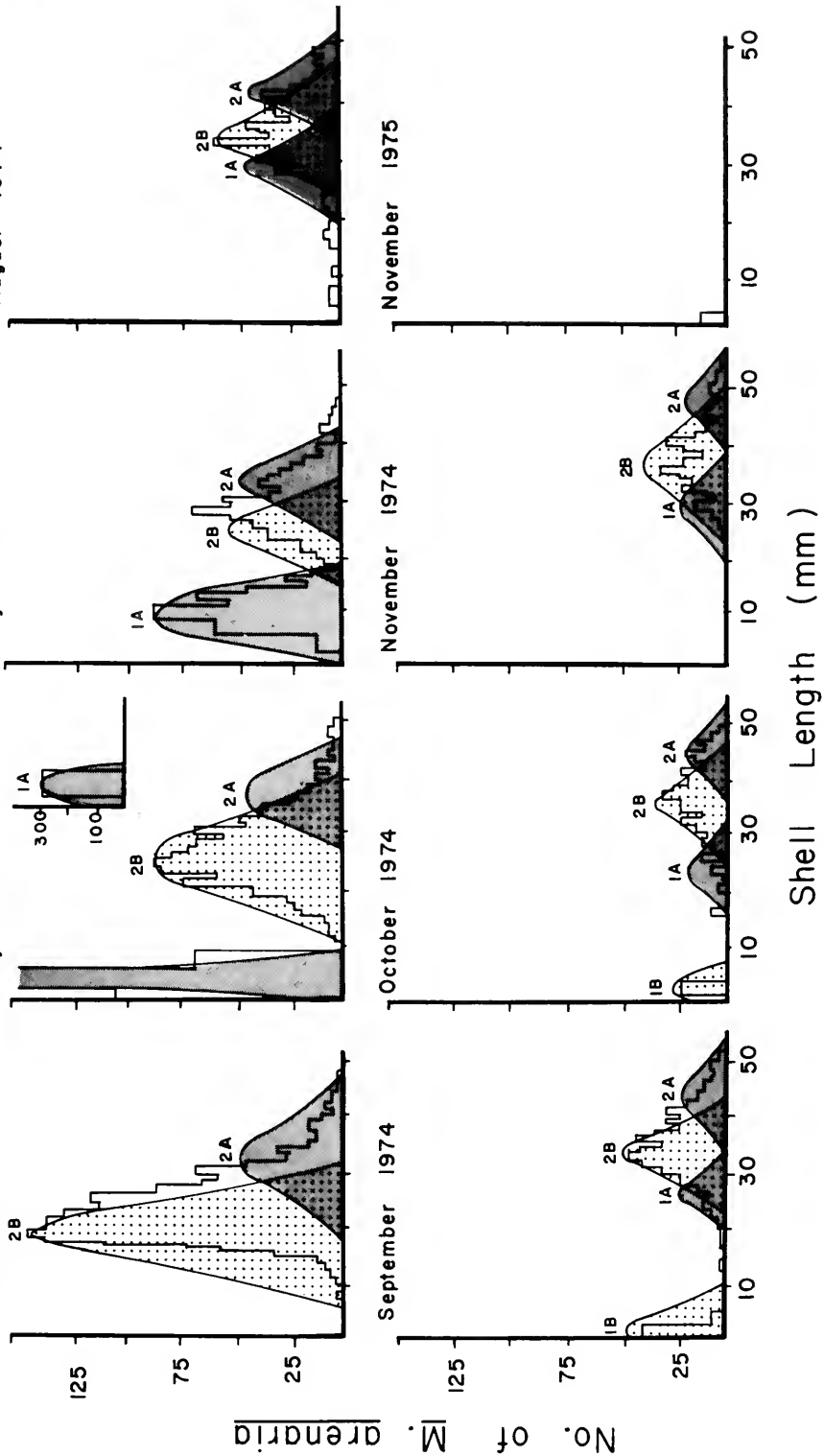

FIGURE 6.—Size-frequency distributions of *Mya arenaria* during October 1973, May-November 1974, and November 1975. Normal curves obtained by probability paper analysis are indicated by shading. Numerals indicate the year class of each cohort (0 = 1975; 1 = 1974; 2 = 1973) and letters denote the season in which the set occurred (A = spring; B = summer).

and 1974 approximated 8-yr monthly means so the bimodal pattern was not an atypical response to above average temperatures. Nevertheless, the temperature patterns of this locale are probably influenced substantially by local topography. More than 60% of the total area of the Annisquam River system is <6 m deep, 30% being intertidal (Jerome et al. 1968). Early spring warming and fall cooling trends would be expected here due to these nearshore influences. Lastly, it appears that the bimodal spawning pattern emerging here may be typical of some populations of *M. arenaria* found as far north as Plum Island Sound. A spring set of juvenile clams occurs annually on intertidal flats in Ipswich, Mass., (Richard Sheppard pers. commun.) and large numbers of 2- to 4-mm clams appeared in the May and June samples of Smith et al. (1955). Such evidence indicates that a semiannual pattern may be more prevalent in northern Massachusetts than once believed.

Orton (1920) first noted that some animals in temperate regions spawn when the temperature exceeds a critical level characteristic of the species, while for others the rate of change is important. Nelson (1928) reported 10°-12°C as the critical spawning temperature for *M. arenaria*; Belding (1930) reported the exceptionally high figure of 22°C. The data for Gloucester indicate that spawning can occur with equal likelihood at either of the supposedly critical temperatures provided that the gonad is ripe. The significant temperature appears to be that at which maturation of the gonad occurs. Similar significance of maturation temperature had been reported for the oyster, *Crassostrea virginica*, by Loosanoff and Davis (1950).

Gonadal oocyte counts provide an accurate measure of fecundity in *M. arenaria* since all oocytes are stored in the gonad prior to spawning and nearly total evacuation takes place at spawning. The fecundity values for *M. arenaria* indicate that the largest females produce the largest number of oocytes. This increase is undoubtedly due to increased gonad size made possible by increased shell volume. Average oocyte production by a 60-mm clam during a single breeding season (two spawning periods) is about 120,000; lifetime production would be in the order of 1.5×10^6 oocytes. Although fecundity of *M. arenaria* is large, as is typical of species with planktonic larvae (Thorson 1950), these estimates are considerably lower than early unsubstantiated ones for this species (Belding 1930), as well as those reported for other marine bivalves such as *Crassostrea virginica* and the hard-shell clam, *Mercenaria mercenaria* (Galtsoff 1930; Davis and Chanley 1956).

High fecundity, however, is offset by high mortality during pelagic life, metamorphosis, and early settlement. It appears that sources of mortality such as predation, disease, and bottom character are more critical factors in explaining fluctuations in recruitment than variability in fecundity rates or spawning frequency. The spawning cycles in which the greatest number of oocytes were released did not correlate with periods of highest recruitment. In terms of spat densities, spring recruitment in both years studied was higher than summer recruitment. Success of some year classes and failure of others indicate that fluctuations in clam populations are largely natural occurrences and may result from things other than fluctuations in the number of oocytes or the number of juveniles or byssus-stage young.

Spawning times and fecundities of individual females are critical factors in determining first, what constitutes a satisfactory breeding stock and secondly, how to protect it. Numerous studies have been conducted on methods of improving soft-shell clam fisheries (Belding 1930; Turner 1949, 1950; Smith et al. 1955; Smith[3]). Regulatory efforts have ranged from predator control to establishment of legal size limits for clams, closed seasons, and restocking of barren flats. All this work has proceeded in the near absence of basic information of the reproduction and population dynamics of the clam. The dwindling yields of clams on the New England coasts indicate the ineffectiveness of present regulatory procedures and the need for revised management practices.

In Massachusetts, any clam over 2 in long (51 mm) may be harvested. In effect this practice maximizes the removal of the reproductively most valuable individuals in the population. Murphy (1968), using genetic models, has shown that adult longevity and iteroparity (= repeated reproduction) are important adaptations for population stability in species like *M. arenaria* which exist under conditions of uncertain preadult survival and relatively stable adult survival (Brousseau

[3]Smith, O. R. 1952. The results of experimental soft clam farming in Plum Island Sound, Massachusetts. Third annual conference on clam research, U.S. Fish and Wildl. Service, clam investigations, Boothbay Harbor, Maine, p. 46-48. Unpubl. rep.

1976). Consequently, long-term stability of the resource is endangered by present harvesting practices which reduce the normal 10-12 yr lifespan of *M. arenaria* to 2 yr. Revision of existing regulations to include protection of sufficient breeding stock may be an effective way of insuring the long-term stability of the resource and minimizing the harmful effects of human predation.

ACKNOWLEDGMENTS

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DIEL MOVEMENTS OF LARVAL YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*, DETERMINED FROM DISCRETE DEPTH SAMPLING

W. G. SMITH, J. D. SIBUNKA, AND A. WELLS[1]

ABSTRACT

A 72-h study to investigate diel movements of yellowtail flounder larvae indicated that they exhibited pronounced vertical movements that were repetitious from day to day. Collections at 3-h intervals with 20-cm bongo nets revealed that larvae were near the surface at night, and mostly at a depth of 20 m during the day. Ascent and descent occurred largely at sunset and sunrise, respectively. Thermal gradients at 10 to 20 m and 30 to 40 m had no apparent influence on the vertical movements. Amplitude of the movements increased with the size of larvae. Recently hatched larvae remained near the shallow thermal gradient. Intermediate sized larvae migrated from middepths during the day to surface and near-surface at night. Large larvae moved throughout the water column. The incidence of feeding was low but a daily feeding pattern was evident. Most larvae with gut contents were collected from 1900 to 0100 h on the first day; from 1600 to 2200 h on the second day; and from 1600 to 0100 h on the third day. The near-absence of gut contents in larvae caught during morning daylight hours suggests that the onset of feeding is triggered by something other than, or in addition to, light. Wind driven circulation near the surface was thought to transport larvae at night, when they moved towards the surface. Subsurface circulation was sluggish and ineffective as a transporting mechanism.

Diel migrations by larval fishes play an important but largely unexplored role in dispersion during planktonic development. We became cognizant of the need to investigate this role after our initial ichthyoplankton survey, a series of cruises in the Middle Atlantic Bight to determine when and where coastal fishes spawn and to trace the dispersal of planktonic eggs and larvae (Clark et al. 1969). Despite a full schedule of field work, the survey was only partially successful. We learned where and when many fishes spawn and recognized seasonal shifts in spawning areas (see Smith 1973; Fahay 1974; Kendall and Reintjes 1975; Smith et al. 1975), but we were unsuccessful in tracking disperson away from the spawning grounds.

After realizing the shortcomings of the survey, we began to speculate on the significance of diel migrations and how they might interact with circulation to affect dispersion, especially where the water column is thermally stratified and surface and subsurface currents differ in velocity. We theorized that a study of the diel movements of fish larvae, when related to our survey data and to known circulation patterns, might provide us with better information on larval transport than we could obtain from continued surveys. In June 1972 we conducted a 72-h study of the diel movements of larval yellowtail flounder, *Limanda ferruginea* (Storer), an important species in the New England trawl fishery, and the most abundant flatfish larvae collected during our survey of the Middle Atlantic Bight. Our primary objectives were to determine whether the young flatfish undergo diel migrations, whether the migrations are repetitious in time and extent, and how they interact with circulation to affect dispersion.

Yellowtail flounder range from the Gulf of St. Lawrence to Chesapeake Bay. Their center of abundance lies between the western Gulf of Maine and southern New England (Bigelow and Schroeder 1953). They spawn from March to September in the Middle Atlantic Bight. Spawning progresses from south to north as the season advances. The peak of the season in the bight occurs in early May with heaviest spawning off New York and northern New Jersey. Based on the catch of larvae <4 mm, Smith et al. (1975) determined that most spawning takes place between 4° and 9°C.

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METHODS

We selected the general area for the 72-h study from results of the 1965-66 survey (Smith et al. 1975). The specific site, 98 km south of Montauk Point, N.Y., was selected by making trial plankton tows until we found the patch of larvae (Figure 1). To stay within the patch, we deployed a free-drifting parachute drogue similar to that described by Volkmann et al. (1956). The parachute was attached 18 m below the staff buoy on our drogue.

We sampled at 3-h intervals, from 1000 h on 15 June to 0700 h (EDT) on 18 June 1972. Temperature and salinity observations preceded each tow during the first 2 days. We continued to take temperatures at 3-h intervals on the third day but recorded salinity data at 6-h intervals. When we started sampling, the summer solstice was only 6 days hence and a day was divided into 15 h of daylight and 9 h of darkness. Sunrise and sunset were at about 0530 h and 2030 h, respectively. By sampling at 3-h intervals, we made five tows during daylight and three tows at night during each day.

Plankton samples were taken with an array of four 20-cm bongos fitted with 0.505-mm mesh nets. Each tow lasted 15 min. Towing speed was 5 kn (3 m/s). We chose the 20-cm bongo over the larger 61-cm bongo to keep both plankton volumes and numbers of fish larvae at levels that would not exceed our laboratory capabilities. Catch comparison tests between the 20- and 61-cm nets revealed no significant differences in the catch of larvae (Bjørke et al. 1974; Posgay et al.[2]).

Readings obtained from digital flow meters were used to calculate the amount of water sampled by one side of each bongo. With the exception of the surface-sampling net, the bongos were attached to the towing wire to sample near depths where temperature changes were greatest. They sampled at 8 m, which was just above the shallower of the two temperature gradients; at 20 m, below the shallow gradient; and at 48 m, which was below the deep thermal gradient and about 17 to 20 m above bottom. We preserved the contents from only the metered side of each bongo. Bathykymographs (BKG) were attached above two of the three subsurface nets to monitor sampling depth profiles. The sequence of attachment changed with each tow. Resultant BKG traces indicated that the average towing depth of each subsurface net was ±2 m of the intended sampling depth. The bongos did not have opening-closing devices. We tried to minimize contamination during setting and retrieval by snapping the three subsurface nets onto the towing wire and lowering them into the water while the ship maintained just enough way to stay on course. Immediately after affixing the 8-m net, vessel speed was increased. The surface net was snapped in place and lowered into the water as the ship approached

[2]Posgay, J. A., R. R. Marak, and R. C. Hennemuth. 1968. Development and tests of new zooplankton samplers. Int. Comm. Northwest Atl. Fish., Res. Doc. 68/85, 7 p.

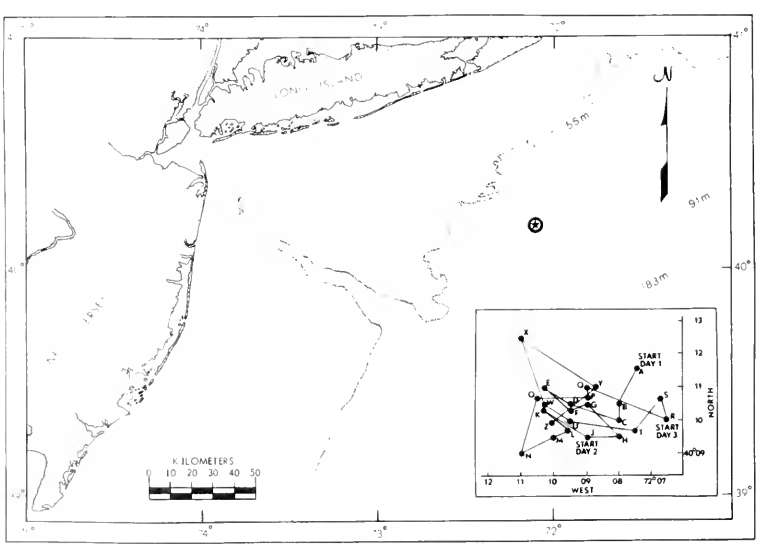

FIGURE 1.—Site of 72-h study of diel movements of yellowtail flounder larvae. Insert shows theoretical track of drogue and its position at 3-h sampling intervals.

towing speed. At the end of each tow the nets were retrieved as we slowed to a stop.

All yellowtail flounder larvae from each sample of <100 fish were counted and measured to the nearest 0.1 mm SL. If the count exceeded 100, a subsample of about 25% was randomly selected and measured. Then the number of larvae in each size increment was adjusted so that the sum corresponded with the total sample size. Despite our efforts to minimize sampling contamination while setting and retrieving the nets, subsurface nets sampled more water than the surface net. To compensate for contamination, we standardized the volume of water filtered by each net by using the mean amount of water filtered by the surface net (88.8 m^3) as the standard. We then adjusted the catch of each net to correspond with the adjusted amount of water filtered. These changes accounted for average reductions in the catch of <1.0% in the surface net, 3.4% in the 8-m net, 4.4% in the 20-m net, and 13.4% in the 48-m net or a net reduction of 4.7% of the total catch.

We inspected digestive tracts of young flounders for indications of a feeding pattern, i.e., presence or absence of gut contents, that might be related to vertical movements. We were able to make these observations simply by using a microscope and incident lighting.

After grouping the adjusted larval catches into four size categories, ≤4.0, 4.1 to 8.0, 8.1 to 10.0, and >10.0 mm, we examined the data for homogeneity of sampling variance by comparing within station catches by depth. Daylight tows were considered replicates, as were night tows. Standard deviations were proportional to the means in the raw data, indicating that sampling variance was not homogeneous. The variance was stabilized by transforming the data to $\log_{10}(x + 1)$. We used the UCLA BMD computer program 02V, a multifactor ANOVA program (Dixon 1973), to test for differences in mean catches by day, depth, time (day vs. night), and size of larvae (Table 1). To meet a program prerequisite, we balanced the number of day and night tows used in the analysis by randomly selecting three of the five tows for each daytime period.

TABLE 1.—Analysis of variance of data collected during study of diel movements of yellowtail flounder larvae. Variables include days, time (day vs. night), capture depth, and length of larvae, grouped into size categories of ≤4.0, 4.1 to 8.0, 8.1 to 10.0, and >10.0 mm. Data were transformed to $\log_{10}(x + 1)$ and pertain to 3 day tows and 3 night tows taken during each day of the 3-day study.

Source of variation	df	S.S.	M.S.	F
1 (days)	2	0.21	0.11	0.93
2 (day-night)	1	23.83	23.83	208.40**
3 (depth)	3	16.81	5.60	48.99**
4 (size of larvae)	3	73.49	24.50	214.53**
1, 2	2	0.23	0.11	1.01
1, 3	6	1.79	0.30	2.61*
1, 4	6	1.45	0.24	2.11
2, 3	3	43.63	14.54	127.18**
2, 4	3	3.94	1.31	11.47**
3, 4	9	14.86	1.65	14.44**
1, 2, 3	6	2.20	0.37	3.21**
1, 2, 4	6	0.45	0.07	0.66
1, 3, 4	18	2.37	0.13	1.15
2, 3, 4	9	13.13	1.46	12.76**
1, 2, 3, 4	18	2.80	0.15	1.36
Within replicates	192	21.95	0.11	
Total	287	223.14		

*$P \leq 0.05$.
**$P \leq 0.01$.

RESULTS

Light conditions and sea state varied during the 3-day study in response to changing weather. The sky was cloudy when we began sampling on 15 June. Seas were moderate, stirred by 2 days of brisk south to southwesterly winds of 15 to 20 kn (7-10 m/s). On the 16th the sky cleared but southerly winds persisted. The 17th was cloudy with intermittent periods of light rain until evening when dense fog set in. We completed field work in heavy rain on the morning of the 18th. There was little or no measurable wind during the last 24 h of sampling.

Water temperature in the Middle Atlantic Bight increases rapidly in the spring and the water column becomes thermally stratified during the summer (Norcross and Harrison 1967). At the time and site of our study, the surface temperature averaged 15.0°C, the bottom 5.7°C. A thermal gradient of about 5°C, the predecessor of the more strongly defined summer thermocline, occurred at depths between 10 and 20 m. A second, weaker gradient existed between 30 and 40 m. Salinity increased from 31.3‰ at the surface to 32.8‰ near the bottom. The most pronounced change in salinity occurred at about the same depths as the shallow thermal gradient (Figure 2).

Drift of the drogue was erratic and sluggish throughout the 72-h study. In 3 days it crossed its previous path 16 times, travelled a net distance of only 5.4 km in a southwesterly direction, and was never more than 7.2 km from the starting point. Net direction of drift was into the wind and the drogue travelled the greatest distance on the third day, when there was little or no wind. Because the drogue's direction of drift changed at approximately 6-h intervals, we concluded that tidal

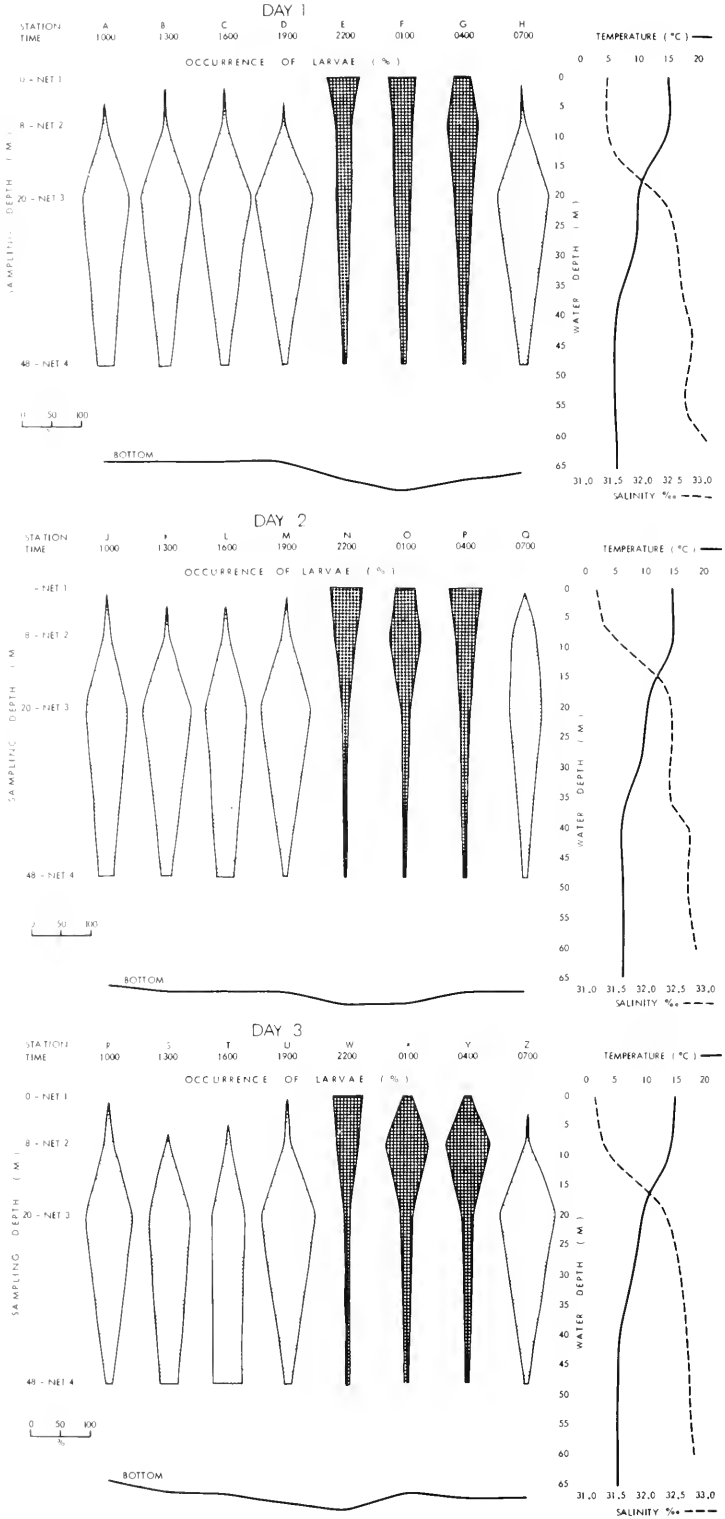

FIGURE 2.—Vertical distribution of yellowtail flounder larvae at 3-h intervals, based on percent contribution of adjusted catches in each of four nets. Mean temperature and salinity profiles during each day of the 3-day study are shown at right.

circulation was largely responsible for its movements (see Figure 1 insert).

The analysis of variance indicated that we stayed within the same patch of larvae throughout the study. Daily mean differences in both the number and size of larvae were not significant. There was, however, a highly significant difference between means of day and night catches, and between catches at the four depths sampled. We attributed these differences to diel movements and the resultant shift in the distribution of most larvae toward the surface, where two nets fished, at night. The diel movements were repetitious in time and extent. There was no significant difference in means of catches within daylight and night tows, or in their depth distribution at a given time during each day (Table 1).

Larvae were most abundant in the 20-m net during daylight tows on the first day. None were caught by the surface net and the combined catch of the nets at 8 and 48 m contributed $<15\%$ of the daytime catch. The distribution of larvae changed significantly after dark. By 2200 h the catch in the surface net was greater than the combined catch of the other three nets and more than double that of any other net. When combined, the surface and 8-m catches accounted for nearly 77% of the 2200-h catch. At 0100 h larvae remained most abundant at the surface and, although the surface catch was less than at 2200 h, again the upper two nets accounted for $>70\%$ of the catch (Figure 2). At 0400 h, the last nighttime tow, most larvae were caught at 8 m (Table 2).

The vertical movements of larvae throughout the second day were similar to those on the first day. Most larvae were taken at 20 m on each of the five daylight tows. Except for a single specimen in the 1600-h tow, none were caught at the surface during daylight. By 2200 h the distribution again changed significantly. Like the first night, the surface catch was greater than the total catch of the other three nets. The combined catch at the surface and 8 m made up 88% of the 2200-h catch. Unlike the first night, larvae were less abundant at the surface than at 8 m at 0100 h but the upper two nets again contributed $>80\%$ of the catch (Figure 2). At 0400 h larvae reoccurred in greatest numbers at the surface. This increase in the surface catch at 0400 h did not occur on the previous day (Table 2).

Results of tows on the last day were much like those on the first 2 days. Larvae were most abundant at 20 m on all five daylight tows. Only one larva was taken at the surface, that at 1900 h. By 2000 h the distribution of larvae shifted towards the surface. The young flounder repeated their behavior of the previous day by descending at 0100 h. Most were at 8 m and, for the first time, the 20-m net caught more larvae than the surface net on a night tow. Despite the somewhat deeper distribution, the combined catch of the surface and 8-m nets contributed nearly 80% of the 0100-h catch (Figure 2). The distribution of larvae at 0400 h was much like that at 0100 h. It differed from the other two 0400-h tows in that the contribution of the surface net was greatly reduced, and that of the 8-m net greatly increased (Table 2).

The amplitude of diel movements increased with size of larvae but, within each of the four size groups, the movements were similar each day (Figure 3). The vertical movements of larvae ≤ 4.0 mm were relatively insignificant compared with those of larger larvae. During daylight hours the recently hatched larvae were at an average depth of about 24 m, at night 20 m, a difference of only 4 m. Larvae 4.1 to 8.0 mm long were more active. They moved vertically from an average depth of 24 m during the day to about 9 m at night. The trend continued with larvae 8.1 to 10.0 mm long. During the day were at an average depth of 29 m. At night they ascended to an average depth of 5 m. Larvae >10.0 mm exhibited the most pronounced vertical movements. During the day they were at an average depth of 41 m, at night 7 m.

By not having a net near bottom, we failed to sample the entire depth range of larvae. However, it appears that our nets encompassed the depth distribution for nearly all larvae <10.0 mm. Only 5% of those <10.0 mm were caught in the 48-m net and we assume that their numbers continued to decline below that depth. On the other hand, the daytime distribution of larvae >10.0 mm may have been deeper than our results indicate. Almost half (46%) of the daytime catch of larvae >10.0 mm was caught in the deep net. None were caught at depths <20 m, and most (77%) of the large larvae caught at 20 m during the day were collected at 0700 h, probably during their morning descent.

The incidence (percent) of larvae with visible gut contents was as high as 40% at one station but only 6% of the larvae caught during the 3-day study contained visible gut contents. The overall incidence was low, but our results indicate that most feeding occurred at about the same time on all 3 days. We found the highest incidence from

TABLE 2.—Adjusted catch of yellowtail flounder larvae by size group, depth, and time. Results are presented by day, beginning with the initial daylight tow, although we began sampling at 1000 h (Station A) and finished at 0700 h (Station Z).

			Day 1								Day 2						
	Hour	Net	Size group (mm)				Total				Size group (mm)				Total		
Stn.	of tow	depth (m)	<4	4-8	8-10	>10	No.	%	No./m³	Stn.	<4	4-8	8-10	>10	No.	%	No./m³
Day tows																	
H	0700	Surf	0	0	0	0	0	0	0	Q	0	0	0	0	0	0	0
		8	0	21	1	0	22	5	0.2		0	125	76	0	201	42	2.3
		20	26	350	15	0	391	84	4.4		0	153	95	15	263	54	3.0
		48	1	38	7	4	50	11	0.6		0	14	2	3	19	4	0.2
		Total	27	409	23	4	463	100			0	292	173	18	483	100	
A	1000	Surf	0	0	0	0	0	0	0	J	0	0	0	0	0	0	0
		8	2	6	0	0	8	1	0.1		0	48	12	0	60	11	0.7
		20	84	447	8	0	539	76	6.1		25	315	22	1	363	67	4.1
		48	0	85	68	12	165	23	1.9		2	87	26	7	122	22	1.4
		Total	86	538	76	12	712	100			27	450	60	8	545	100	
B	1300	Surf	0	0	0	0	0	0	0	K	0	0	0	0	0	0	0
		8	0	12	1	0	13	3	0.1		0	15	8	0	23	4	0.3
		20	25	411	16	0	452	82	5.1		15	325	74	4	418	82	4.7
		48	6	51	20	7	84	15	0.9		5	49	11	5	70	14	0.8
		Total	31	474	37	7	549	100			20	389	93	9	511	100	
C	1600	Surf	0	0	0	0	0	0	0	L	0	1	0	0	1	<1	<0.1
		8	0	12	2	0	14	4	0.2		1	16	4	0	21	6	0.2
		20	15	285	24	1	325	85	3.7		29	173	31	3	236	67	2.7
		48	0	33	6	3	42	11	0.5		13	68	11	4	96	27	1.1
		Total	15	330	32	4	381	100			43	258	46	7	354	100	
D	1900	Surf	0	0	0	0	0	0	0	M	0	0	0	0	0	0	0
		8	0	13	0	0	13	1	0.1		1	62	19	0	82	13	0.9
		20	22	864	18	0	904	96	10.2		24	444	60	2	530	83	6.0
		48	0	14	9	6	29	3	0.3		0	14	6	8	28	4	0.3
		Total	22	891	27	6	946	100			25	520	85	10	640	100	
All day tows:																	
		Surf	0	0	0	0	0	0	0		0	1	0	0	1	<1	<0.1
		8	2	64	4	0	70	2	0.2		2	266	119	0	387	15	0.9
		20	172	2,357	81	1	2,611	86	5.9		93	1,410	282	25	1,810	72	4.1
		48	7	221	110	32	370	12	0.8		20	232	56	27	335	13	0.8
		Total	181	2,642	195	33	3,051	100			115	1,909	457	52	2,533	100	
Night tows:																	
E	2200	Surf	10	922	342	30	1,304	54	14.7	N	4	795	215	24	1,038	53	11.7
		8	13	421	93	18	545	23	6.1		29	504	111	36	680	35	7.7
		20	61	411	53	15	540	22	6.1		16	169	17	3	205	11	2.3
		48	1	21	2	0	24	1	0.3		1	23	2	1	27	1	0.3
		Total	85	1,775	490	63	2,413	100			50	1,491	345	64	1,950	100	
F	0100	Surf	4	329	126	20	479	43	5.4	O	0	374	146	24	544	30	6.1
		8	10	268	29	2	309	27	3.5		0	886	62	18	966	54	10.9
		20	49	230	11	1	291	26	3.3		29	216	10	5	260	15	2.9
		48	3	34	3	0	40	4	0.5		1	22	0	0	23	1	0.3
		Total	66	861	169	23	1,119	100			30	1,498	218	47	1,793	100	
G	0400	Surf	4	274	33	4	315	25	3.5	P	5	551	126	0	682	47	7.7
		8	11	505	59	7	582	47	6.6		12	338	102	18	470	33	5.3
		20	46	244	7	5	302	25	3.4		12	227	0	0	239	17	2.7
		48	7	27	0	0	34	3	0.4		5	35	2	2	44	3	0.5
		Total	68	1,050	99	16	1,233	100			34	1,151	230	20	1,435	100	
All night tows:																	
		Surf	18	1,525	501	54	2,098	44	7.9		9	1,720	487	48	2,264	44	8.5
		8	34	1,194	181	27	1,436	30	5.4		41	1,728	275	72	2,116	41	7.9
		20	156	885	71	21	1,133	24	4.3		57	612	27	8	704	13	2.6
		48	11	82	5	0	98	2	0.4		7	80	4	3	94	2	0.4
		Total	219	3,686	758	102	4,765	100			114	4,140	793	131	5,178	100	
All tows:																	
		Surf	18	1,525	501	54	2,098	27	3.0		9	1,721	487	48	2,265	29	3.2
		8	36	1,258	185	27	1,506	19	2.1		43	1,994	394	72	2,503	32	3.5
		20	328	3,242	152	22	3,744	48	5.3		150	2,022	309	33	2,514	33	3.5
		48	18	303	115	32	468	6	0.7		27	312	60	30	429	6	0.6
		Total	400	6,328	953	135	7,816	100			229	6,049	1,250	183	7,711	100	

1900 to 0100 h on the first day; from 1600 to 2200 h on the second day; and from 1600 to 0100 h on the third day. The evening ascent toward the surface occurred during the time of peak feeding, but the incidence of feeding remained highest in larvae caught at 20 m before, during, and after the evening ascent (Figure 4). We concluded that essential prey organisms occur throughout the water column and that diel movements and feeding are not directly related.

DISCUSSION

When Sette (1943) studied the early life history of Atlantic mackerel, *Scomber scombrus,* in the Middle Atlantic Bight in1929, he made four tows,

TABLE 2.—Continued.

Stn	Hour of tow	Net depth (m)	Day 3 Size group (mm) <4	4-8	8-10	>10	Day 3 Total No.	%	No./m³	3-day total Size group (mm) <4	4-8	8-10	>10	3-day total No.	%	No./m³ (avg.)
Day tows:																
Z	0700	Surf	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		8	1	13	5	0	19	3	0.2	1	159	82	0	242	15	0.9
		20	11	271	218	71	571	93	6.4	37	774	328	86	1,225	79	4.6
		48	0	17	2	3	22	4	0.2	1	69	11	10	91	6	0.3
		Total	12	301	225	74	612	100		39	1,002	421	96	1,558	100	
R	1000	Surf	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		8	0	17	32	0	49	13	0.6	2	71	44	0	117	7	0.4
		20	6	151	123	15	295	79	3.3	115	913	153	16	1,197	74	4.5
		48	0	21	5	2	28	8	0.3	2	193	99	21	315	19	1.2
		Total	6	189	160	17	372	100		119	1,177	296	37	1,629	100	
S	1300	Surf	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		8	0	0	2	0	2	1	<0.1	0	27	11	0	38	3	0.1
		20	47	150	9	0	206	71	2.3	87	886	99	4	1,076	80	4.0
		48	3	42	24	12	81	28	0.9	14	142	55	24	235	17	0.9
		Total	50	192	35	12	289	100		101	1,055	165	28	1,349	100	
T	1600	Surf	0	0	0	0	0	0	0	0	1	0	0	1	<1	<0.1
		8	1	5	0	0	6	3	0.1	2	33	6	0	41	4	0.2
		20	25	106	3	0	134	53	1.5	69	564	58	4	695	71	2.6
		48	1	66	35	10	112	44	1.3	14	167	52	17	250	25	0.9
		Total	27	177	38	10	252	100		85	765	116	21	987	100	
U	1900	Surf	0	1	0	0	1	<1	<0.1	0	1	0	0	1	<1	<0.1
		8	0	30	7	0	37	6	0.4	1	105	26	0	132	6	0.5
		20	14	467	46	0	527	89	5.9	60	1,775	124	2	1,961	90	7.4
		48	0	11	6	10	27	5	0.3	0	39	21	24	84	4	0.3
		Total	14	509	59	10	592	100		61	1,920	171	26	2,178	100	
All day tows:																
		Surf	0	1	0	0	1	<1	<0.1	0	2	0	0	2	<1	<0.1
		8	2	65	46	0	113	5	0.3	6	395	169	0	570	7	0.4
		20	103	1,145	399	86	1,733	82	3.9	368	4,912	762	112	6,154	80	4.6
		48	4	157	72	37	270	13	0.6	31	610	238	96	975	13	0.7
		Total	109	1,368	517	123	2,117	100		405	5,919	1,169	208	7,701	100	
Night tows:																
W	2200	Surf	4	574	235	28	841	53	9.5	18	2,291	792	82	3,183	54	11.9
		8	8	374	206	28	616	39	6.9	50	1,299	410	82	1,841	31	6.9
		20	12	68	6	0	86	6	1.0	89	648	76	18	831	14	3.1
		48	0	23	3	2	28	2	0.3	2	67	7	3	79	1	0.3
		Total	24	1,039	450	58	1,571	100		159	4,305	1,285	185	5,934	100	
X	0100	Surf	5	197	43	0	245	10	2.8	9	900	315	44	1,268	23	4.8
		8	0	1,488	274	16	1,778	70	20.0	10	2,642	365	36	3,053	56	11.5
		20	32	412	3	0	447	17	5.0	110	858	24	6	998	18	3.7
		48	7	57	0	1	65	3	0.7	11	113	3	1	128	3	0.5
		Total	44	2,154	320	17	2,535	100		140	4,513	707	87	5,447	100	
Y	0400	Surf	0	55	36	4	95	6	1.1	9	880	195	8	1,092	26	4.1
		8	4	851	209	31	1,095	71	12.3	27	1,694	370	56	2,147	51	8.1
		20	24	257	10	0	291	19	3.3	82	728	17	5	832	20	3.1
		48	11	38	3	1	53	4	0.6	23	100	5	3	131	3	0.5
		Total	39	1,201	258	36	1,534	100		141	3,402	587	72	4,202	100	
All night tows:																
		Surf	9	826	314	32	1,181	21	4.4	36	4,071	1,302	134	5,543	36	6.9
		8	12	2,713	689	75	3,489	62	13.1	87	5,635	1,145	174	7,041	45	8.8
		20	68	737	19	0	824	14	3.1	281	2,234	117	29	2,661	17	3.3
		48	18	118	6	4	146	3	0.5	36	280	15	7	338	2	0.4
		Total	107	4,394	1,028	111	5,640	100		440	12,220	2,579	344	15,583	100	
All tows:																
		Surf	9	827	314	32	1,182	15	1.7	36	4,073	1,302	134	5,545	24	2.6
		8	14	2,778	735	75	3,602	46	5.1	93	6,030	1,314	174	7,611	33	3.6
		20	171	1,882	418	86	2,557	33	3.6	649	7,146	879	141	8,815	38	4.1
		48	22	275	78	41	416	6	0.6	67	890	253	103	1,313	5	0.6
		Total	216	5,762	1,545	234	7,757	100		845	18,139	3,748	552	23,284	100	

morning, noon, evening, and midnight, off Fire Island to investigate the vertical distribution of eggs and larvae. Royce et al. (1959) included a cursory presentation of data on yellowtail flounder larvae from Sette's series of discrete depth tows. Although Sette's nets were towed slower (1 kn vs. 5 kn) and the flounder larvae were smaller ($\bar{x}$ = 3.9 mm vs. $\bar{x}$ = 6.7 mm) than ours, the results of the two studies are similar in several aspects. For example, Royce et al. (1959) reported larvae at the surface at night, but not during daylight; the night catch was double the daytime catch; and the catch dropped off sharply in their deep net at night. Their larvae were most concentrated at a depth of 10 m on all four tows. Although this appears to differ from our results, we have shown that larvae <4 mm do not participate in the diel migrations but remain within a limited depth stratum. Thus

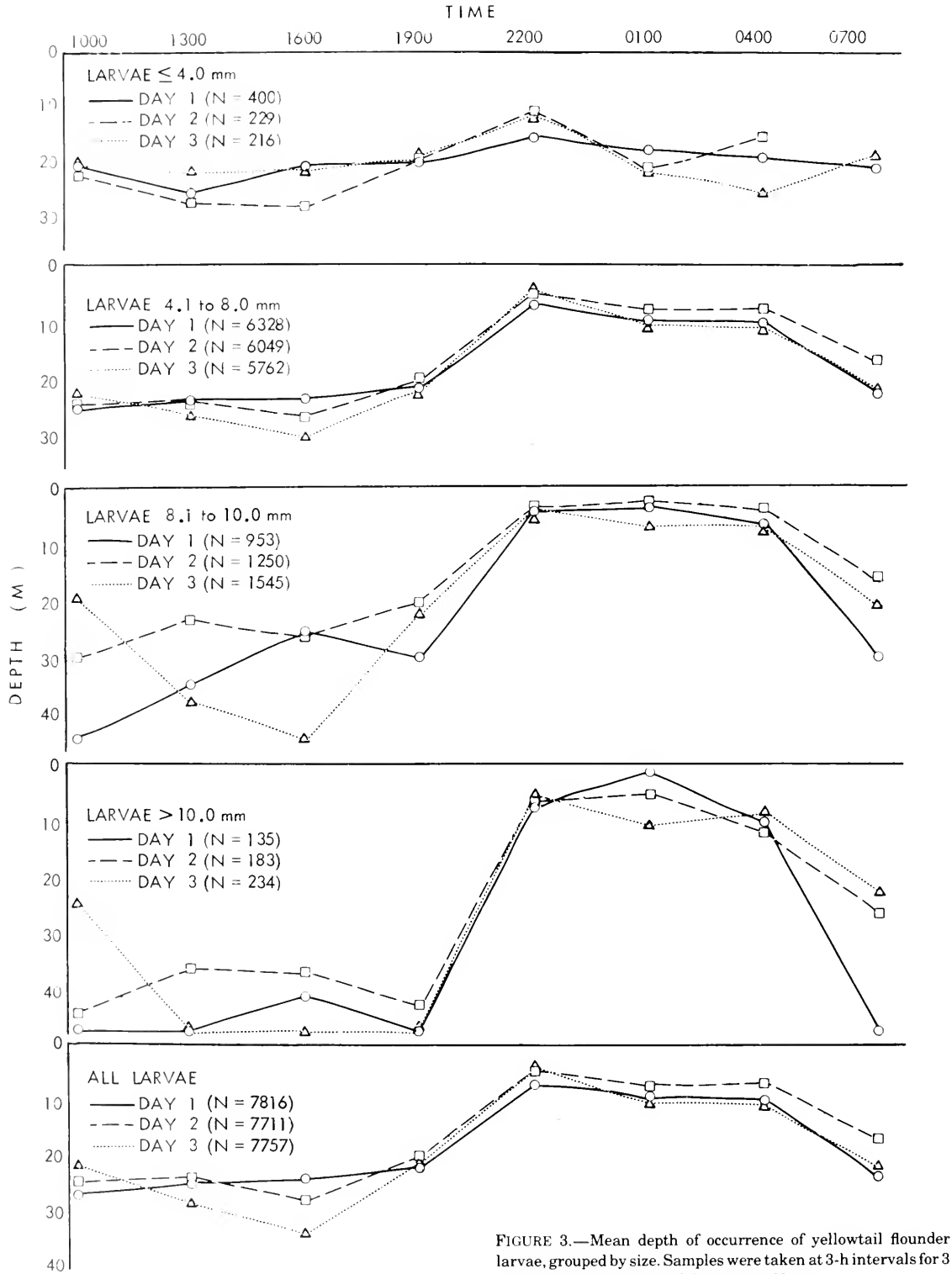

FIGURE 3.—Mean depth of occurrence of yellowtail flounder larvae, grouped by size. Samples were taken at 3-h intervals for 3 days. Water depth ranged from 63 to 68 m.

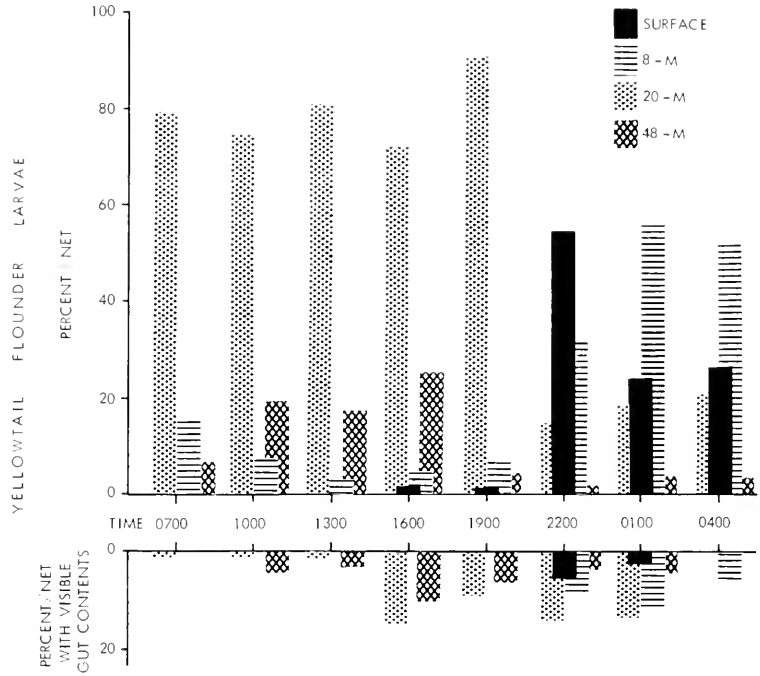

FIGURE 4.—Percent of yellowtail flounder larvae by depth and time (upper graph); and percent of larvae with visible gut contents by depth and time (lower graph). Figure represents averaged results from 3-day study.

the small larvae exhibited similar behavior in both studies. Although their larvae were concentrated at shallower depths than ours, in both cases the temperature was about 10°C where larvae <4 mm were most abundant. See Sette (1943) for temperature profile pertaining to data presented by Royce et al. (1959).

A *t*-test on our adjusted catch data from the 15 daylight tows and 9 night tows indicated that the catch at night was significantly greater than the daytime catch. Some of this difference might result from avoidance during daylight but, based on our fast towing speed, which would curtail avoidance, and results of gear performance tests by Bjørke et al. (1974) and Posgay et al. (see footnote 2), which showed the 20-cm bongo to be an effective sampler, we concluded that the greater catch at night was largely attributable to a change in the vertical distribution of larvae and our sampling depths. Comparisons of day:night catch ratios of daily catches and catches at 20 m support our conclusion. Whereas the day:night catch ratios of the adjusted catch (larvae per cubic meter) were 1:1.56, 1:2.04, and 1:2.66 on days 1 through 3, respecitvely, the reverse was true at 20 m, where the ratios were 2.30:1, 2.57:1, and 2.10:1. Night catches were greater than day catches because most larvae migrated towards the surface at night, where two nets fished. The resultant concentration of larvae in a confined depth stratum, and the "extra" net fishing within the stratum where larvae were concentrated, accounted for the significantly greater catch with less sampling effort at night. After descending during the early morning hours, larvae were largely subjected to capture at 20 m, where the daytime catch was more than twice as great as the catch at night. If avoidance were the principal factor in the day:night differences, we would expect larger catches at all depths at night.

Both Bridger (1958) and Wood (1971) found that the daytime distribution of herring, *Clupea harengus,* larvae depended on light conditions. Their larvae were nearer the surface on cloudy days than on sunny days. Although weather conditions changed from partly cloudy to sunny, followed by fog and rain, and sea conditions changed from moderate to calm as winds diminished, yellowtail flounder larvae showed little variation in their diel movements during our 3-day study. We caught only two larvae at the surface during daylight hours. On all 3 days larvae began to ascend after 1900 h and were at the surface in greatest numbers at 2200 h. During the early morning hours of darkness their numbers decreased at the surface but the young fish did not disappear from the surface until sometime between 0400 and 0700 h. Judging from our results and those of Royce et

al. (1959), we presume both the daily ascent and descent occurred near sunset and sunrise, respectively.

Ahlstrom (1959) studied the vertical movements of larvae of several fishes off the coast of California. He found no evidence that larvae moved through the thermocline. His collections showed that they migrated vertically but the movements were usually restricted to the upper mixed layer. In contrast, neither the salinity gradient at 10 to 20 m nor the temperature gradients beginning at 10 and 30 m had a noticeable effect on the vertical movements of yellowtail flounder larvae in our study. Our collections indicate that the small flounder that migrated between middepths and the surface routinely tolerated salinity differences of 1.5‰ and temperature changes of 5°C, and those that moved throughout the water column withstood changes of about 10°C. Such rapid changes in temperature seem deleterious but our survey collections indicated that larvae of most flatfishes spawned in the Middle Atlantic Bight are physiologically adapted to wide ranges in temperature. For example, in 1966, when yellowtail flounder spawned mostly at bottom temperatures between 4° and 9°C, we caught their larvae where the surface temperature was 5°C in April and 23°C in August (Smith et al. 1975).

The amplitude of the vertical migrations by yellowtail flounder larvae increased in proportion to their size. Similar behavior was reported for larval haddock, *Melanogrammus aeglefinus* (Miller et al. 1963), and larval *Clupea harengus* (Seliverstov 1974). Recently hatched yellowtail flounder remained most abundant beneath the shallow thermal gradient, whereas late-stage larvae exhibited extensive vertical migrations that included most or all of the water column. Larvae >10 mm probably spend some time on the bottom. Bigelow and Schroeder (1953) reported that young yellowtail flounder descend to the bottom when 14 mm long. Royce et al. (1959) concluded that they seek bottom when 12 to 19 mm long. Judging from this information and the advanced stage of development of some larvae we caught near the surface after dark, we concluded that the change from a pelagic to a demersal life is not abrupt. Larvae making the transition to a demersal life continue to migrate towards the surface at night. This nocturnal behavior might reflect a gradual dietary change from planktonic to benthic organisms. Although we are unsure of how long they continue the vertical migrations, the 20.7-mm SL specimen collected during our survey (see Smith et al. 1975) might represent the maximum size at which they ascend toward the surface.

In his review of the "critical period" concept, May (1974) pointed out that field studies of larval feeding have produced highly variable results. He cited several investigations that found the feeding incidence of clupeoid larvae very low, others that found it very high, and discussed theories that have been advanced to explain this variability. They include rapid digestion; nutrition from dissolved organics; low food requirements; daily feeding patterns; defecation upon capture and preservation; escapement by healthy, feeding larvae; and food availability. Our data on yellowtail flounder larvae support at least two of these theories, namely, a daily feeding pattern and rapid digestion. Both the highest and lowest incidence of feeding occurred at predictable times on all 3 days and, with the exception of five specimens, the guts of all larvae appeared to be empty within hours after the period of maximum feeding.

Several studies report that fish larvae feed most actively at high light intensities, but others differ. For example, Kjelson et al. (1975) found the digestive tract of young Atlantic menhaden, *Brevoortia tyrannus;* pinfish, *Lagodon rhomboides;* and spot, *Leiostomus xanthurus,* fullest at midday. Rudakova (1971) estimated that an average of 25% of the Atlantic herring, *Clupea harengus harengus,* larvae that he caught fed during the day, only 3.2% at night. Feeding studies by Blaxter (1965), Schumann (1965), and Braum (1967) support the above studies. On the other hand, Marak (1974) reported that young redfish, *Sebastes marinus,* fed during day or night and Blaxter (1969) found that larval sole, *Solea solea,* feed at night. Shelbourne (1953) reported that all postlarval plaice, *Pleuronectes platessa,* that he collected between 1400 and 2000 h had food in their guts. The percent of feeding larvae declined to between 70 and 80% in his samples collected from 2000 to 0200 h, then dropped sharply until daylight when it again increased to 100% for a short time.

Our results resemble Shelbourne's (1953), except that we caught fewer feeding larvae and we did not find an indication of feeding at sunrise. The near absence of feeding larvae during daylight morning hours suggests that something other than, or in addition to, light triggers feeding by yellowtail flounder larvae. It appeared to us that feeding intensity increased during afternoon and evening hours. Larvae that had food in their guts

at 2200 and 0100 h might have fed after dark or they might have stopped feeding after sunset. Further study is needed to determine whether yellowtail flounder larvae feed at night.

After analyzing 10 yr of drifter releases, Bumpus (1973) reported that surface currents in the Middle Atlantic Bight occasionally reach speeds of 15 mi/day (27 km/day), but they are usually less than 10 mi/day (18 km/day). He estimated bottom drift at 0.5±0.2 mi/day (0.9±0.4 km/day) and speculated that circulation near bottom was so random and sluggish that it was unrealistic to derive drift rates of bottom water from his data, except from nearshore releases, which stranded within a reasonable time frame. Howe (1962) concluded that coastal circulation between Cape Cod and New York was largely attributable to short-term wind effects and that waters inside the 90-m isobath were comparatively stagnant during the first half of the year. The sluggish performance of our drogue supports Howe's results and indicates that the velocity of middepth drift at the time and location of our study was similar to Bumpus' description of bottom circulation.

Returns from drift bottle releases indicate that surface water generally moves westward off Long Island then southward along the Middle Atlantic States (Bumpus and Lauzier 1965). However, both Norcross and Stanley (1967) and Bumpus (1969) found evidence of surface current reversals in the Middle Atlantic Bight during the summer, and Doebler (1966) showed that the direction of surface water transport off Delaware responded rapidly to changes in wind direction. On the basis of these reports, we assume that the brisk south to southwest wind during the first 48 h of our study propelled surface water towards southern New England. Although yellowtail flounder larvae were not at the surface during the day, 44% of our night catches were taken at the surface during the first two nights. During this time wind probably influenced their horizontal displacement. By passing the 15 h of daylight at subsurface depths, it appears from the net drift of our drogue that the larvae were transported in the opposite direction to that at night.

Assuming that our drogue's erratic and sluggish drift is representative of middepth circulation off Long Island in the spring, when spawning by yellowtail flounder peaks, and that effects of spring and summer winds on circulation are usually limited to a few days at a time, we conclude that wind driven currents in the study area do not play a major role in dispersing the larvae. Our conclusion is supported by Royce et al. (1959). Similarities in patterns of distribution between eggs and larvae led them to conclude that larvae were demersal before much horizontal drift occurred. It seems worth noting here that the smallest larvae, those least able to swim with directed movements, did not ascend to the surface at night. They remained below the shallow thermal gradient, where they were unaffected by wind-driven circulation.

Whether or not our interpretation of the effects of currents on the distribution of yellowtail flounder larvae is correct, it is clear to us that researchers must investigate the diel movements of larvae they are studying before hypothesizing on how circulation affects the distribution and survival of young fishes. It is common practice to overlook or ignore larval behavior and relate the transport of larvae from both day and night collections by obliquely towed nets to surface circulation. In many cases, this oversight produces an exaggerated estimate of the distance larvae are transported and, perhaps, an erroneous estimate of the direction of transport.

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BIOECONOMIC CONTRIBUTION OF COLUMBIA RIVER HATCHERY FALL CHINOOK SALMON, 1961 THROUGH 1964 BROODS, TO THE PACIFIC SALMON FISHERIES

ROY J. WAHLE AND ROBERT R. VREELAND[1]

ABSTRACT

This experiment was designed to estimate the contribution to sport and commercial fisheries of the 1961 through 1964 broods of fall chinook salmon, *Oncorhynchus tshawytscha*, from 13 rearing facilities on the Columbia River. These facilities reared 90% of the Columbia River hatchery fall chinook salmon during the four brood years. Marks common to all facilities were applied to 21.3 million of the 213 million 1961-64 brood fish released. Special marks were applied to 9.6 million fish at 11 of the study hatcheries. Sampling for the marks took place from 1963 through 1969.

During the 7 yr of sampling, 65,620 chinook salmon with common and 22,090 fish with special marks were estimated to have been caught in marine commercial and sport fisheries from Pelican, Alaska, to Avila Beach, Calif., and Columbia River fisheries. The potential contribution for the four broods from the 13 study facilities, after adjustment for the effects of marking, was 1,433,300 fish. The value of the contribution was estimated at $12,027,000. Costs applicable to rearing were $2,859,700, yielding an average benefit to cost ratio of 4.2 to 1. Benefit to cost ratios at the 11 special mark hatcheries ranged from 0.3 to 1 to 17.1 to 1.

The Columbia River Development Program (subsequently referred to as "Program"), initiated in 1949, was created to counteract the severe loss of salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, resulting from the expansion of water-use projects in the Columbia River system. The Program is a cooperative effort of fish management agencies of the States of Oregon, Washington, and Idaho and the Federal Government and is administered by the Columbia Fisheries Program Office, National Marine Fisheries Service, NOAA, Portland, Oreg. The Program's role has included two major functions: 1) the protection and improvement of stream environment which has included improvement of natural habitat, such as clearing obstructions from nearly 2,000 mi of tributary streams, building 87 fishways past natural barriers, and installation of 570 screens in diversion ditches and canals; and 2) the production of fish in hatcheries which has been accomplished by the construction or modernization of 21 salmon and steelhead hatcheries on the lower Columbia River and tributaries. A supplementary function of the Program is funding operational improvement studies to complement the hatchery system. Major achievements have been: 1) improved marking techniques through development of the implanted coded wire fish tag (Bergman et al. 1968); 2) increased natural production through rehabilitation of chinook salmon runs in the Clearwater River system in Idaho and the Willamette River system in Oregon; 3) determination of the physiological factors controlling downstream salmonid smolt migration through understanding the development of osmotic and ionic regulation in coho salmon (Conte et al. 1966), chinook salmon (Wagner et al. 1969), and steelhead trout (Conte and Wagner 1965), thus improving hatchery release timing; 4) reduced natural competition and predation through the development of Squaxin,[2] a selective toxin to squawfish (MacPhee and Ruelle 1969); and 5) improved fish diets through development of the Oregon Moist Pellet (Hublou 1963).

There are two major reasons for concentrating on hatchery produced salmon and steelhead trout: their life histories allow successful hatchery propagation and these species are historically and economically important to the United States. Over the past three decades Pacific salmon have ranked first or second in landed value of commercial

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

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finfishes to U.S. fishermen. The net economic value of salmon sport fishing in the United States was $77.7 million in 1970 (Wahle et al. 1974).

Initially, Program hatcheries were constructed to emphasize rearing of fall chinook salmon rather than coho and spring chinook salmon and steelhead trout because of a serious decline of this run in the early 1950's (Van Hyning 1973).

Releases of migrant size fall chinook salmon have ranged from 10 million fish from 6 hatcheries in 1949 to 94 million fish from 17 hatcheries in 1973. Prior to the study reported by Worlund et al. (1969), little was known about the contribution of these releases to the commercial and sport fisheries. Some marking experiments had demonstrated that hatchery releases contribute to fisheries, but because such experiments were limited and designed for other purposes, the contribution had not been estimated.

Although reports were written for each of the four broods of fall chinook salmon (Worlund et al. 1969; Rose and Arp[3]; Arp et al.[4]; Wahle et al.[5]), brood years were not compared and individual hatchery contributions, values, and benefits were not evaluated or compared. No new studies of this scale on the Columbia River have been initiated to supersede the 1962 through 1969 data. In addition, the contributions, values, and benefits in the individual brood year reports are not comparable with those presented for Columbia River hatchery coho salmon (Wahle et al. 1974). Therefore, we compiled this report to supplement, summarize, and, in some cases, replace previously reported Columbia River hatchery fall chinook salmon contribution and value data.

The marking study discussed in this paper, initiated in 1962 by the Columbia Fisheries Program Office, was designed to estimate the contribution of Columbia River hatchery-reared fall chinook salmon to the fisheries. The effort was brought about by the Bureau of the Budget (now the Office of Management and Budget) which had declared a moratorium on hatchery construction until there was proof that further expansion would be economically justified.

The experiment was confined to 12 hatcheries and 1 rearing pond that during the marking phase of the study propagated nearly 90% of all fall chinook salmon artificially reared in the Columbia River system. Locations of the participating and nonparticipating hatcheries rearing fall chinook salmon during the study period are shown in Figure 1. The marking of four brood years, 1961 through 1964, began in 1962 and data collection was completed in 1969.

This report contains: 1) the experimental design; 2) a description of the field operations; 3) estimation of 10 individual hatchery contributions, values to fisheries, benefit to cost ratios for study facilities, and comparisons between hatcheries; 4) the contributions, values, and benefit to cost ratios for each brood year marked for all participating hatcheries combined, with a comparison of brood years; and 5) the contribution and value to the Pacific Coast fisheries of fall chinook salmon from all Columbia River hatcheries.

EXPERIMENTAL DESIGN

The experimental procedures for this study were the same for the four brood years. The design of the study is described by Worlund et al. (1969), and will be reviewed here. In general, 10% of the fall chinook salmon production from the participating hatcheries was marked by clipping fins and maxillary bones. The commercial and sport fisheries along the Pacific Coast were sampled for these marks. Individual and collective hatchery contributions can be estimated from: 1) proportion of fish marked, 2) number of marks actually recovered, 3) fractions of the total catches sampled for marks by time and area in each fishery, and 4) information on any bias associated with application or detection of marks. The execution of this entire study required the cooperation of personnel from the following agencies: the Alaska Department of Fish and Game, the Fisheries Research Board of Canada (now the Department of Environment), the Washington Department of Fisheries, the Fish Commission of Oregon and the Oregon Game Commission (now the Oregon Department of Fish and Wildlife), the California Department of Fish and Game, the Bureau of Commercial Fisheries (now the National Marine

[3]Joe H. Rose, and Arthur H. Arp. 1970. Contribution of Columbia River hatcheries to harvest of 1962 brood fall chinook salmon (*Oncorhynchus tshawytscha*). Unpubl. manuscr., 27 p. U.S. Fish Wildl. Serv., Bur. Commer. Fish., Columbia Fish. Program Off., Portland, Oreg.

[4]Arthur H. Arp. Joe H. Rose, and Steven K. Olhausen. 1970. Contribution of Columbia River hatcheries to harvest of 1963 brood fall chinook salmon (*Oncorhynchus tshawytscha*). Unpubl. manuscr., 33 p. Natl. Mar. Fish. Serv., Columbia Fish. Program Off., Portland, Oreg., Econ. Feasibility Rep.

[5]Roy J. Wahle, Arthur H. Arp, and Steven K. Olhausen. 1972. Contribution of Columbia River hatcheries to harvest of 1964 brood fall chinook salmon (*Oncorhynchus tshawytscha*). Unpubl. manuscr., 31 p. Natl. Mar. Fish. Serv., Columbia Fish. Program Off., Portland, Oreg., Econ. Feasibility Rep.

Fisheries Service), and the U.S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife.

Allocation of Marks

The experiment was limited to 13 rearing facilities on the Columbia River. The hatchery locations ranged from Big Creek Hatchery, the lowermost station, 40 km (25 mi) above the Columbia River mouth, to Klickitat Hatchery, the uppermost station, 290 km (180 mi) above the Columbia River mouth (Figure 1).

Approximately 10% of the production at each of the 13 facilities was marked with a common mark

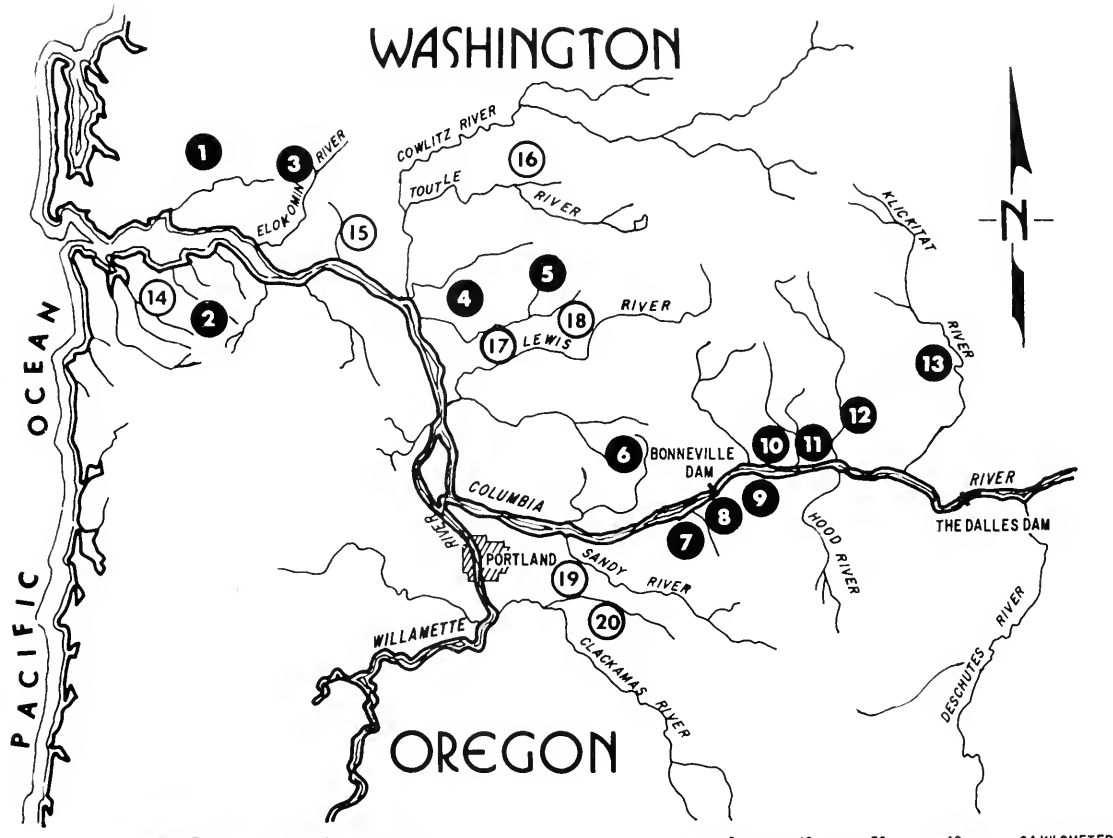

FIGURE 1.—Locations of participating and nonparticipating Columbia River hatcheries rearing fall chinook salmon, 1961-64 broods.

(Table 1). This mark consisted of clipping the adipose fin (Ad) and a right or left maxillary (RM or LM). The maxillary clip was alternated from one brood year to the next. In addition, a portion (as discussed later) of the production at 11 of the study hatcheries was marked with special marks. A portion of four broods at Spring Creek National Fish Hatchery and Kalama River hatcheries (in this study, Kalama Falls and Lower Kalama Hatcheries were treated as one facility) were marked with the following special mark: adipose, a ventral, and a maxillary clip. Spring Creek was assigned the adipose, left ventral (LV), and left or right maxillary clip. The maxillary clip was alternated among brood years. The 1961 brood was marked Ad-LV-RM, the 1962 brood was marked Ad-LV-LM, and so on. Kalama River hatcheries were assigned the adipose, right ventral (RV), and left or right maxillary clip. Again, the maxillary clip was alternated among brood years. Combinations of a single ventral and maxillary were alternated among eight other hatcheries: Elokomin, OxBow, Grays River, Cascade, Klickitat, Big Creek, Bonneville, and Little White Salmon. Two different hatcheries were marked with this combination for each brood year.

TABLE 1.—Releases of marked fall chinook salmon from Columbia River study hatcheries, 1961-64 broods.

Brood	Hatchery	Mark[1]	Number marked	Percent production marked
1961	All hatcheries	Ad-RM	5,446,439	10.15
	Spring Creek	Ad-LV-RM	1,133,019	10.37
	Kalama	Ad-RV-RM	475,964	9.70
	Elokomin	LV-RM	480,533	30.51
	OxBow	RV-RM	450,446	9.90
1962	All hatcheries	Ad-LM	5,249,079	10.00
	Spring Creek	Ad-LV-LM	866,892	10.31
	Kalama	Ad-RV-LM	437,669	9.52
	Grays River	LV-LM	241,494	17.76
	Cascade	RV-LM	541,158	12.83
1963	All hatcheries	Ad-RM	5,986,464	9.96
	Spring Creek	Ad-LV-RM	751,243	10.06
	Kalama	Ad-RV-RM	456,158	9.34
	Klickitat	LV-RM	521,610	18.06
	Big Creek	RV-RM	579,967	29.21
1964	All hatcheries	Ad-LM	4,638,237	9.92
	Spring Creek	Ad-LV-LM	600,953	9.17
	Kalama	Ad-RV-LM	319,412	9.14
	Bonneville	LV-LM	957,110	9.68
	Little White Salmon	RV-LM	797,345	9.53

[1]Ad: Adipose; LV: Left ventral; RV: Right ventral; LM: Left maxillary; RM: Right maxillary.

Sources of Variation and Error

Two major sources of variation in contributions to fisheries are differences among brood years and differences among hatcheries. To evaluate the differences among broods, four broods were marked. The variations among hatcheries were evaluated by special marking at four hatcheries for each brood year.

One possible source of error in estimating contributions is the combination of differential relative survival and differential maturation time for marked and unmarked fish. If the difference in marked and unmarked ratios at release and return were due primarily to delayed maturation caused by marking, then marked fish may have been subjected to more intense fishing pressure due to a longer time in the ocean. This could mean the ratio of marked to unmarked fish in the fisheries would be greater than the ratio at release from the hatcheries. If this were true, the potential contributions would be overestimated in this report. However, since we are making the best estimate of contribution and benefit for the hatcheries, we are assuming all differences in marked to unmarked ratios at release and return are due to differential survival between marked and unmarked fish. This point is discussed in detail under assumption 4.

Straying of wild fish into the hatcheries, thus diluting the marked to unmarked ratios at return, is another source of variation and/or error. This dilution would reduce the relative survival rates for marked fish. To minimize this effect of variation and/or error, average relative survival figures for common and special marked fish were calculated and used in the contribution computations.

Estimating Procedures

A formal account of the estimating procedures is presented in the report by Worlund et al. (1969). Simple numerical examples will be used to explain the procedure in this report. Estimating the potential contributions and values of hatchery fall chinook salmon required four steps. First, the number of marked and unmarked hatchery releases had to be estimated. Second, the estimated catch of marked fish was calculated. Third, the total contribution of hatchery fish was estimated. Fourth, dollar values were applied to the contribution estimates.

Hatchery Releases

The numbers of marked and unmarked fish in hatchery releases were estimated by sampling the hatchery population with a 10-part sampler (see Marking and Release Procedures). This device

was precalibrated from a number of trials with known numbers of fish to find the average percentage retained by a single closed pocket. The following example illustrates the fish enumeration procedure for a pond of fall chinook salmon. Suppose a precalibrated pocket is found to remove a 10.1% sample. Also, suppose after passing all the fish in a pond through the sampler, the number of fish retained by the closed pocket is found to be 20,200. The total number of fish in that pond is then estimated as 20,200/0.101 = 200,000. Suppose further that of the 20,200 fish retained in the pocket, 2,020 fish are found to be marked. Then 2,020/20,200 = 10% of the estimated 200,000 fish in the pond, or 20,000 are estimated to be marked and 180,000 unmarked. The total release, numbers marked (common and special) and unmarked, were estimated for a hatchery by summing data from all ponds.

Catch of Marked Fish

To estimate the catch of marked fish in a given area and fishery, the following values were needed by time period: total catch; number of fish examined for marks; number of marked fish by species, mark type, and age; and the proportion of each age-group in the total catch. The sampling seasons were stratified into relatively small time units (usually 2-wk periods). The estimated catches of a particular mark were summed over the entire fishing season for a given area and fishery. For example, during the period from 26 June through 9 July 1966 in the Ilwaco sport fishery, 1,193 chinook salmon from a total catch of 5,664 were examined for marks, for a 21.1% sample. Samplers found one Ad-LM marked 1964-brood (2-yr-old) fall chinook salmon during this period. Then the estimated catch of 1964-brood Ad-LM marked fall chinook salmon during this period was 1/0.2106 = 5. Catches of 1964-brood Ad-LM marked chinook salmon for the Ilwaco sport fishery in 1966 were summed for 13 time periods. This resulted in an estimated catch of 196 Ad-LM marked fish.

This procedure was carried out for each port sampled and each mark found. Catch data for each time-location stratum were provided by management agencies. Commercial catches were estimated from total landing weights and average fish size data or from total numbers of salmon landed and species composition estimates. Sport catches were estimated from measures of total effort and catch-per-unit-effort or from salmon punch cards and independent sampling. All catch and sampling information was transferred to computer cards and estimates were calculated by computer. Unpublished reports of catch and mark data were produced for 1963 through 1969 by the Seattle Biological Laboratory, Bureau of Commercial Fisheries (now the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA).

Contribution of Hatchery Fish

Maxillary regeneration occurred during the ocean lives of some of the common and special marked chinook salmon, resulting in partial marks (see Assumptions). For example, a 1961-brood Kalama Ad-RV-RM mark could have regenerated to an Ad-RV mark, or a 1962-brood Ad-LM common mark could have regenerated to an Ad-only mark. Partial marks were a result of this regeneration and/or an occurrence of naturally marked fish. If partial marks due to regeneration were not claimed as part of the marked hatchery fish total, the hatchery contribution would be underestimated considerably. Therefore, we examined the ocean catches of chinook salmon with partial marks to determine the number that could be claimed as hatchery fish.

A comparison of maxillary regeneration rates of marked fish held at Bowman Bay (Worlund et al. 1969) and the occurrence of Ad-SV (adipose-single ventral) and Ad-only partial marks in the fisheries (Table 2), led us to believe Ad-LV, Ad-RV, and Ad-only marks occurred because of maxillary re-

TABLE 2.—Percent partial mark occurrence in the ocean and Columbia River fisheries and in hatchery returns, 1961-64 broods.

Region	Brood	Partial marks[1]		
		Ad-SV[2]	Ad	SV
Ocean fisheries	1961	15.8	14.6	74.9
	1962	18.8	23.5	72.7
	1963	8.0	9.1	36.4
	1964	12.8	15.2	39.7
Columbia River fisheries	1961	10.3	7.8	51.0
	1962	17.4	5.0	57.4
	1963	9.5	6.0	7.0
	1964	8.0	7.2	28.3
Hatchery returns	1961	10.9	16.1	27.7
	1962	19.8	22.0	20.0
	1963	8.3	8.6	2.0
	1964	11.2	17.2	12.5

[1]Figures are ratios, averaged for all years by brood, of estimated numbers of partial marks to estimated sum of partial marks and corresponding complete marks expressed in percent.
[2]SV signifies "single ventral." Marks of same general type are combined

generation. This belief is also supported by the absence of Ad-LV and Ad-RV marks in the 1965-brood catches of chinook salmon (Bureau of Commercial Fisheries[6, 7, 8]; Fish Commission of Oregon[9]). The Ad-V marks were not assigned to the 1965-brood fish. Thus, we have claimed all Ad-RV, Ad-LV, and Ad-only marked chinook salmon as hatchery fish.

However, the percentage occurrence of SV marks in the fisheries was much higher than 1) the maxillary regeneration rate, 2) the occurrence of Ad-SV marks in the fisheries, and 3) the occurrence of SV marks in hatchery returns. Thus, we concluded SV marks occurred because of maxillary regeneration and natural marks.

Two steps were required to determine the number of SV marked fish we would claim as part of the hatchery production. First, we assumed the maxillary regeneration rate for all special marked hatcheries was the same. The partial mark percentages for Kalama River and Spring Creek combined were calculated for each fishery, year, and brood. For example, in the 1964 Washington commercial fisheries the estimated catch of 1961-brood Ad-LV-RM and Ad-RV-RM full marked fish was 1,001 and Ad-LV and Ad-RV partial marked fish was 232. The partial mark percentage for this year, fishery, and brood was then 232/1,001 = 23%.

Second, full mark recoveries from other special mark hatcheries (Elokomin, OxBow, Grays River, Cascade, Klickitat, Big Creek, Bonneville, and Little White) for the corresponding brood, year of recovery, and fishery were multiplied by the Kalama-Spring Creek percentages. For example, the estimated full mark recoveries of Elokomin and OxBow 1961-brood chinook salmon in the 1964 Washington commercial fisheries were 48 and 58 fish respectively. The SV marked fish claimed as part of Elokomin and OxBow hatcheries' production were then $48 \times 0.23 = 11$ and $58 \times 0.23 = 13$ respectively. In cases where the calculated claimed partial marks were greater than the partial marks actually recovered, all partial marked fish were claimed. No SV marked fish were claimed for the southeastern Alaska or California fisheries because few Columbia River hatchery special marked fish were captured in these fisheries.

The claimed partial marked fish estimates by year and fishery were summed for each special mark hatchery. The sums are the number of partial marked fish we claimed as part of the special mark hatcheries' catch (Table 3).

Loss of maxillaries due to hooking occurred during the ocean lives of the marked fall chinook salmon (author's pers. obs.), resulting in the possible misidentification of marks. In some cases a marked chinook salmon was assigned to a certain brood year from scale analysis, but the fish had the wrong maxillary mark for that brood. For example, 1961-brood Ad-LM marked chinook salmon, 1962-brood Ad-LV-RM marked fish, 1963-brood LV-RM marked chinook salmon, and so on (see Table 1 for correct marks for each brood) were reported to have been caught in the fisheries. In some cases, double maxillary marks (1961-brood Ad-RM-LM, 1963-brood Ad-LV-RM-LM, etc.) were reported to have been caught.

Duplication of marks or use of marks with the opposite maxillary for the same brood year were prevented by the Pacific Marine Fisheries Com-

TABLE 3.—Estimated catches of 1961- to 1964-brood fall chinook salmon from Columbia River study hatcheries with full marks, misidentified marks, partial marks, and partial marks claimed as study hatchery fish by brood and hatchery.

Brood	Hatchery	Full marks	Misidentified marks[1]	Partial marks	Partial marks claimed	Total estimated marks
1961	All study	18,906	621	2,710	2,710	22,237
	Spring Creek	3,553	115	732	732	4,400
	Kalama	1,955	34	186	186	2,175
	Elokomin	174	18	533	43	235
	OxBow	266	19	594	51	336
1962	All study	6,008	512	1,366	1,366	7,886
	Spring Creek	769	26	172	172	967
	Kalama	498	48	113	113	659
	Grays River	177	8	373	30	215
	Cascade	140	21	418	30	191
1963	All study	19,856	489	1,838	1,838	22,183
	Spring Creek	2,210	48	149	149	2,407
	Kalama	1,053	60	144	144	1,257
	Klickitat	1,048	702	396	108	1,858
	Big Creek	772	71	479	71	914
1964	All study	11,085	489	1,740	1,740	13,314
	Spring Creek	3,798	99	509	509	4,406
	Kalama	849	54	102	102	1,005
	Bonneville	649	43	210	70	762
	Little White	274	6	392	23	303

[1] Double maxillary clips or the opposite maxillary for a particular brood year.

[6] Bureau of Commercial Fisheries. 1969. Data report: Columbia River fall chinook salmon hatchery contribution study: 1967 sampling season. Unpubl. manuscr., 519 p. U.S. Fish Wildl. Serv., Bur. Commer. Fish., Seattle Biol. Lab.

[7] Bureau of Commercial Fisheries. 1970. Data report: Columbia River fall chinook salmon hatchery contribution study: 1968 sampling season. Unpubl. manuscr., 437 p. U.S. Fish Wildl. Serv., Bur. Commer. Fish., Seattle Biol. Lab.

[8] National Marine Fisheries Service. 1971. Data Report: Columbia River fall chinook salmon hatchery contribution study: 1969 sampling season. Unpubl. manuscr., 283 p. Natl. Mar. Fish. Serv., Seattle Biol. Lab.

[9] Fish Commission of Oregon. 1972. 1970 fin-mark sampling and recovery report for salmon and steelhead from various Pacific coast fisheries. Unpubl. manuscr., 102 p. Fish Comm. Oreg., Biom. Sect., Clackamas.

mission. We are assuming aging was correct (see Assumptions). Therefore, we have assumed marked fall chinook salmon with a double maxillary or the wrong maxillary for a particular brood were misidentified. Thus we claimed these marked fish as part of the Columbia River hatchery marked fall chinook salmon catch (Table 3).

Therefore, estimated catches of Columbia River hatchery marked fall chinook salmon (Tables 3, 8-14) include full, misidentified, and claimed partial marked fish.

Before estimating the contribution of hatchery fall chinook salmon if no marking had taken place (hereafter referred to as potential contribution), the survivals of common marked fish had to be calculated. Three methods were used to estimate the common mark relative survival and a median relative survival was calculated from the three answers.

METHOD 1.—All 13 study facilities were combined and four sums—marked releases, unmarked releases, marked returns, and unmarked returns—were obtained for each brood year. The marked to unmarked ratio at return was then divided by the marked to unmarked ratio at release. The formula is:

$$\frac{\frac{\text{Marked returns}}{\text{Unmarked returns}}}{\frac{\text{Marked releases}}{\text{Unmarked releases}}} = \text{Relative survival.}$$

METHOD 2.—If wild fish strayed into the study hatcheries, diluting the marked to unmarked ratios at return, method 1 would underestimate relative survival. Thus to allow for straying, in method 2 we have calculated relative survivals using releases and returns from four selected hatcheries, Cascade, OxBow, Little White Salmon, and Spring Creek, on streams with no natural runs of fall chinook salmon. Relative survivals were estimated for each brood in the same manner as described in method 1.

METHOD 3.—Even for the four selected hatcheries, straying of wild fish into hatcheries is a possibility, resulting in an underestimated relative survival. To account for this possibility, a method was devised to estimate the number of wild fish straying into the four selected hatcheries. This was done in four steps. First, since the selected hatcheries are between Bonneville and The Dalles Dams, an estimate of the maximum number of fall chinook salmon spawning between the dams was obtained by subtracting both the Indian and sport fall chinook salmon catches between Bonneville and The Dalles Dams as well as The Dalles Dam fall chinook salmon count from the Bonneville Dam fall chinook salmon count. Second, the maximum number of fish spawning at sites other than the selected hatcheries was obtained by subtracting the four hatcheries returns from the total spawners between the dams. Third, the age of fish spawning at sites other than the selected hatcheries was approximated by applying age data from Columbia River gillnet fall chinook salmon catches. Fourth, straying factors (from observed straying of fish marked at Spring Creek Hatchery) were applied by brood and age to the wild spawners to obtain the estimate of wild fish straying into the selected hatcheries. These estimates are maximum since we cannot account for mortalities, uncounted fish passing through navigation locks, double counting of fish that fall back over dam spillways and again ascend the fish ladders, or fish straying from the four hatcheries. Also, we assumed wild fish had the same straying pattern as the hatchery fish in this study, i.e., they strayed to sites near their area of origin.

Once the brood estimate of the number of wild fish entering the hatcheries was obtained, it was subtracted from the appropriate unmarked returns. The resulting unmarked hatchery return quantity for each brood was then used in the formula described in method 1 to calculate the third estimated common mark relative survival.

Examples of the calculations used to obtain the three values for the common mark relative survivals are presented by Worlund et al. (1969). The median common mark relative survivals for the 1961-64 broods of Columbia River study hatchery fall chinook salmon are:

Brood	*Common mark relative survival*
1961	0.608
1962	0.477
1963	0.372
1964	0.448

Special mark relative survivals also had to be calculated to estimate contributions of special marked hatcheries. Calculating special mark relative survivals for each hatchery was impossible because seven hatcheries (Elokomin, OxBow,

Grays River, Cascade, Klickitat, Bonneville, and Little White) had too few special mark returns to obtain reliable estimates of marked to unmarked ratios at return. Thus returns to only three hatcheries (Spring Creek, Kalama, and Big Creek), having sufficient special mark returns, were used to calculate average special mark relative survivals for each brood. However, if special marked fish from the other seven hatcheries had lower relative survivals than the average, the contributions of these hatcheries would be underestimated using this method.

Relative survivals of special marks to common marks were first calculated using the formula:

$$\frac{\text{Special mark return/Common mark return}}{\text{Special mark release/Common mark release}}.$$

The relative survivals are:

Brood	*Spring Creek*	*Kalama River*	*Big Creek*
1961	0.526	0.800	—
1962	0.617	0.472	—
1963	0.535	0.498	0.797
1964	0.535	0.731	—

From these values we concluded that special marked fish survived between 50 and 80% as well as common marked fish. Multiplying the common mark relative survivals by 50 and 80% for each brood year yielded the following average special mark relative survivals:

Brood	*Survival*
1961	0.395
1962	0.310
1963	0.242
1964	0.291

The next step was to determine the mark proportions at release for common and special marks for each brood year. Special marks were excluded from the calculation of the common mark proportions. This was done for two reasons: special marked fish had a lower relative survival than the common or unmarked fish, and the special marks could be identified in the fisheries and related back to specific hatcheries. The common marked fish had to be treated as unmarked fish in calculating the special mark proportions at release because common mark catches could not be related to specific hatcheries. These mark porportions at release are presented in Table 4.

TABLE 4.—Mark percentages at release for common and special marked fall chinook salmon by brood year and hatchery.

Mark type and hatchery	Percent of brood marked			
	1961	1962	1963	1964
Common marks[1]				
All hatcheries	10.7	10.4	10.4	10.5
Special marks[2]				
Spring Creek[3]	7.8	7.3	7.6	7.0
Kalama River	9.7	9.5	9.3	9.1
Elokomin	30.5	—	—	—
OxBow	9.9	—	—	—
Grays River	—	17.8	—	—
Cascade	—	12.8	—	—
Klickitat	—	—	18.1	—
Big Creek	—	—	29.2	—
Bonneville	—	—	—	9.7
Little White Salmon	—	—	—	9.5

[1]Special marks not included.
[2]Common marks included with unmarked releases.
[3]Includes Big White Salmon pond releases.

The potential contributions of the hatchery fall chinook salmon were calculated by dividing the estimated catch of marks by the marked fish relative survival times the mark proportion at release. The formula for calculating the potential contributions of Spring Creek, Kalama River, and other special mark hatcheries is:

$$\frac{\text{Estimated catch of spec. marks}}{(\text{Spec. mark relative survival})(\text{Spec. mark propor. at rel.})}.$$

The potential contribution of all study facilities was calculated with the formula:

$$\frac{\text{Estimated catch of common marks}}{(\text{Common mark relative survival})(\text{Common mark propor. at rel.})}$$

+ Potential catch of spec. marks.

The potential catch of special marks is an estimate of the special marks that would have been caught if marking had not caused differential mortality. The formula used to calculate this potential catch is:

$$\frac{\text{Estimated catch of special marks}}{\text{Special mark relative survival}}.$$

Value of Hatchery Contribution

With estimates of the potential contribution of Columbia River hatchery fall chinook salmon, the potential value of the catches could be calculated from average weight and unit price data. The average weights for the commercially caught fish were obtained from common marked fish. Total weights of hatchery fish caught in the commercial fisheries are underestimated with this method be-

cause marked fish are smaller than unmarked fish (Cleaver 1969). Weights for the ocean troll fisheries are dressed weights and those for Columbia River net fisheries are round weights. Ex-vessel market prices have been used to represent estimated net values for commercially caught fish. The ex-vessel prices were obtained from Washington Department of Fisheries records for the appropriate years and age of fish. (D. Ward, Washington Department of Fisheries, pers. commun.) Washington troll prices were used for other commercial fisheries on the Pacific Coast.

The net value for salmon and steelhead sport fishing is estimated to be $20/day of fishing. This value results from reconciling the existing research that is closely related to estimated net economic values of Columbia River sport caught salmon. The maximum potential benefits from sport fishing at a single market price is predicted at $20/fishing day (Brown et al.[10]). The salmon catch per angler trip data were obtained from Washington, Oregon, and California publications (Campbell and Locke 1964, 1965, 1966, 1967, 1968, 1969; Nye and Ward undated a, b; Greenhood and Mackett 1967; Haw et al. 1967; Heimann and Frey 1968a, b; Heimann and Carlisle 1970; Pinkas 1970). An estimate of 1.09 salmon/angler trip was obtained by averaging data for the three States over the appropriate years. The $20/angler trip was divided by 1.09 salmon/angler trip to yield a value of $18.35/salmon. This value was used in the ocean sport and Columbia River sport fisheries for all broods and years of capture.

Assumptions

Six assumptions are required in our method for estimating contributions of hatchery fall chinook salmon to the fisheries. Three basic assumptions are: 1) a marked fish is identifiable as a marked fish throughout life, 2) all fish detected and reported with the kind of mark applied at the hatcheries are hatchery fish, and 3) chinook salmon are correctly aged from scale examinations and information on size of fish and date of capture. Two assumptions as to the behavior of marked and unmarked hatchery fish are: 4) marked and unmarked hatchery fish have the same survival rates and maturity schedules, and 5) marked and unmarked hatchery fish have the same ocean distribution and are equally vulnerable to the fisheries. Finally, because part of all hatchery releases bear the same mark, we assume: 6) common marks were applied to the same proportion of each hatchery's production in a given year.

The appropriateness of the estimating procedures is dependent on the validity of these assumptions. Assumption 1 was tested by holding marked fish in saltwater ponds for periodic examination of the condition of the mark. There was no regeneration of the adipose fin. However, regeneration of ventral fins and maxillary bones did occur. In most cases, the ventral fin regenerated to <25% of its original size. Greater regeneration was identifiable by deformation of the fin rays.

The high occurrence of maxillary regeneration (7-12%) for the 1961- and 1962-brood chinook salmon resulted in the removal of more of the maxillary bone in the 1963- and 1964-brood fish. This change in marking procedure resulted in a smaller percentage of fish with regenerated maxillaries (1-3%).

Since single and double fin marks were associated with maxillary clips, even when maxillaries completely regenerated, the fish were identifiable as marked fish. Thus we believe assumption 1 to be true.

The validity of assumption 2, the absence of natural marks on hatchery and wild fish, was tested in two ways: First, over 30 million hatchery fingerlings were examined during marking for naturally missing adipose and ventral fins. Only 156 missing adipose and 201 missing ventral fins (none together) were observed indicating the insignificance of naturally occurring marks on these fish. Second, the occurrence of natural marks outside the hatchery system was checked by examining 1965-brood chinook salmon catches for study marks. The allocation of study marks to any 1965 brood on the Pacific Coast was to have been prevented. Unfortunately, the attempt to prevent the application of study marks to this brood was not completely successful. However, no adipose-ventral-maxillary combinations were applied and none were found in the fisheries. Any occurrence of natural marks like those claimed as hatchery marks has been accounted for under Estimating Procedure. Therefore, we believe assumption 2 has been satisfied.

Assumption 3 was evaluated by testing scale

[10]William G. Brown, Ashok K. Singh, and Jack A. Richards. 1972. Influence of improved estimating techniques on predicted net economic values for salmon and steelhead. Unpubl. manuscr., 26 p. Oreg. State Univ., Agric. Exp. Stn., Corvallis.

readers with chinook salmon scales of known age. Scales from 400 marked fish of known age were submitted to six readers: two from the Fish Commission of Oregon and one each from the Fisheries Research Board of Canada, Washington Department of Fisheries, Oregon Game Commission, and Bureau of Commercial Fisheries. Length of fish and date of capture were available for each scale. The six scale readers correctly aged 83% of the 400 test scales (Worlund et al. 1969). Thus, we believe that assumption 3 is reasonably well satisfied.

The equality of marked and unmarked survival rates and maturity schedules, assumption 4, needs some additional study. A lowering of the marked to unmarked ratio at the hatchery from the time of release to the time of return indicated possible problems with this assumption. There are several possible reasons for this change in marked to unmarked ratio. They are: 1) errors in estimating the number of marked and/or unmarked hatchery fish at the time of release; 2) a difference in distribution or timing of marked and unmarked fish, resulting in the marked fish being exposed to a more intense fishery; 3) a selectivity of some fisheries for marked fish; 4) a greater amount of straying for marked fish than unmarked fish; 5) a difference in maturation schedule for marked and unmarked fish; 6) differential survival between marked and unmarked fish because of marking; and 7) mistakes in aging unmarked hatchery returns.

It is unlikely the difference in the marked to unmarked ratios at the time of release and return could have been caused entirely by mistakes in estimating the ratio at release. The differences were too great, considering the randomness of the estimating procedures and the number of hatcheries involved. There is no way to determine nor reason to believe differences in distribution, timing, or straying between marked and unmarked fish caused the differences in the ratios at release and return. Nor is there any way to determine or reason to believe any fishery was selective for marked fish. Thus we rejected these as possible reasons for the change in marked to unmarked ratios between the time of release and return.

There is some indication a difference in time of maturing did occur between marked and unmarked fish (Cleaver 1969). Examination of the marked to unmarked ratios at the hatcheries by year of return shows a trend of increasing ratios. This indicates the marked fish did not mature as soon as the unmarked fish. The marked fish appeared to stay in the ocean longer and thus were subject to a higher natural and fishing mortality.

It is also possible clipping fins and maxillary bones caused mortality after the fish were released from the hatchery. The unmarked fish would obviously not be subjected to this mortality.

Mistakes in aging of unmarked hatchery returns could easily have occurred because of the poor condition of the fish when entering the hatchery. The scales had been partially resorbed, making them difficult to read. Since the same marks were used in alternate brood years, the mark and size of the fish would aid the aging procedure for the marked fish. This would result in more accurate aging of marked than unmarked fish. However, the errors in aging unmarked fish could have been self cancelling. Possible errors in aging seemed to be a very minor reason for the differences in the marked to unmarked ratios.

Thus the two most probable reasons for the change of marked to unmarked ratios from the time of release to return were differences in maturation schedule and differential survival of marked and unmarked fish. These two problems probably acted in combination. Since we have no way of separating the effects of delayed maturity and differential survival and since we are making the best estimate of hatchery contribution, we are assuming the change in marked to unmarked ratio was due only to differences in survival of marked and unmarked fish. Correction factors were applied to adjust for the differential survival.

The validity of assumption 5, equal ocean distribution and vulnerability to the fisheries for marked and unmarked fish, is supported by ocean tagging studies showing similar ocean distribution for marked and unmarked hatchery fish (Cleaver 1969).

Common marks were applied to 10 or 11% of the production at the 13 study facilities for the four brood years, 1961 through 1964 (Table 4). The percentages ranged from 9 to 11 among the hatcheries for each brood. With these ranges we feel assumption 6, application of common marks to the same proportion of each hatchery's production, is satisfied.

FIELD OPERATIONS

Marking and Release Procedures

Artificial propagation procedures were similar at all 13 study facilities. Adult fall chinook salmon

returned to these facilities and were spawned during September and October. Fry reached free swimming stage in February or March and were then placed in ponds. They were reared 90 to 120 days in the hatchery and released at an average length of 6 to 8 cm (2-3 in). Since there was considerable variation in time and size of release between hatcheries and brood years, we have included Table 5 to complete the release procedure record. After the hatchery fall chinook salmon spent 1 to 6 yr in the ocean, where they were available to sport and commercial fisheries from southeastern Alaska to central California, they matured and returned to the Columbia River.

The marking phase of this study extended from June 1962 through June 1965. Approximately 10% of the 1961-64 broods were marked. A "10-part sampler," a modified sampling tool (Worlund et al. 1969), was used to obtain the sample of fish for marking. The sampler consisted of a cylindrical liner containing a circular metal frame. The frame was divided into 10 equal pie-shaped sections with a zipper-bottomed net pocket hung from each section. To obtain a sample for marking, the zippers on one or more pockets were closed, the frame and liner were placed in a water-filled tub, and 18 kg (40 lb) of fish were placed into the liner. The closed pocket, or pockets, retained the desired sample when the liner and frame were lifted. The fish remaining in the tub were placed into another pond. This procedure was followed until all chinook salmon in each pond were processed. In the case of the special mark hatcheries, two or more pockets were closed. One pocket retained the fish for common marking and the other pockets retained those for special marking. The intention was to apply special marks to between 500,000 and 1.0 million chinook salmon at each of the special mark hatcheries. We felt this number would provide a statistically sound number of special mark recoveries for each hatchery. The hatchery manager's estimate of the number of fall chinook salmon on hand at the time of sampling was used to determine how many pockets to close at each hatchery to obtain the desired sample for special marking. These estimates were sometimes inaccurate, resulting in a smaller or larger sample than had been desired.

Fish to be marked were anesthetized with MS-222 (tricaine methanesulfonate). The fins and maxillary bones were clipped with bent-nosed scissors. Marked fish were held in hatchery troughs until they recovered from the anesthetic, then returned to the group of unmarked fish from which they came. Mark quality control was maintained by sampling 100 marked fish per marker at irregular periods each day and grading them according to quality of mark. Each year over 100,000 marked fish were sampled and graded. This grading indicated a high mark quality was attained.

The entire production of fall chinook salmon at the study hatcheries was sampled with the 10-part sampler prior to release to estimate the marked and unmarked releases. The "10%" samples were set aside and resampled to obtain a "1%" sample which was sorted into marked and unmarked groups, counted, and weighed. The counts and the estimate of the proportion removed by the particular sampler were used to estimate the numbers of marked and unmarked fish released.

Over 213 million 1961-64-brood fall chinook salmon were released from the study hatcheries. Of these, 21.3 million were given the common mark and 9.6 million were given a special mark (Table 1).

TABLE 5.—Size and date of release of 1961-64 broods of fall chinook salmon from Columbia River hatcheries participating in the fall chinook salmon study by hatchery and brood.

	1961 brood		1962 brood		1963 brood		1964 brood	
Hatchery	Size[1]	Date	Size[1]	Date	Size[1]	Date	Size[1]	Date
Grays River	169	5/24/62	141	5/31/63	114	6/1/64	108	5/26/65
Elokomin	202	5/24/62	206	5/20/63	181	5/9/64	134	5/12/65
Kalama Falls	356-202	6/1-7/31/62	226	6/4/63	198	6/15/64	177	6/20/65
Washougal	187-107	5-6/62	180	5/22/63	153	5/25/64	139	5/2/65
Little White	180	6/22/62	227- 83	6/5-8/15/63	200	6/18/64	177	6/65
Spring Creek	289-173	4/9-5/11/62	282-149	4/8-6/13/63	273-206	4/12-5/12/64	250-142	4/11-5/4/65
Big White	182	5/11/62	190	6/17/63	181	5/12/64	85	6/29/65
Klickitat	166	4/23/62	164	4/20/63	148	4/29/64	132	5/5/65
OxBow	217	5/10/62	195	5/14/63	189	5/6/64	170	6/19/65
Cascade	318	5/20/62	192	6/24/63	215	6/12/64	146	6/29/65
Bonneville	312	6/6/62	152	6/19/63	136	6/26/64	154	6/24/65
Big Creek	174	5/2/62	137	5/7/63	102	5/13/64	91	6/2/65
Lower Kalama	261	6/2/62	199	5/18/63	139	5/18/64	169	5/18/65

[1]Fish per pound.

Mark Recovery

The sampling phase of this study began in 1963 and was completed in 1969. Table 6 shows the marks and the age of the marked fish in the fisheries during these years. Sampling and catch estimation procedures are explained under Catch of Marked Fish. Sampling for these fish occurred in the major ocean sport and commercial fisheries from southeastern Alaska to central California, the Columbia River fisheries (Figure 2, Table 7), at parent hatcheries, and certain natural spawning grounds (Worlund et al. 1969; Rose and Arp see footnote 3; Arp et al. see footnote 4; Wahle et al. see footnote 5). During the first sampling year, 1963, only Washington and Oregon ocean fisheries, Columbia River fisheries, and hatchery returns were examined for marks. In 1964, the sampling was expanded to include most chinook salmon fisheries from Avila Beach, Calif. to Pelican, Alaska. The Puget Sound sport fishery was not sampled in 1964. The British Columbia purse seine fishery was not sampled in 1966. The sampling of the southeastern Alaska gillnet fishery

TABLE 6.—Ages of marked Columbia River fall chinook salmon in catches and escapements by brood (1961-64) and sampling years (1963-69).

Brood	Mark[1]	Hatchery	Year of sampling						
			1963	1964	1965	1966	1967	1968	1969
			Years old						
1961	Ad-RM	12 hatcheries	2	3	4	5			
	Ad-LV-RM	Spring Creek	2	3	4	5			
	Ad-RV-RM	Kalama	2	3	4	5			
	RV-RM	OxBow	2	3	4	5			
	LV-RM	Elokomin	2	3	4	5			
1962	Ad-LM	12 hatcheries		2	3	4	5		
	Ad-LV-LM	Spring Creek		2	3	4	5		
	Ad-RV-LM	Kalama		2	3	4	5		
	RV-LM	Cascade		2	3	4	5		
	LV-LM	Grays River		2	3	4	5		
1963	Ad-RM	12 htacheries			2	3	4	5	
	Ad-LV-RM	Spring Creek			2	3	4	5	
	Ad-RV-RM	Kalama			2	3	4	5	
	LV-RM	Klickitat			2	3	4	5	
	RV-RM	Big Creek			2	3	4	5	
1964	Ad-LM	12 hatcheries				2	3	4	5
	Ad-LV-LM	Spring Creek				2	3	4	5
	Ad-RV-LM	Kalama				2	3	4	5
	RV-LM	Little White Salmon				2	3	4	5
	LV-LM	Bonneville				2	3	4	5
No. of marks in catches and escapements			5	10	15	20	15	10	5

[1]Ad: adipose; LV: left ventral; RV: right ventral; LM: left maxillary; and RM: right maxillary

TABLE 7.—Areas where catches were examined for marked fall chinook salmon of Columbia River origin by port or zone of landing and type of fishery.

Area sampled	Sport fishery	Commercial fisheries			
	Rod and reel	Troll	Gill net	Dip net	Purse seine
Southeast Alaska		Zones 1, 3-15, 18, 22	Zones 1, 6, 8, 11, 15, 18, 19		
British Columbia		Alaska area Zones 29, 40-43, Area C.	Zones 29, 40, 41-43		Zones 40-43
Washington ocean	Sekiu	Seattle	Juan de Fuca Strait		
	Neah Bay	Neah Bay	Grays Harbor		
	La Push	La Push	Willapa Bay		
	Westport	Westport			
	Ilwaco	Ilwaco			
Puget Sound	Zones 6-12				
Oregon ocean	Warrenton	Astoria, Tillamook			
	Depoe Bay	Nestucca, Depoe Bay			
	Newport	Newport			
	Florence	Florence			
	Reedsport	Reedsport			
	Coos Bay	Coos Bay			
	Gold Beach	Port Orford			
	Brookings	Brookings			
California ocean	Crescent City	Crescent City			
	Eureka	Eureka			
	Fort Bragg	Fort Bragg			
	San Francisco	San Francisco			
	Monterey	Monterey			
Columbia River	Zones 1-5		Zones 1-6	Klickitat River	

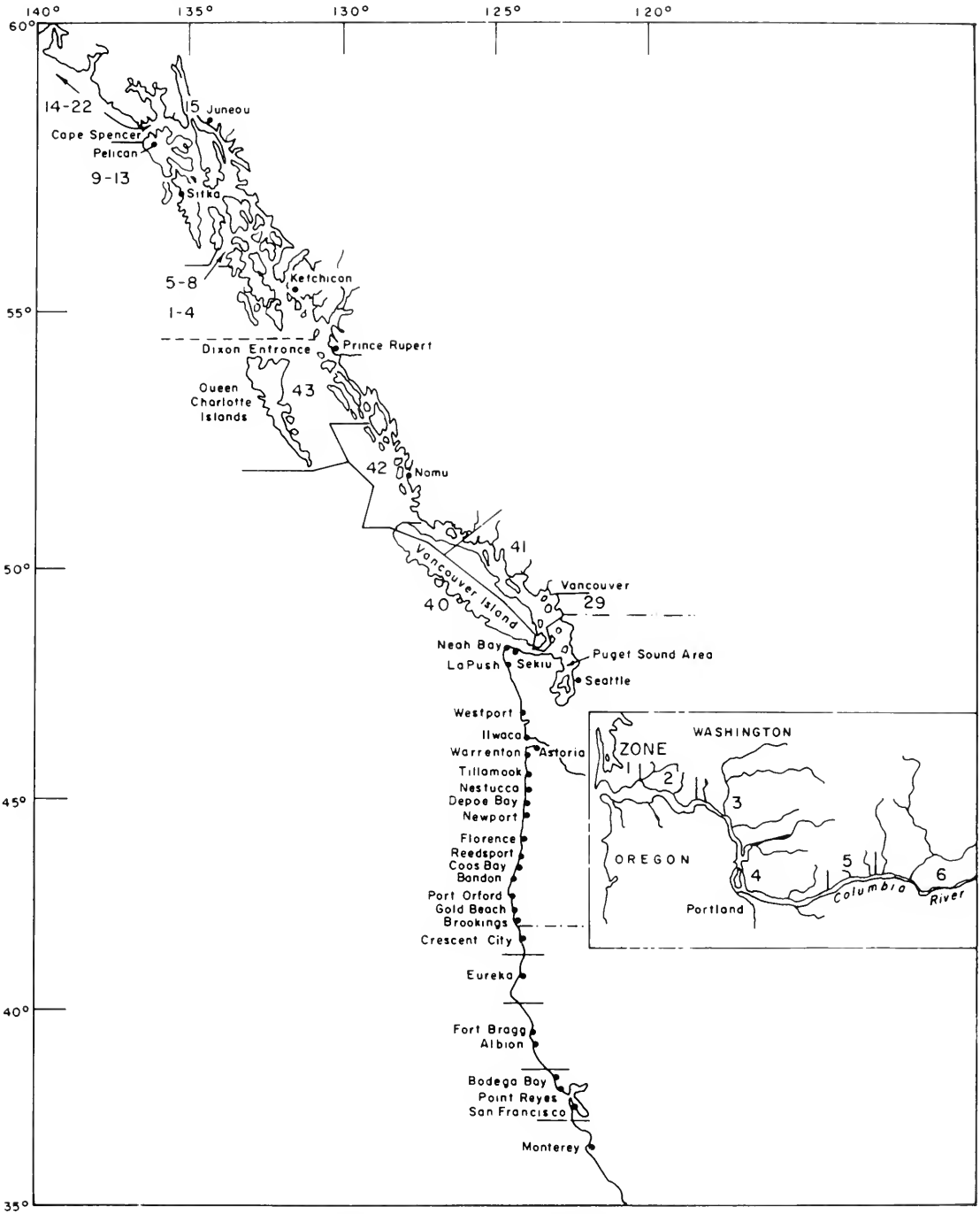

FIGURE 2.—Ports and zones sampled for marked fall chinook salmon of Columbia River origin.

was discontinued after 1966 and the Alaska troll fishery sampling stopped after 1967. Over the 7 yr of sampling, 3.3 million chinook salmon were examined for marks and 208,000 were sampled for age. This was an average sampling percentage of 20 and 1% for marks and age, respectively. The yearly mark sampling rate ranged from 14 to 28% of the catch and the age sampling ranged from 1 to 4%.

Enumeration of Returns

Returns to all study facilities were counted and examined for marks. Age, length, and sex data were also collected from 25 to 50 unmarked chinook salmon/wk at each hatchery. Returns to five other Columbia River hatcheries (Abernathy, Speelyai, Toutle, Klaskanine, and Sandy) were also examined for marks. Total hatchery returns for the 1961-64 broods of fall chinook salmon were 155,783, of which 8,527 were marked.

Hatchery and adjacent fall chinook salmon spawning streams were surveyed to estimate natural spawning of hatchery fish. The Klickitat, Big White Salmon, Little White Salmon, Wind, Washougal, Kalama, Lewis, Elokomin, and Grays Rivers and Plympton and Big Creeks were surveyed in 1964, 1965, and 1966. The surveys were designed to estimate the total spawning population and to gather mark, age, and length data. During the 3 yr, 62,400 chinook salmon were examined of which 1,600 were marked. The stream surveys were discontinued after 1966 because of a funding reduction.

INDIVIDUAL HATCHERY MARK CATCH AND POTENTIAL CONTRIBUTION, 1961-64 BROODS

In this study 12 hatcheries and one rearing pond were marked with a common mark for four brood years. All but two of these facilities (Big White Salmon Pond and Washougal Hatchery) had a portion of at least one brood year's production marked with a special mark. A portion of all four brood years' production at Spring Creek and the two Kalama River hatcheries were marked with special marks. This special marking was done to give an indication of the migration patterns and contributions to the fisheries for each individual hatchery in the study. The estimated catches and potential contributions will now be presented for each hatchery with special marks.

Spring Creek National Fish Hatchery, 1961-64 Broods

Spring Creek Hatchery was allocated the Ad, LV, combination mark for the four brood years. The RM mark was used in combination with the Ad-LV mark for the 1961 and 1963 broods and the LM mark was used with the 1962 and 1964 broods. Approximately 10% of Spring Creek's production was marked for each brood year. The number of fish given special marks ranged from 1.1 million for the 1961 brood to 600,000 for the 1964 brood.

Spring Creek special marked chinook salmon were available to the ocean and Columbia River fisheries from 1963 through 1969. During this 7-yr period, we estimated 12,180 special marked fish were recovered in the fisheries (Table 8). Over 65% of the fish were captured in their third year of life, with nearly 27% taken as 4-yr-olds. Ocean recoveries occurred primarily from the Columbia River mouth north to the west coast of Vancouver Island. Fisheries in the marine areas took 74% of the fish, with 26% being caught in the Columbia River commercial fisheries (Figure 3).

The potential contribution of Spring Creek chinook salmon (had no marking taken place) was estimated at 401,700 fish for the four broods combined. The average Spring Creek contribution to the fisheries for the four broods combined was 12

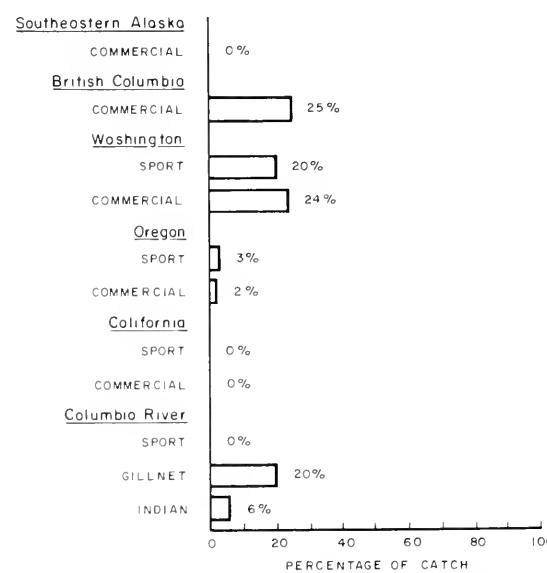

FIGURE 3.—Percentage of catch of 1961- to 1964-brood fall chinook salmon from Spring Creek National Fish Hatchery taken by area and fishery, 1963-69.

TABLE 8.—Estimated catches of special marked fall chinook salmon from Spring Creek National Fish Hatchery and potential contributions by fishery type and brood (1961-64), 1963-69.

Brood year and fishery type	Estimated catch of marked fish by year							Catch	Potential contribution (in thousands)
	1963	1964	1965	1966	1967	1968	1969		
1961:									
Marine sport	156	488	129	0	—	—	—	773	18.9
Marine commercial	4	2,031	269	5	—	—	—	2,309	56.4
Columbia River sport	0	14	16	0	—	—	—	30	0.7
Columbia River gillnet	11	388	633	17	—	—	—	1,049	25.6
Columbia River Indian[1]	11	147	81	0	—	—	—	239	5.8
Total	182	3,068	1,128	22	—	—	—	4,400	107.4
1962:									
Marine sport	—	34	142	28	0	—	—	204	6.4
Marine commercial	—	0	234	135	14	—	—	383	12.0
Columbia River sport	—	0	0	0	0	—	—	0	0.0
Columbia River gillnet	—	10	242	88	0	—	—	340	10.6
Columbia River Indian[1]	—	0	40	0	0	—	—	40	1.3
Total	—	44	658	251	14	—	—	967	30.3
1963:									
Marine sport	—	—	120	368	133	0	—	621	25.5
Marine commercial	—	—	23	966	282	9	—	1,280	52.6
Columbia River sport	—	—	0	0	0	0	—	0	0.0
Columbia River gillnet	—	—	15	151	203	7	—	376	15.4
Columbia River Indian[1]	—	—	14	13	95	8	—	130	5.3
Total	—	—	172	1,498	713	24	—	2,407	98.8
1964:									
Marine sport	—	—	—	378	685	87	10	1,160	43.5
Marine commercial	—	—	—	7	1,634	582	16	2,239	83.9
Columbia River sport	—	—	—	0	0	0	0	0	0.0
Columbia River gillnet	—	—	—	15	260	351	19	645	24.2
Columbia River Indian[1]	—	—	—	0	201	156	5	362	13.6
Total	—	—	—	400	2,780	1,176	50	4,406	165.2

[1]Setnet and dip net fisheries.

fish per 1,000 released and 2.3 fish per pound of fish released.

Kalama River Hatcheries, 1961-64 Broods

The production at Kalama Falls Salmon Hatchery and Lower Kalama Salmon Hatchery was combined for this study. Common and special marks were applied to the production at both facilities. The Ad, RV, and M special mark was allocated to the Kalama facilities. The RM clip was used with the 1961 and 1963 broods, and the LM mark was used with 1962 and 1964 broods. For all brood years, approximately 10% of both hatcheries' fall chinook salmon production was marked with a special mark.

We estimated 5,096 chinook salmon with special marks from Kalama River hatcheries were captured in the ocean and Columbia River fisheries from 1963 through 1969 (Table 9). Generally for the four brood years, over half of the Kalama fish were caught in their fourth and fifth years of life. However, the age distribution did vary by brood year. The 1961 and 1964 broods were over 60% 4- and 5-yr-old fish while these two age-groups contributed less than 50% to the 1962- and 1963-brood catches. The Kalama chinook salmon contributed to the Alaska fisheries primarily as 4-yr-olds; and the larger the Canadian catch, the larger the Alaskan catch. In 1968 the Canadian catch of Kalama fish was large and no sampling took place in the Alaska fisheries. Thus a significant contribution to Alaska of 1964-brood Kalama fall chinook salmon in 1968 could have been missed.

The potential contribution of Kalama River hatcheries fall chinook salmon totaled 172,400 fish for the four brood years (Table 9). The contributions ranged from a low of 22,300 fish for the 1962 brood to a high of 56,800 fish for the 1961 brood. The average contribution for all four broods combined was 43,100. This is an average potential contribution to Pacific coast fisheries of 9.6 fish for each 1,000 smolts released and 2.0 fish caught for every pound of fish released.

Kalama chinook salmon contributed primarily to British Columbia, Washington, and Columbia River gillnet fisheries (Figure 4). The largest contribution was to British Columbia followed by Washington, Columbia River, Oregon, and Alaska, in that order.

TABLE 9.—Estimated catch of special marked fall chinook salmon from Kalama River hatcheries and potential contributions by fishery type and brood (1961-64), 1963-69.

Brood year and fishery type	Estimated catch of marked fish by year							Catch	Potential contribution (in thousands)
	1963	1964	1965	1966	1967	1968	1969		
1961									
Marine sport	23	78	103	9	—	—	—	213	5.6
Marine commercial	0	618	683	106	—	—	—	1,407	36.7
Columbia River sport	0	0	0	0	—	—	—	0	0.0
Columbia River gillnet	0	38	402	111	—	—	—	551	14.4
Columbia River Indian[1]	0	0	4	0	—	—	—	4	0.1
Total	23	734	1,192	226	—	—	—	2,175	56.8
1962									
Marine sport	—	0	84	11	8	—	—	103	3.5
Marine commercial	—	0	240	194	23	—	—	457	15.5
Columbia River sport	—	0	0	16	0	—	—	16	0.5
Columbia River gillnet	—	6	21	46	10	—	—	83	2.8
Columbia River Indian[1]	—	0	0	0	0	—	—	0	0.0
Total	—	6	345	267	41	—	—	659	22.3
1963									
Marine sport	—	—	140	167	66	12	—	385	17.0
Marine commercial	—	—	0	366	320	53	—	739	32.7
Columbia River sport	—	—	0	0	0	0	—	0	0.0
Columbia River gillnet	—	—	7	32	44	50	—	133	5.9
Columbia River Indian[1]	—	—	0	0	0	0	—	0	0.0
Total[1]	—	—	147	565	430	115	—	1,257	55.6
1964									
Marine sport	—	—	—	38	61	40	0	139	5.2
Marine commercial	—	—	—	0	132	533	69	734	27.6
Columbia River sport	—	—	—	0	0	17	0	17	0.6
Columbia River gillnet	—	—	—	3	0	41	68	112	4.2
Columbia River Indian[1]	—	—	—	0	3	0	0	3	0.1
Total	—	—	—	41	196	631	137	1,005	37.7

[1]Setnet and dip net fisheries.

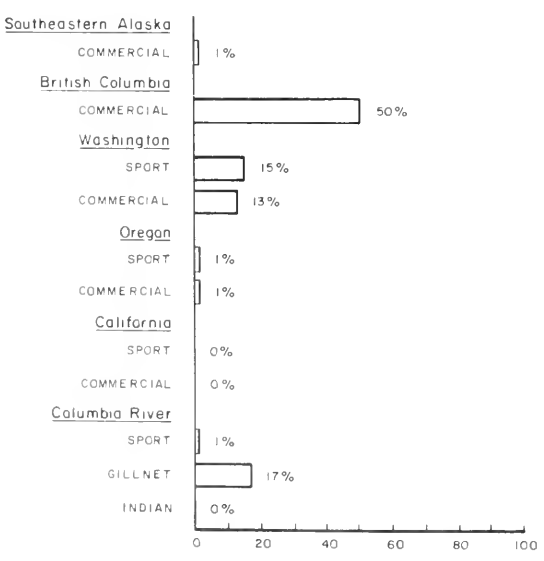

FIGURE 4.—Percentage of catch of 1961- to 1964-brood fall chinook salmon from Kalama River hatcheries taken by area and fishery, 1963-69. Percentages do not add to 100% due to rounding.

Elokomin and OxBow Hatcheries, 1961 Brood

A portion of the 1961-brood fall chinook salmon productions at Elokomin and OxBow Hatcheries were given special marks. At Elokomin Hatchery, 480,500 or 30% of the production was LV-RM clipped. Approximately 450,400 or 10% of OxBow's fall chinook salmon production was marked with a RV-RM clip. These fish contributed to the fisheries from 1963 through 1966.

During the 4 yr, 235 Elokomin and 336 OxBow fish with special marks were estimated to have been caught (Table 10). Chinook salmon from both hatcheries were taken primarily as 3-yr-olds. A larger portion of Elokomin fish than OxBow fish were taken as 4-yr-olds, and a larger portion of OxBow than Elokomin fish were taken as 2- and 5-yr-olds. Potential contributions were estimated at 2,000 and 8,500 fish for Elokomin and OxBow respectively. The catch per 1,000 fish released at Elokomin Hatchery was 1.3 fish and at OxBow 1.9 fish. The catches per pound of fish released at Elokomin and OxBow Hatcheries were 0.2 and 0.4 fish respectively.

About one-half of the catch from the two hatch-

TABLE 10.—Estimated catch of 1961-brood special marked fall chinook salmon and potential contribution from Elokomin and OxBow Hatcheries by fishery type, 1963-66.

Hatchery and fishery type	Estimated catch of marked fish by year				Total catch	Potential contribution (in thousands)
	1963	1964	1965	1966		
Elokomin Hatchery						
Marine sport	0	25	31	0	56	0.5
Marine commercial	0	109	23	9	141	1.2
Columbia River sport	0	0	0	0	0	0.0
Columbia River gillnet	0	6	30	0	36	0.3
Columbia River Indian[1]	0	2	0	0	2	0.0
Total	0	142	84	9	235	2.0
OxBow Hatchery						
Marine sport	18	78	6	16	118	3.0
Marine commercial	0	107	41	6	154	3.9
Columbia River sport	0	0	17	0	17	0.4
Columbia River gillnet	0	27	3	14	44	1.1
Columbia River Indian[1]	3	0	0	0	3	0.1
Total	21	212	67	36	336	8.5

[1]Setnet and dip net fisheries.

eries occurred in the Washington fisheries. (Figure 5). Nearly 30% of the Elokomin catch was taken in the Washington commercial fisheries. Washington sport fishermen took over one-fourth of the OxBow catch. Fish from Elokomin appear to have a more northerly distribution than those from OxBow.

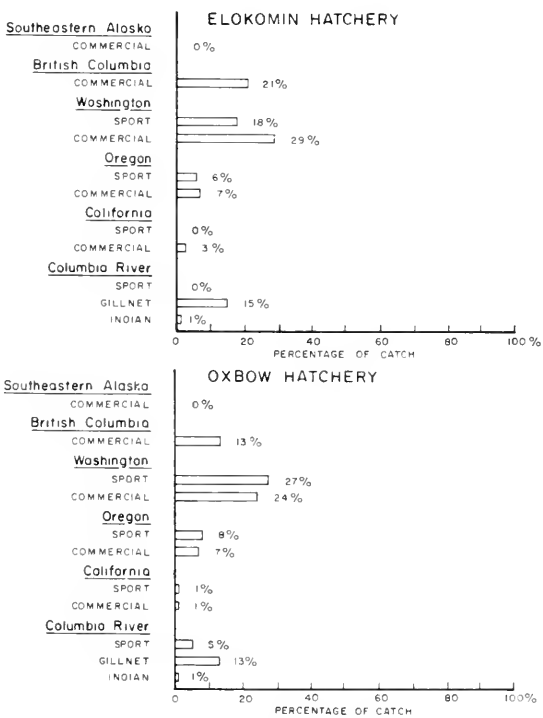

FIGURE 5.—Percentage of 1961-brood fall chinook salmon from Elokomin and OxBow Hatcheries taken by area and fishery, 1963-66.

Grays River and Cascade Hatcheries, 1962 Brood

The 1962-brood fall chinook salmon at Grays River Hatchery were given a LV-LM special clip and the Cascade fish were RV-LM clipped. Special marks were applied to approximately 18% or 241,500 Grays River and 13% or 541,200 Cascade Hatchery fish. These fish contributed to the fisheries from 1964 through 1967.

Approximately equal numbers of Grays River and Cascade fall chinook salmon with special marks were estimated to have been taken in the fisheries (Table 11). Fish from both hatcheries were caught almost exclusively as 3- and 4-yr-olds. Few were taken as 2's and 5's. The potential contributions of Grays River and Cascade were 3,900 and 4,800 fish, respectively. For each 1,000 chinook salmon released at Grays River Hatchery, 2.9 were caught in the fisheries and 0.4 fish were caught per pound of fish released. The contribution from Cascade Hatchery was 1.1 chinook salmon per 1,000 released and 0.2 per pound of fish released.

The catch distributions of Grays River and Cascade Hatcheries were very different (Figure 6); for example, a much greater portion of Cascade's than Grays River's fish were taken in the British Columbia fishery. Most of Grays River's fish (65%) but only 24% of Cascade's fish were taken in the Washington sport fishery.

Klickitat and Big Creek Hatcheries, 1963 Brood

A LV-RM special mark was applied to 18% or 521,600 1963-brood fall chinook salmon at Klick-

TABLE 11.—Estimated catch of 1962-brood special marked fall chinook salmon and potential contribution from Grays River and Cascade hatcheries by fishery type, 1964-67.

Hatchery and fishery type	Estimated catch of marked fish by year				Total catch	Potential contribution (in thousands)
	1964	1965	1966	1967		
Grays River Hatchery						
Marine sport	0	89	50	0	139	2.5
Marine commercial	3	29	35	4	71	1.3
Columbia River sport	0	0	0	0	0	0.0
Columbia River gillnet	0	0	5	0	5	0.1
Columbia River Indian[1]	0	0	0	0	0	0.0
Total	3	118	90	4	215	3.9
Cascade Hatchery						
Marine sport	0	19	28	0	47	1.2
Marine commercial	0	66	38	3	107	2.7
Columbia River sport	0	0	0	0	0	0.0
Columbia River commercial	3	6	24	0	33	0.8
Columbia River Indian[1]	0	0	4	0	4	0.1
Total	3	91	94	3	191	4.8

[1] Setnet and dip net fisheries

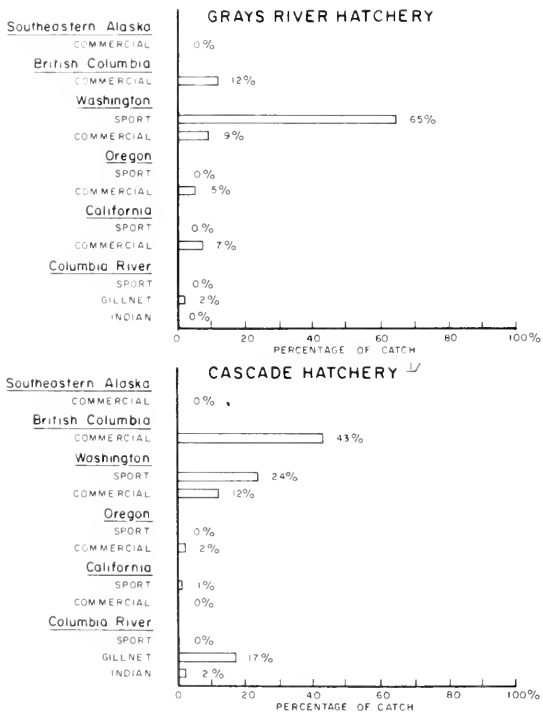

FIGURE 6.—Percentage of catch or 1962-brood fall chinook salmon from Grays River and Cascade Hatcheries taken by area and fishery, 1964-67. Percentages do not add to 100% due to rounding.

itat Hatchery. At Big Creek Hatchery nearly 30% or 580,000 1963-brood chinook salmon were given RV-RM special clips. These fish contributed to the fisheries from 1965 through 1968.

The estimated catches of chinook salmon with special marks from Klickitat and Big Creek Hatcheries were 1,858 and 914 fish, respectively (Table 12). The Klickitat fish were caught primarily as 3- and 4-yr-olds, except in the ocean sport fishery where 2-yr-olds were predominant. In the marine commercial and Columbia River fisheries, the predominant age class was 3-yr-olds. Nearly 60% of Big Creek's special marked fish were caught in their third year of life, and about one-third were taken as 4-yr-olds.

Klickitat and Big Creek Hatcheries' potential contributions to the fisheries were 42,500 and 12,900 fish, respectively. From Klickitat the contribution was 14.7 fish per 1,000 released and 2.2 fish for each pound of fish released. The contribution per 1,000 chinook salmon released at Big Creek was 6.5 fish and 0.7 fish for each pound of fish released.

Distribution of both facilities' catches can be compared by examination of Figure 7. Thirty-nine percent of Klickitat's fish were taken in the British Columbia commercial fisheries compared with 16% for Big Creek, suggesting a more northerly distribution for Klickitat fish. Although Big Creek fish pass through only a small portion of the Columbia River commercial fishery, the portion taken in this fishery is larger (19%) than the Klickitat portion (10%). Over half of Big Creek's estimated catch was taken in the Washington marine fisheries.

Bonneville and Little White Salmon Hatcheries, 1964 Brood

About 10% (957,100) of the 1964-brood Bonneville Hatchery fall chinook salmon were marked with a LV-LM clip. The RV-LM mark was applied to about 10% (797,300) of the Little White

TABLE 12.—Estimated catch of 1963-brood special marked fall chinook salmon and potential contribution from Klickitat and Big Creek hatcheries by fishery type, 1965-68.

Hatchery and fishery type	Estimated catch of marked fish by year				Total catch	Potential contribution (in thousands)
	1965	1966	1967	1968		
Klickitat Hatchery:						
Marine sport	161	146	81	0	388	8.9
Marine commercial	3	633	617	32	1,285	29.4
Columbia River sport	0	0	0	0	0	0.0
Columbia River commercial	0	72	45	0	117	2.7
Columbia River Indian[1]	0	47	21	0	68	1.5
Total	164	898	764	32	1,858	42.5
Big Creek Hatchery:						
Marine sport	70	209	73	0	352	5.0
Marine commercial	0	240	144	7	391	5.5
Columbia River sport	0	0	0	0	0	0.0
Columbia River commercial	0	93	78	0	171	2.4
Columbia River Indian[1]	0	0	0	0	0	0.0
Total	70	542	295	7	914	12.9

[1]Setnet and dip net fisheries.

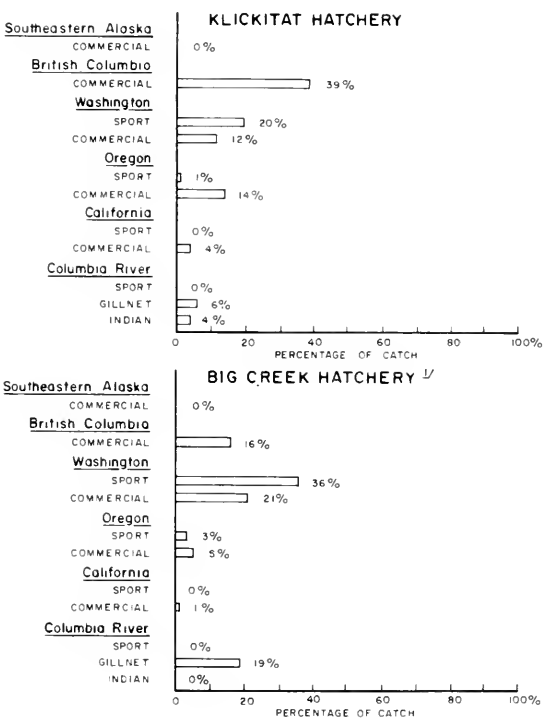

FIGURE 7.—Percentage of catch of 1963-brood fall chinook salmon from Klickitat and Big Creek Hatcheries taken by area and fishery, 1965-68. Percentages do not add to 100% due to rounding.

Salmon National Fish Hatchery 1964-brood fish. Both groups contributed to the fisheries from 1966 through 1969.

The estimated catches of special marked fish from Bonneville and Little White Salmon Hatcheries were 762 and 303 fish respectively. Significant numbers of Bonneville special mark chinook salmon were caught in the ocean fisheries as 2-, 3-, and 4-yr-olds, while the Little White fish contributed as 3's and 4's (Table 13). The largest numbers of both hatcheries' fish were taken in the ocean commercial fisheries.

The potential contributions for Bonneville and Little White were 27,100 and 11,000 fish, respectively. Bonneville produced 2.7 fish per 1,000 or 0.4 fish per pound of fish released. Little White produced 1.3 fish per 1,000 or 0.2 fish per pound of fish released.

The distribution of the Bonneville Hatchery catch was more southerly than that of Little White Salmon Hatchery (Figure 8). Nearly 50% of the catch from both facilities occurred in the Washington fisheries. The British Columbia fisheries took most of the remaining Little White catch (41%).

Common Mark Catch and Potential Contribution All Study Facilities Combined, 1961-64 Broods

An Ad-M common mark was applied to a portion of the 1961-64-brood fall chinook salmon production at all 13 study facilities. The RM was clipped from the 1961- and 1963-brood fish, and the LM was clipped from the 1962- and 1964-brood chinook salmon. Common marks were applied to 21,320,000 (approximately 10%) of the 213,014,000 fall chinook salmon released over the four brood years from the 13 study facilities.

We estimated 65,620 common marked fish were caught from 1963 through 1969 (Table 14). On the average over the four broods 76% of the common marked fish were taken in the ocean, with 56% caught in the ocean commercial fisheries. In the

TABLE 13.—Estimated catch of 1964-brood special marked fall chinook salmon and potential contribution from Bonneville and Little White Salmon National Fish hatcheries by fishery type, 1966-69.

Hatchery and fishery type	Estimated catch of marked fish by year				Total catch	Potential contribution (in thousands)
	1966	1967	1968	1969		
Bonneville Hatchery:						
Marine sport	99	70	95	0	264	9.4
Marine commercial	62	230	172	8	472	16.8
Columbia River sport	0	0	0	0	0	0.0
Columbia River commercial	0	0	17	5	22	0.8
Columbia River Indian[1]	4	0	0	0	4	0.1
Total	165	300	284	13	762	27.1
Little White Salmon Hatchery:						
Marine sport	0	40	37	0	77	2.8
Marine commercial	4	84	125	0	213	7.7
Columbia River sport	0	0	0	0	0	0.0
Columbia River commerical	0	5	8	0	13	0.5
Columbia River Indian[1]	0	0	0	0	0	0.0
Total	4	129	170	0	303	11.0

[1]Setnet and dip net fisheries.

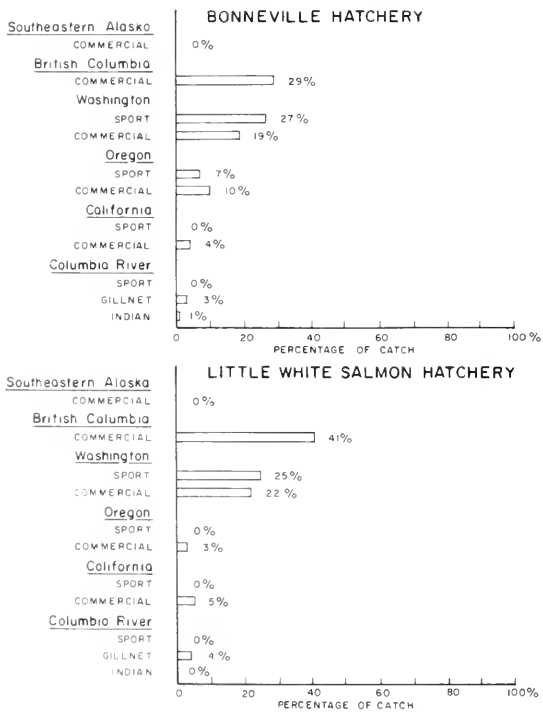

FIGURE 8.—Percentage of catch of 1964-brood fall chinook salmon from Bonneville and Little White Salmon Hatcheries taken by area and fishery, 1966-69.

ocean fisheries, the 3-yr-old exceeded the 4-yr-old catch. However, in the river the 4-yr-old catch was larger than the 3-yr-old. The Columbia River fall chinook salmon sport fishery was small and few marked fish were observed.

The potential contribution for the four broods combined was 1,433,300 fall chinook salmon. The contribution ranged from a low of 165,200 fish for the 1962 brood to a high of 602,200 for the 1963 brood. The contribution figures in Table 14 include fish with common and special marks as well as unmarked fish from the 13 study facilities. The average catch to release ratio was 6.7 fish per 1,000 released, with ratios of 6.7, 3.1, 10.0, and 6.5 for the 1961-64 broods respectively. The average catch per pound released was 1.2 fish with ratios by brood of 1.4, 0.6, 1.7, and 0.9 fish per pound released. The catch was distributed primarily among the British Columbia commercial (34%), the Washington marine sport and commercial (38%), and the Columbia River gillnet (19%) fisheries (Figure 9).

CATCH TO ESCAPEMENT AND SURVIVAL

Returns to Columbia River hatcheries, both study and nonstudy, and to streams adjacent to these hatcheries were examined for marked chinook salmon (see Enumeration of Returns).

Mark return data were used to estimate catch to escapement ratios and total survival percentages for each special mark hatchery and all study hatcheries combined (Table 15). Only marked catches and escapements were used to develop the estimates to eliminate possible inflation of escapement values due to unmarked wild fish in hatchery returns. Survival estimates were calculated by dividing the potential marked catches and escapements by the marked releases. Potential marked catches and escapements are those that would be expected if marking did not cause post release mortalities. Potential marks were es-

TABLE 14.—Estimated catches of common marked fall chinook salmon and potential contribution from all Columbia River study hatcheries by fishery type and brood, 1963-69.

Brood year and fishery type	Estimated catch of common marked fish by year							Total Catch	Potential contribution[1] (in thousands)
	1963	1964	1965	1966	1967	1968	1969		
1961									
Marine sport	576	2,091	613	82	—	—	—	3,362	54.8
Marine commercial	3	8,778	3,034	366	—	—	—	12,181	198.1
Columbia River sport	0	21	0	0	—	—	—	21	0.4
Columbia River gillnet	98	1,651	3,407	197	—	—	—	5,353	86.8
Columbia River Indian[2]	50	852	411	7	—	—	—	1,320	21.0
Total	727	13,393	7,465	652	—	—	—	22,237	361.1
1962									
Marine sport	—	204	773	166	27	—	—	1,170	25.1
Marine commercial	—	79	2,981	1,490	108	—	—	4,658	97.0
Columbia River sport	—	12	8	0	0	—	—	20	0.5
Columbia River gillnet	—	31	879	680	21	—	—	1,611	33.9
Columbia River Indian[2]	—	11	392	21	3	—	—	427	8.7
Total	—	337	5,033	2,357	159	—	—	7,886	165.2
1963									
Marine sport	—	—	1,304	3,140	594	56	—	5,094	139.4
Marine commercial	—	—	71	9,016	3,317	284	—	12,688	344.5
Columbia River sport	—	—	0	0	0	0	—	0	0.0
Columbia River gillnet	—	—	88	1,194	2,168	315	—	3,765	101.0
Columbia River Indian[2]	—	—	38	103	453	42	—	636	17.3
Total	—	—	1,501	13,453	6,532	697	—	22,183	602.2
1964									
Marine sport	—	—	—	797	1,966	466	4	3,233	74.2
Marine commercial	—	—	—	53	4,757	2,492	108	7,410	169.8
Columbia River sport	—	—	—	0	0	0	0	0	0.1
Columbia River gillnet	—	—	—	27	692	1,034	188	1,941	43.9
Columbia River Indian[2]	—	—	—	1	405	307	17	730	16.8
Total	—	—	—	878	7,820	4,299	317	13,314	304.8

[1]Special marks included.
[2]Setnet and dip net fisheries.

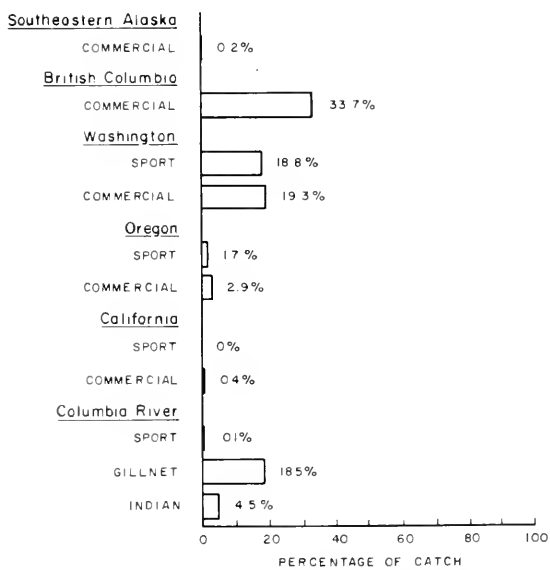

FIGURE 9.—Percentage of catch of 1961- to 1964-brood fall chinook salmon from 13 Columbia River study facilities taken by area and fishery, 1963-69. Percentages do not add to 100% due to rounding.

timated by dividing the mark recoveries by the appropriate special or common marked to unmarked relative survivals (see Contribution of Hatchery Fish).

Catch to escapement and survival estimates are of limited value for several reasons. First, adjacent tributary streams were surveyed during only three of the seven return years of the study (1964-66). Survey data are unavailable for at least one return year for each brood. Thus, all catch to escapement ratios are probably overestimated and survivals underestimated. Second, only a portion of the fish returning to the streams could be examined for marks. Total mark recoveries had to be estimated from the survey samples. Third, in some cases fish were delayed in entering adult holding facilities and may have strayed to other areas. Thus, some marked hatchery fish may not have been counted. Fourth, use of average relative survivals limited the accuracy of potential mark catches and returns and thus the total survival percentages. Relative survivals for individual hatcheries could have differed greatly from the averages.

Catch to escapement ratios and total survivals are needed to develop values for fisheries compensation and enhancement projects related to water use projects on the Columbia River system. Thus,

TABLE 15.—Marked catches and escapements, catch to escapement ratios, and total survivals for fish from each special mark hatchery and all study facilities combined, 1961-64 broods.

Hatchery	Brood	Marked catch	Marked escapement	Catch to escapement	Potential marked catch and escapement[1]	Marked releases	Total survival
Spring Creek	1961	4,400	613	7.2:1	12,691	1,133,019	0.011
	1962	967	92	10.5:1	3,416	866,892	0.004
	1963	2,407	374	6.4:1	11,492	751,243	0.015
	1964	4,406	228	19.3:1	15,924	600,953	0.026
Kalama River	1961	2,175	238	9.1:1	6,109	475,964	0.013
	1962	659	38	17.3:1	2,248	437,669	0.005
	1963	1,257	106	11.9:1	5,632	456,158	0.012
	1964	1,005	41	24.5:1	3,595	319,412	0.011
Elokomin	1961	235	33	7.1:1	678	480,533	0.001
OxBow	1961	336	99	3.4:1	1,101	450,446	0.002
Grays River	1962	215	5	43.0:1	710	241,494	0.003
Cascade	1962	191	6	31.9:1	635	541,158	0.001
Klickitat	1963	1,858	129	14.4:1	8,210	521,610	0.016
Big Creek	1963	914	380	2.4:1	5,347	579,967	0.009
Bonneville	1964	762	27	28.2:1	2,711	957,110	0.003
Little White Salmon	1964	303	37	8.2:1	1,168	797,345	0.001
All study facilities[2]	1961	22,237	3,399	6.5:1	42,164	5,446,439	0.008
	1962	7,886	675	11.7:1	17,948	5,249,079	0.003
	1963	22,183	2,737	8:1	66,989	5,986,464	0.011
	1964	13,314	856	15.6:1	31,629	4,638,237	0.007

[1]Assuming no mortality due to marking
[2]Includes common marks only

despite the limitations, we have included the values in this report.

Catch to escapement ratios for special mark hatcheries (Table 15) ranged from 2.4 to 1 (Big Creek, 1963 brood) to 43 to 1 (Grays River, 1962 brood). Average catch to escapements for Spring Creek and Kalama River hatcheries were 9.3 to 1 and 12.0 to 1 respectively. The catch to escapement ratios for all hatcheries combined, common marks only, show much less yearly variation than those for the special mark hatcheries. The average catch to escapement, all hatcheries and broods combined, was 8.6 to 1. Only common marks were combined for all hatcheries because these marks show only the variations among broods, not those among marks.

Total survivals ranged from 0.1% (Elokomin, 1961 brood; Cascade, 1962 brood; Little White Salmon, 1964 brood) to 2.6% (Spring Creek, 1964 brood). Average survivals for Spring Creek and Kalama River hatcheries were 1.3 and 1.0% respectively. For all hatcheries combined, the average survival was 0.7%.

Examination of Table 15 does not reveal any relationship between catch to escapement ratios and survivals. For example, at Spring Creek the 1964 brood had the highest catch to escapement ratio and percent survival. At Kalama River hatcheries, the 1964 brood had the highest catch to escapement ratio and the second highest survival value. The 1961 brood had the lowest catch to escapement and highest survival. For all study facilities, the 1964 brood had the highest catch to escapement ratio, and the 1963 brood had the highest total survival. The 1964 and 1961 broods had nearly equal survivals, but markedly different catch to escapements. The major reason for high 1964 brood catch to escapement ratios is the absence of adjacent stream surveys during three of the four return years for this brood.

ECONOMIC EVALUATION

A major purpose of this paper is to develop benefit to cost ratios for each of the special mark hatcheries and for each brood of the combined study facilities. To develop these ratios, the cost of rearing the four broods of chinook salmon and their potential value to the fisheries had to be estimated. The development of benefit to cost ratios is explained in detail by Worlund et al. (1969) and Wahle et al. (1974), but certain modifications will be discussed here briefly.

The values and benefit to cost ratios are higher in this report than those reported in our previous reports for five reasons: 1) the interest rate applied to capital costs is lower in this report (Wahle et al. 1974), 2) the sport value used is higher (see Value of Hatchery Contribution), 3) a lower marked fish relative survival figure was used for the 1961-brood (see Contribution of Hatchery Fish), 4) misidentified and partial marks were included in this report (see Contribution of Hatchery Fish), and 5) the potential catch contribution figures were used in this report rather than estimated catches (see Contribution of Hatchery Fish).

Cost Accounting and Value Estimation

Costs in Table 16 include capital and operation and maintenance costs applicable to the rearing of fall chinook salmon at each study facility. Capital costs for each facility were amortized over a 30-yr period from1940 to 1970 and divided among the species reared at the facilities. Capital costs applied to fall chinook salmon at all study facilities combined were $193,867, $169,616, $193,102, and $186,437 for the 1961-64 broods respectively.

Operation and maintenance costs were divided into two categories at each facility: fish food and drugs, and other operational costs. Operational costs other than food and drugs include costs for labor, personal services, travel, transportation of items, communication services, equipment, supplies and materials, and administration. Total operational and maintenance costs for the 1961-64 broods were $554,171, $489,947, $534,146, and $538,418 respectively.

Estimation of values is described under Value of Hatchery Contribution. Basically, the weights of commercial catches in each fishery were multiplied by the appropriate ex-vessel prices. The numbers of sport caught fish in all fisheries were multiplied by $18.35.

Valuation of the Potential Contributions

The value of the potential contribution to the fisheries of fall chinook salmon from Spring Creek National Fish Hatchery and Big White Salmon Pond were combined (Table 16). This was done because Spring Creek Hatchery personnel operated the Big White Pond, and Spring Creek fall chinook salmon stock was reared in the pond. Thus available Spring Creek operation and maintenance, and capital costs include the Big White facility. Values of Big White contributions were estimated using the ratio:

$$\frac{\text{Spring Creek value}}{\text{Spring Creek releases}} = \frac{\text{Big White value}}{\text{Big White releases}}.$$

For example, the 1961-brood Spring Creek value was $797,300. Releases were 10,925,933 and 3,545,865 1961-brood chinook salmon for Spring Creek and Big White respectively (Worlund et al. 1969). Thus, the Big White Salmon Pond value was estimated at $258,700. Values for the other broods were calculated in the same manner.

TABLE 16.—Values of the potential contributions, costs of rearing, and benefit (B) to cost (C) ratios for fish from each special mark hatchery and all study facilities combined, 1961-64 broods.[1]

Hatchery	Brood	Value ($)	Cost ($)	B/C ratio
Spring Creek[2]	1961	1,056,000	99,900	10.5/1
	1962	373,900	84,800	4.4/1
	1963	1,131,400	99,200	11.4/1
	1964	1,917,300	112,000	17.1/1
Kalama River	1961	481,900	100,700	4.8/1
	1962	199,800	104,700	1.9/1
	1963	582,000	97,600	6.0/1
	1964	392,700	110,700	3.5/1
Elokomin	1961	16,900	53,400	0.3/1
OxBow	1961	93,100	42,100	2.2/1
Grays River	1962	56,100	38,800	1.4/1
Cascade	1962	44,800	57,800	0.8/1
Klickitat	1963	373,200	32,800	11.4/1
Big Creek	1963	141,400	33,700	4.2/1
Bonneville	1964	279,300	81,000	3.4/1
Little White Salmon	1964	108,200	99,400	1.1/1
All study facilities	1961	2,738,800	748,000	3.7/1
	1962	1,306,100	659,600	2.0/1
	1963	5,224,100	727,200	7.2/1
	1964	2,758,000	724,900	3.8/1

[1]Values and costs rounded to the nearest $100.
[2]Includes Big White Salmon Pond values and costs

Combined Spring Creek and Big White values ranged from $373,900 (1962 brood) to $1,917,300 (1964 brood). The average value was $1,119,600. The costs averaged approximately $100,000 per brood. Benefit to cost ratios ranged from 4.4 to 1 to 17.1 to 1 and averaged 11.2 to 1. The 1961 brood had the largest contribution to the fisheries, yet the 1963 and 1964 broods had higher values. The reason for this is the increase in prices paid for troll caught fish from 1963 to 1969.

Values for the Kalama River hatcheries ranged from $199,800 (1962 brood) to $582,000 (1963 brood). The 1963 brood value was larger than the 1961 brood despite a smaller contribution for the 1963 brood. Again this was due to higher prices paid for troll chinook salmon in the later years of the study and also a larger 1963 than 1961 brood contribution to Washington and Oregon ocean sport fisheries. The average benefit over the four broods was $414,100. The average cost of rearing was $103,400 per brood. Benefit to cost ratios varied from 1.9 to 1 to 6.0 to 1 and averaged 4.0 to 1. The value of Elokomin Hatchery's potential contribution was $16,900 for the 1961 brood and the cost of rearing was $53,400. The benefit to cost ratio was then 0.3 to 1. OxBow's 1961 brood value was $93,100 and costs were $42,100 for a benefit to cost ratio of 2.2 to 1. The ratio was much higher for OxBow because OxBow chinook salmon contributed more heavily to ocean sport fisheries than Elokomin fish.

Contributions of 1962-brood Grays River and Cascade Hatchery fish were valued at $56,100 and

$44,800 respectively. The Grays River value is higher because of a larger contribution to the ocean sport fishery. The costs of rearing were $38,800 at Grays River and $57,800 at Cascade. The benefit to cost ratios were 1.4 to 1 and 0.8 to 1 for Grays River and Cascade respectively.

Klickitat and Big Creek Hatcheries' potential contributions of 1963-brood chinook salmon were valued at $373,200 and $141,400 respectively. The costs of rearing were $32,800 and $33,700 for the two hatcheries respectively. Benefit to cost ratios were 11.4 to 1 for Klickitat Hatchery and 4.2 to 1 for Big Creek Hatchery.

The values of the 1964 brood potential contributions were estimated at $279,300 for Bonneville Hatchery and $108,200 for Little White Salmon National Fish Hatchery. Rearing costs were $81,000 and $99,400 for the respective facilities. The benefit to cost ratios were 3.4 to 1 and 1.1 to 1 for Bonneville and Little White respectively.

Values of potential contributions for all study facilities combined ranged from $1,306,100 for the 1962 brood to $5,224,100 for the 1963 brood and averaged $3,006,800. Costs ranged from $659,600 to $748,000 for the 1962 and 1961 broods respectively. The average rearing costs were $714,900 per brood. Benefit to cost ratios ranged from 2.0 to 1 (1962 brood) to 7.2 to 1 (1963 brood) and averaged 4.2 to 1.

During the later years of the study, fall chinook salmon carcasses from study hatcheries were sold to commercial processors or donated to various institutions and groups. The value of these carcasses was determined from the average price paid by commercial processors. The estimated value was $31,467 for the 1963 brood (Arp et al. see footnote 4) and $42,000 for the 1964 brood (Wahle et al. see footnote 5). Thus the total value of 1963- and 1964-brood study hatchery fall chinook salmon was $5,255,600 and $2,800,000 respectively.

DISCUSSION

Brood Year Comparison

The 1963-brood Columbia River hatchery fall chinook salmon had the best potential contribution and value to the Pacific coast fisheries (Tables 16, 17). The 1963 brood had a potential contribution of 602,900 fish or 10 fall chinook salmon caught for every 1,000 releases and 1.7 fish per pound released. The 1963 brood contribution and catch to release ratios were followed in order by the 1961, 1964, and 1962 broods. The benefit to cost ratios followed a similar pattern, with the best ratio (7.2 to 1) for the 1963 brood followed by the 1964, 1961, and 1962 broods. The 1964 brood had a lower potential contribution than the 1961 brood, but a higher benefit to cost ratio because of higher prices paid for salmon when the 1964 brood was in the fisheries. Also total rearing costs for the 1964 brood were lower than the 1961 brood because fewer fish were raised.

The ocean distribution of the fall chinook salmon for all hatcheries combined was similar for all

TABLE 17.—Potential contributions, numbers of smolts released, pounds of smolts released, contribution in fish caught per 1,000 released, and contribution per pound released for each special mark hatchery and all study facilities combined, 1961-64 broods.

Hatchery	Brood	Contribution (in thousands)	Releases (in thousands)		Contribution	
			Number	Pounds	Per 1,000 released	Per pound released
Spring Creek	1961	107.4	10,925.9	48.0	9.8	2.2
	1962	30.3	8,408.3	48.9	3.6	0.6
	1963	98.8	7,467.6	34.7	13.2	2.8
	1964	165.2	6,554.5	42.4	25.2	3.9
Kalama River	1961	56.8	4,906.8	16.8	11.6	3.4
	1962	22.3	4,599.3	21.0	4.8	1.1
	1963	55.6	4,883.9	26.8	11.4	2.1
	1964	37.7	3,496.6	21.0	10.8	1.8
Elokomin	1961	2.0	1,575.0	8.1	1.3	0.2
OxBow	1961	8.5	4,550.0	21.0	1.9	0.4
Grays River	1962	3.9	1,359.8	9.6	2.9	0.4
Cascade	1962	4.8	4,217.9	21.9	1.1	0.2
Klickitat	1963	42.5	2,888.2	19.5	14.7	2.2
Big Creek	1963	12.9	1,985.8	19.4	6.5	0.7
Bonneville	1964	27.1	9,887.6	62.1	2.7	0.4
Little White Salmon	1964	11.0	8,365.6	47.3	1.3	0.2
All study facilities	1961	361.1	53,653.2	250.9	6.7	1.4
	1962	165.2	52,470.0	278.5	3.1	0.6
	1963	602.2	60,112.1	350.7	10.0	1.7
	1964	304.8	46,778.6	322.2	6.5	0.9

four brood years (Table 18). Washington marine fisheries took the largest catch of Columbia River study hatchery fall chinook salmon followed by British Columbia, Columbia River, and Oregon fisheries. The combined Washington commercial and sport marine catches from the 1961-63 broods were equal to or greater than the British Columbia commercial catch and were between 33 and 39% of the catch of Columbia River study hatchery fall chinook salmon. For the 1964 brood the Washington catch was over 1½ times as large as the British Columbia catch and approached one-half of the total 1964-brood study hatchery fall chinook salmon catch. The British Columbia commercial catch ranged from 27 to 39% of the study hatchery fall chinook salmon catch. The combined Columbia River sport and commercial catch by brood ranged from 20 to 30% of the study hatchery catch. The Oregon ocean portion of the catch ranged from 1 to 9%. The California portion was 1% or less. Less than 0.5% of Columbia River study hatchery fish were taken in the Alaska fisheries, but these fisheries were incompletely sampled.

Kalama River and Spring Creek hatcheries, the only hatcheries with special marks all four brood years, did not follow the combined hatchery pattern. For the Kalama River hatcheries the 1961 brood had the largest contribution and best catch to release ratio, followed in order by the 1963, 1964, and 1962 broods (Table 17). The benefit to cost ratios, however, did not follow this pattern primarily because of higher prices paid for salmon in the later years of the study. The 1963 brood had the best benefit to cost ratio, followed by the 1961, 1964, and 1962 broods respectively (Table 16).

Distribution of the Kalama fish was more northerly than the combined distribution for all study hatcheries (Table 18). About 1% of the Kalama fish were caught in the Alaska fisheries during the years when these fisheries were sampled. The British Columbia portion of the Kalama contribution ranged from 42 to 60%. The Washington marine fisheries took from 23 to 43% of the Kalama fall chinook salmon. When the Washington catch was at its highest (1963 brood), the British Columbia catch was at its lowest. The Columbia River sport and commercial catches of Kalama fish ranged from 11 to 26%. In general, the larger the percentage taken by the British Columbia and Washington fisheries, the smaller the percentage of Kalama fish taken by the Columbia River fisheries. The Oregon ocean fisheries took 1 to 3% of the Kalama chinook salmon and the California fisheries took very few Kalama fish.

The brood year comparison of Spring Creek contribution also differed from the comparison of all hatcheries combined. The 1964 brood showed the best potential contribution followed by the 1961, 1963, and 1962 broods (Table 17). The catch to release and benefit to cost ratios were best for the 1964 brood followed by the 1963, 1961, and 1962 broods (Table 16).

The ocean distribution of the Spring Creek

TABLE 18.—Percentage of catch of Columbia River study hatchery fall chinook salmon taken by each fishery, 1961-64 broods.[1]

Hatchery	Brood	Fishery					
		Alaska	British Columbia	Washington	Oregon	California	Columbia River
Spring Creek	1961	0	23	43	4	1	30
	1962	0	18	41	2	0	39
	1963	0	34	41	3	(2)	21
	1964	0	24	45	7	(2)	23
Kalama River	1961	2	48	23	1	(2)	26
	1962	1	58	24	2	0	15
	1963	2	42	43	3	0	11
	1964	0	60	23	3	1	13
Elokomin	1961	0	21	47	13	3	16
OxBow	1961	0	13	51	15	2	19
Grays River	1962	0	12	74	5	7	2
Cascade	1962	0	43	36	2	1	19
Klickitat	1963	0	39	32	15	4	10
Big Creek	1963	0	16	57	8	1	19
Bonneville	1964	0	29	46	17	4	4
Little White	1964	0	41	47	3	5	4
All study facilities	1961	(2)	33	33	3	(2)	30
	1962	(2)	39	33	1	1	26
	1963	(2)	36	39	5	(2)	20
	1964	(2)	27	44	9	(2)	20

[1]Percentages may not add to 100 due to rounding
[2]Less than 0.5%.

Hatchery fall chinook salmon was more southerly than those of the Kalama or combined study hatcheries (Table 18). The British Columbia catch ranged from 18 to 34% of the total Spring Creek contribution. The Washington marine fisheries took 41 to 45%. The catch of Spring Creek fish in the Oregon ocean fisheries ranged from 2 to 7%. The maximum California take of these fish was just over 0.5%. The Columbia River catch of Spring Creek fish (21 to 39%) was higher than the percent catch of Kalama or all hatcheries combined. This is to be expected since the Spring Creek chinook salmon are exposed to more river fisheries because of the upriver location of the hatchery.

Hatchery Comparison

A hatchery comparison is made difficult by the great differences in contribution between brood years. Thus these comparisons are not a reflection of the value of any particular hatchery as a fall chinook salmon station nor are they a criticism of rearing techniques at any of the hatcheries. In general, the best catch to release and benefit to cost ratios occurred for the 1963-brood special marked hatchery fish (Tables 16, 17). The poorest ratios generally occurred for the 1962-brood special mark hatchery chinook salmon. This follows the pattern of the common marked fish. The 1964-brood Spring Creek fall chinook salmon had the best catch to release and benefit to cost ratios of 10 special mark hatcheries. The Cascade Hatchery 1962-brood chinook salmon had the poorest catch to release ratio, and the 1961-brood Elokomin Hatchery fish had the poorest benefit to cost ratio.

The general distribution of fall chinook salmon from special mark hatcheries was similar in that a majority of the fall chinook salmon were caught north of the Columbia River mouth in the Washington and British Columbia ocean fisheries (Table 18). However, the percent catch of each hatchery's fish varied greatly within each fishery. The percent catch ranged from 12% (Grays River 1962-brood falls) to 60% (Kalama 1964 brood) in the British Columbia fisheries. Percent catch by Washington ocean fisheries ranged from 23% for 1961- and 1964-brood Kalama River fish to 74% for 1962-brood Grays River chinook salmon. Washington fisheries took the largest portion of the catch for all but Kalama, Cascade, and Klickitat hatcheries. The British Columbia exceeded the Washington catch for these facilities except for the 1963-brood Kalama fish where the Washington catch was slightly higher. As the percentage of the catch taken by the British Columbia fisheries increased, the percentage taken by other fisheries (particularly Washington) naturally decreased. Percent catches in the Oregon fisheries ranged from 1 to 17% for 1961-brood Kalama and 1964-brood Bonneville fish respectively. In the California fisheries, percentages ranged from 0% for Spring Creek and Kalama fish to 7% for Grays River fish. Columbia River catch portions ranged from 2 to 39% for the Grays River and Spring Creek 1962-brood fish respectively.

COLUMBIA RIVER HATCHERY CONTRIBUTION TO PACIFIC COAST FISHERIES

This report covers the contributions of 13 fall chinook salmon study facilities on the Columbia River for brood years 1961 through 1964. These broods were also released from other hatcheries on the Columbia system. From 1962 through 1965, seven nonparticipating facilities released fall chinook salmon during one or more years (Table 19). Experimental releases made from three facilities were not included. A total of 26 million 1961-64-brood fall chinook salmon migrants were released from nonstudy hatcheries. We have assumed nonstudy hatchery releases had the same distribution and contribution as the study facility average. In this way, we have incorporated the catches of nonstudy hatchery fall chinook salmon into those from study hatcheries to estimate the total contribution and value of Columbia River 1961-64-brood hatchery fall chinook salmon. From 1963 through 1969 the estimated total catch in the fisheries sampled of the 1961-64-brood chinook salmon, wild and hatchery, was 9,894,200 (Table 20). Marine sport and commercial catches include three races of chinook salmon, i.e., spring, summer, and fall. Columbia River catches include

TABLE 19.—Releases of 1961- to 1964-brood migrant fall chinook salmon from Columbia River nonstudy hatcheries.

Hatchery	1961 brood	1962 brood	1963 brood	1964 brood
Abernathy	1,077,519	1,806,164	836,375	719,228
Lewis River	477,462	0	275,965	0
Speelyai	456,550	0	0	0
Toutle	992,559	3,075,052	2,580,198	5,730,659
Klaskanine	568,032	137,132	252,216	191,636
Sandy	231,999	144,848	969,154	1,000,418
Eagle Creek	0	2,435,531	1,427,326	1,054,720
Total	3,804,121	7,598,727	6,341,234	8,696,661

TABLE 20.—Percent contribution of Columbia River hatchery fall chinook salmon in the Pacific coast fisheries sampled for marks, 1961-64 broods.

Region	Fishery type	Estimated catch of hatchery fall chinook salmon[1]	Estimated total catch of chinook salmon[2]	Percent hatchery contribution
Marine fisheries:				
Southeastern Alaska	Commercial	2.6	754.3	0.3
British Columbia	Commercial	496.1	4,048.4	12.3
Washington	Sport	276.3	897.4	30.8
	Commercial	286.0	576.5	49.6
Oregon	Sport	24.6	97.6	25.2
	Commercial	43.0	302.6	14.2
California	Sport	0.4	248.1	0.2
	Commercial	5.6	2,171.0	0.3
Freshwater fisheries:				
Columbia River	Sport	0.9	27.4	3.3
	Gillnet	273.6	658.3	41.6
	Indian[3]	58.5	112.6	52.0
Total	All fisheries	1,467.6	9,894.2	14.8

[1]Includes study and nonstudy Columbia River hatcheries which reared 1961- to 1964-brood fall chinook salmon.
[2]Marine catches include all races of chinook salmon; Columbia River catches include only fall chinook salmon.
[3]Setnet and dip net fisheries.

only fall chinook salmon. We estimated 1,467,600 fish or 14.8% were Columbia River hatchery fall chinook salmon. The proportions of fall chinook salmon in each of the fisheries sampled that were of Columbia River hatchery origin are presented in Figure 10. The percentages are averages obtained by summing the 1961-64-brood fall chinook salmon catches from Columbia River hatcheries and dividing by the total 1961-64-brood chinook salmon catches in the Pacific coast fisheries sampled for marks (Table 20).

The importance of Columbia River hatchery fall chinook salmon to the Pacific coast fisheries is readily evident in Figure 10. Columbia River hatchery fall chinook salmon compose nearly one-half of the Washington commercial and nearly one-third of the Washington marine sport chinook salmon catches. The Oregon ocean sport catch of chinook salmon is one-fourth Columbia River hatchery fall chinook salmon. The low sampling percentage (averaging $<5\%$) may be the reason for the apparent lack of hatchery contribution to the Columbia River sport fall chinook salmon fishery.

The contributions to the fisheries from the seven Columbia River nonstudy hatcheries were 24,100, 22,700, 61,800, and 53,500 fall chinook salmon for the 1961-64 broods respectively. Values of the contributions were calculated using the ratio:

$$\frac{\text{Study hatchery value}}{\text{Study hatchery contribution}} = \frac{\text{Nonstudy hatchery value}}{\text{Nonstudy hatchery contribution}}.$$

The values calculated for the nonstudy hatchery chinook salmon were \$182,900, \$179,100, \$538,700, and \$484,600 for the four broods respectively. The total values for all 1961-64-brood Columbia River hatcheries by brood were \$2,921,700, \$1,485,200, \$5,794,300, and \$3,284,600 respectively.

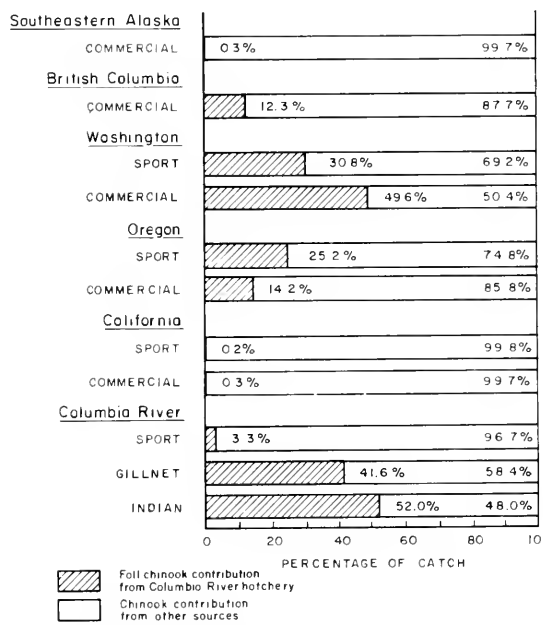

FIGURE 10.—Percentage contribution of 1961- to 1964-brood Columbia River hatchery fall chinook salmon to the total chinook salmon catch in each Pacific coast fishery, 1963-69. Marine fisheries include all races of chinook salmon; Columbia River fisheries include only fall chinook salmon.

SUMMARY

In 1962 a marking experiment was initiated to determine the bioeconomic contribution of Columbia River hatchery fall chinook salmon. From

1962 through 1965, 30.9 million 1961-64-brood fall chinook salmon were marked at 12 Columbia River hatcheries and one rearing pond. Four brood years were marked to examine the differences between broods. A mark common to all 13 facilities was used for each brood. Common marks were applied to 21.3 million fish. To examine the differences between hatcheries, four hatcheries were assigned special marks for each brood. Two hatcheries, Kalama River (in this study Kalama Falls and Lower Kalama Hatcheries were treated as one facility) and Spring Creek, had special marks for all four brood years. Special marks were applied to 9.6 million fish.

Sampling for these marked chinook salmon took place from 1963 through 1969. Major marine sport and commercial fisheries from southeastern Alaska to central California and Columbia River fisheries were sampled for marks, and scale samples were taken for age determination. Mark sampling ranged from 14 to 28% of the catch, and age sampling ranged from 1 to 4% by year. During the 7 yr of sampling, 3.3 million chinook salmon were sampled for marks and 208,000 were sampled for age.

Returns to the 13 study facilities, adjacent streams, and nonstudy hatcheries rearing fall chinook salmon were sampled for marked 1961-64-brood fish. Hatchery returns of these broods numbered 155,800 fish, of which 8,500 were marked. The stream sampling was conducted from 1964 through 1966 with 62,400 chinook salmon examined and 1,600 marked fish found.

Hatchery contribution estimation is dependent on the validity of six assumptions. Where practical, these assumptions were tested with additional studies and data collections. Assumption 1 (that the marks were permanent) was tested by holding marked fish in saltwater ponds for periodic examination. Some regeneration did occur but, since double and triple marks were applied, the marked fish remained identifiable throughout their life. Assumption 2 (that fish detected and reported with the kinds of marks applied at the hatcheries are hatchery fish) was tested by examining hatchery fingerlings and 1965-brood chinook salmon catches for study marks. Over 30 million hatchery fingerlings were examined, and only 201 missing ventral and 156 missing adipose fins (none together) were found. The attempt to keep 1965-brood chinook salmon from being marked with study marks was unsuccessful. However, ocean and Columbia River catches of study marks were adjusted for those marks that appeared to have a natural origin. Assumption 3 (fish were correctly aged from scales) was examined by having six scale readers from State, Provincial, and Federal agencies read 400 scales from fish of known age. The readers correctly aged 83% of the scales. Hatchery returns showed survival adjustments had to be made for assumption 4 (equality of survival and maturity schedules for marked and unmarked fish). Assumption 5 (the equality of ocean distribution and catch vulnerability of marked and unmarked fish) is supported by ocean tagging studies showing similar distributions for marked and unmarked hatchery fish. A 10-part sampler was used to select fish for marking thus insuring the validity of assumption 6 (the marking of equal proportions of each hatchery's production).

Estimated catches of special marked fish from the 10 special mark facilities ranged from 191 (Cascade, 1962 brood) to 4,406 (Spring Creek, 1964 brood). During the 7 yr of sampling, 65,620 common marked fish were estimated to have been caught: 22,237, 1961 brood; 7,886, 1962 brood; 22,183, 1963 brood; and 13,314, 1964 brood.

Columbia River hatchery fish were captured in marine fisheries from Alaska to California. Marine catches were primarily in British Columbia and Washington fisheries. Fall chinook salmon from the Kalama River hatcheries had a more northerly distribution than those from other special mark hatcheries. Kalama fish had the highest percentage catches of any special marked hatchery chinook salmon in Alaska and British Columbia fisheries. The average common marked fish catch distributions in percent of the total chinook salmon catch for the 1961-64 broods combined were: 0.2, Alaska commercial fisheries; 33.7, British Columbia commercial fisheries; 38.1, Washington marine fisheries; 4.6, Oregon ocean fisheries; 0.4, California ocean fisheries; and 23.1, Columbia River fisheries.

The potential contribution of Spring Creek 1961-64-brood fall chinook salmon ranged from 30,300 (1962 brood) to 165,200 (1964 brood) with an average of 100,500 fish per brood. The average catch to release ratio was 12 fish per 1,000 fish released from Spring Creek. The Kalama hatcheries potential contribution ranged from 22,300 (1962 brood) to 56,800 (1961 brood) and averaged 43,100 fish per brood. The average catch to release ratio for the two Kalama facilities was 9.6 fish for each 1,000 released. Potential contributions at the

eight other special mark hatcheries (OxBow, Elokomin, Grays River, Cascade, Klickitat, Big Creek, Bonneville, and Little White Salmon) ranged from 2,000 fish (Elokomin, 1961 brood) to 42,500 (Klickitat, 1963 brood). The range of catch per 1,000 fish released was from 1.1 (Cascade, 1962 brood) to 14.7 (Klickitat, 1963 brood). The potential contribution for all study facilities combined ranged from 165,200 (1962 brood) to 602,200 (1963 brood). The average contribution was 358,500 fall chinook salmon per brood. The average catch per 1,000 smolts released was 6.7 fish.

Catch to escapement ratios ranged from 2.4 to 1 (Big Creek, 1963 brood) to 43.0 to 1 (Grays River. 1962 brood). Total survivals ranged from 0.1% (Elokomin, 1961 brood; Cascade, 1962 brood; Little White Salmon, 1964 brood) to 2.6% (Spring Creek, 1964 brood). Spring Creek Hatchery's average catch to escapement ratio was 9.3 to 1 and the average survival was 1.3%. The average catch to escapement and survival values for the Kalama River hatcheries were 12.0 to 1 and 1.0%. For all facilities and the four broods combined, the average survival was 0.7% and the average catch to escapement was 8.6 to 1.

Spring Creek Hatchery and Big White Pond values were combined because Spring Creek personnel operated the Big White facility making costs inseparable. The average cost of rearing each brood at the two facilities was approximately $100,000. The average value of the potential contribution was $1,119,600. The average benefit to cost ratio was 11.2 to 1. The average cost of rearing the 1961-64 broods of chinook salmon at the two Kalama hatcheries was $103,400. The average benefit from their production was $414,100, yielding a benefit to cost ratio of 4.0 to 1. For the other eight special mark hatcheries, costs ranged from $32,800 (Klickitat, 1963 brood) to $99,400 (Little White, 1964 brood), benefits from $16,900 (Elokomin, 1961 brood) to $373,200 (Klickitat, 1963 brood), and benefit to cost ratios from 0.3 to 1 (Elokomin, 1961 brood) to 11.4 to 1 (Klickitat, 1963 brood). The average cost of rearing the four broods, all study facilities combined, was $714,900. The average benefit was $3,006,800, for an average benefit to cost ratio of 4.2 to 1.

Fall chinook salmon releases from seven nonstudy Columbia River hatcheries totaled 26 million fish for the 1961-64 broods. If we assume these fish had a catch distribution and contribution like the 13 study facilities, then the estimated total catch of fall chinook salmon from all Columbia River hatcheries is 1,467,600 fish. The 1961- to 1964-brood fall chinook salmon caught in marine fisheries sampled from Alaska to California and Columbia River fisheries was 14.8% of the total chinook salmon catch. The portions of the total chinook salmon catch by region originating from fall chinook salmon raised at Columbia River hatcheries were: Alaska, 0.3%; British Columbia, 12.3%; Washington, 38.2%; Oregon, 16.9%; California, 0.2%; and Columbia River, 41.7%.

The 1961-64-brood Columbia River hatchery (study and nonstudy) contributions were valued at $2,921,700, $1,485,200, $5,794,300, and $3,284,600 by brood respectively.

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POLYCHAETOUS ANNELIDS OF THE DELAWARE BAY REGION

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ABSTRACT

Between 1967 and the present, 1,303 quantitative and 887 qualitative samples were taken from 10 different areas in the Delaware Bay region. Four major areas were examined: Delaware Bay proper, two smaller bays, the coastal areas, and offshore on the midcontinental shelf. A total of 125 species of polychaetous annelids representing 34 families and 88 genera were identified. The greatest number of species (95) was collected at the offshore stations, which also had the highest genus to species ratio (1:1.6). Delaware Bay samples contained 83 species and the coastal areas 74 species. The smallest number of species was collected in the small bays (33). The dominant species on the midcontinental shelf were: *Goniadella gracilis, Lumbrinerides acuta, Spiophanes bombyx, Exogone hebes,* and *E. verugera.* In Delaware Bay, *Heteromastus filiformis, Nephtys picta,* and *Glycera dibranchiata* were collected most regularly. The polychaete fauna of three epifaunal assemblages (mussel bed, serpulid "reef," and oyster beds) were also examined. Increasing numbers of *Nephtys picta, Glycera dibranchiata,* and *Heteromastus filiformis* were associated with sediments containing increasing amounts of silt-clay in Delaware Bay. *Lumbrinerides acuta* and *Goniadella gracilis* were associated with poorly sorted coarse sediments (>1 mm) on the continental shelf. A zoogeographic analysis revealed this area to be the southern limit of the range for 11 species and the northern limit for 3 species. The Delaware fauna was more closely related to the northern fauna than to the southern fauna. A summary is given for some recent taxonomic changes in species present in the coastal waters of the eastern United States.

This account was prepared to review the composition, distribution, and general ecology of polychaetous annelids in the Delaware Bay region. The most comprehensive treatment of polychaetes from the northeast Atlantic off the United States was presented by Pettibone (1963a). She reported 183 species from 29 families; cited records of depth, sediment preference, and reproductive condition; and collated and reviewed the works of Webster, Benedict, Verrill, Treadwell, Moore, Hartman, and others. Since then, she has published research on paraonids, spionids, sigalionids, pilargids, and nereids from the northeast Atlantic (Pettibone 1962, 1963b, 1965, 1966, 1970a, b, 1971). Hobson (1971) has added some additional records to the polychaetes of New England. Deepwater polychaetes from the western Atlantic Ocean, including New England, were described by Hartman (1965) and Hartman and Fauchald (1971). Gosner (1971) prepared a key for invertebrates from Cape Hatteras to the Bay of Fundy and listed 213 species of polychaetes. Pratt[3] reviewed the literature on polychaetes from Nantucket to Cape Hatteras.

In nearshore waters off North Carolina, Hartman (1945) reported 104 species of polychaetes and presented information on tube building, reproductive maturity, and faunal associations. Wells and Gray (1964) listed 110 species from the Cape Hatteras area and mainly emphasized the zoogeographic affinities of the polychaetes. Day et al. (1971) analyzed distributional patterns of the benthic fauna across the continental shelf off Beaufort, N.C., from the shore to 200 m in depth. Later, Day (1973) reported 229 species of polychaetes from the shelf study and prepared a guide for the species known from North Carolina. More recently, Gardiner (1975) provided a key to 163 species of errant polychaetes from intertidal and shallow subtidal zones of North Carolina. Wass (1972) compiled a valuable list of the benthic fauna of Chesapeake Bay, including polychaetes, with annotated records of ecological data.

The earliest work on polychaetes in the Delaware Bay area was conducted by Leidy (1855) and Webster (1880, 1886). Polychaetes associated with oyster beds in Delaware were discussed by Maurer and Watling (1973). Wells (1970) and Curtis (1975) described reefs of "sand coral" (*Sabellaria vulgaris*) from the shores of Delaware.

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[3]Pratt, S. D. 1973. Benthic fauna. *In* S. B. Saila (editor), Coastal and offshore environmental inventory, Cape Hatteras to Nantucket Shoals, 5:1-70. Univ. R.I., Mar. Publ. Ser. 2.

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METHODS

Since 1967, a large number of quantitative (1,303) and qualitative (887) samples of benthic invertebrates have been collected throughout the Delaware Bay region. The major collecting areas are designated with letters and presented in Figure 1. Since the objectives of the various surveys differed, the sampling pattern and season, number of samples, frequency of sampling, collecting gear and sieve type, environmental data, and type of analysis also varied (Table 1). A local reference collection was established and verified with the polychaete collection in the U.S. National Museum.

ENVIRONMENTAL SETTING

The general environmental setting is discussed as four major areas: Delaware Bay proper, small bays, coastal areas, and offshore. Polychaetes were collected from a variety of habitats which have been designated as follows:

Delaware Bay area (Figure 1)
- Delaware Bay proper
  - Baywide (A)
  - Bay mouth (B)
  - Midbay (C)
    - Sandy shoals (Brown Shoal, Lower Middle Shoal, Old Bare Shoal)
    - Muddy sand bottom
    - Epifaunal-infaunal assemblages (blue mussel assemblage; calcareous serpulid assemblage)
  - Oyster beds (Delaware Bay; Broadkill, Mispillion, Murderkill, St. Jones, and Leipsic Rivers) (D)
  - Intertidal—Cape Henlopen (E)
- Small Bays
  - Rehoboth and Indian River Bays (F)
- Coastal areas
  - Bethany Beach (G)
  - Hen and Chickens Shoal (H)
  - Off mouth of Delaware Bay (I)
- Offshore
  - Midshelf site (J)

The letters in parentheses refer to letters used to designate areas in Figure 1.

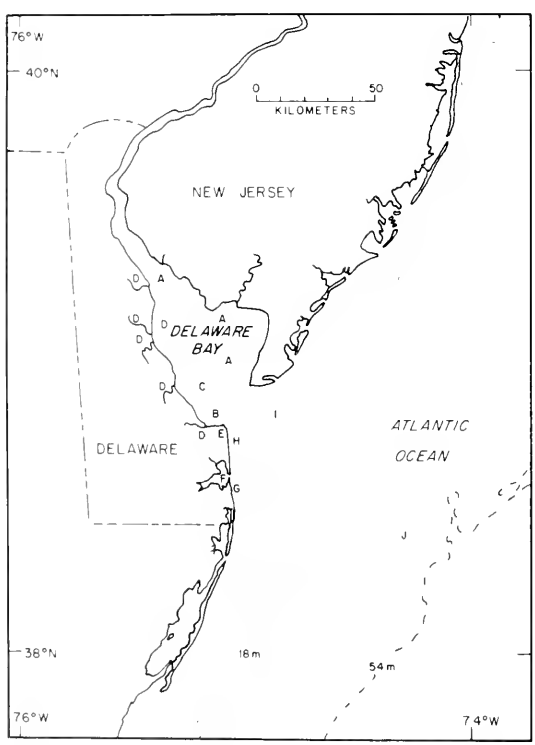

FIGURE 1.—Polychaete sampling in the Delaware Bay region. The sampling areas are: A. baywide, B. bay mouth, C. midbay, D. oyster beds, E. intertidal, F. small bays, G. Bethany Beach, H. Hen and Chickens Shoal, I. off Delaware Bay mouth, and J. midshelf site.

Delaware Bay Proper

The morphology, geology, and sediment distribution of Delaware Bay (Figure 1, A) was described by Shuster,[4] Kraft,[5] Weil (1975), and Watling and Maurer.[6] Salinity values were 5-8‰ at the northern limit of sampling and 30-31‰ near the bay mouth, with the major part of the area being polyhaline (18-30‰) (Table 1). Sediment at the bay mouth was generally medium sand (1-2ϕ), with the coarsest material in the middle of the bay (Figure 2). Sand farther up the bay became finer (2-3.5ϕ), with medium sand in the center channel. Sediments along both sides of the estuary were fine, with as much as 90% silt-clay in some samples. In sediments from the northernmost tran-

[4]Shuster, C. N. 1959. A biological evaluation of the Delaware River Estuary. Univ. Del. Mar. Lab., Inf. Ser., Publ. 3, 77 p.

[5]Kraft, J. C. 1971. A guide to the geology of Delaware's coastal environments. Univ. Del., Coll. Mar. Stud. Publ. No. 2GL039, 220 p.

[6]Watling, L., and D. Maurer (editors). 1976. Ecological studies on benthic and planktonic assemblages in lower Delaware Bay. NSF/RANN. Univ. Del., Coll. Mar. Stud. Publ., 630 p.

TABLE 1.—Summary of collecting and environmental data for Delaware Bay area polychaetous annelids (areas shown in Figure 1).

Area	Sampling pattern, number of samples, frequency of sampling	Collecting gear and processing	Salinity (‰)	Depth (m)	Substrate	Source
Baywide (A)	Transects; 207 samples; summer 1972, 1973	0.1-m² Petersen grab, 1.0-mm mesh seive	5.0-31.0	1.0-50.0	Bay mouth 1-2ϕ, midbay 2-3.5ϕ; Delaware side coarse sand, fine sediment along both shores	Watling and Maurer (see text footnote 5)
Bay mouth (B)	Random spacing, 277 samples; Dec. 1971, Mar. 1972, June 1972	0.1-m² Petersen grab, 1.0-mm mesh sieve	23.0-29.0	1.0-30.0	100% silt-clay, medium to coarse sand in northwest	Maurer et al. (see text footnote 6)
Midbay (C)	Selected stations; 170 samples; May, Aug., Nov. 1974, Feb., May 1975; 60 samples, August 1975	0.1-m² Petersen grab, 1.0-mm mesh sieve; dredges 2.0, 1.0, 0.5, 0.25 mesh sieves	21.0-29.7	3.0-35.0	Well sorted shoal sands, mud (30% silt-clay, calcareous serpulid reef, bimodal sediment with silt and coarse sand)	Watling and Maurer (see text footnote 5)
Oyster beds in rivers, bay (D)	Random spacing; ≥ 800 samples from 1967 to 1971	Oyster dredge, 1 gal sample, 0.25-mm mesh sieve	2.0-33.0 20.0-28.5	0.5-6.0 2.5-8.0	Hard shell bottom intercalated with mud and muddy shell bottom	Maurer and Watling (1973)
Intertidal (E)	Transects; 200 samples; monthly from 1970 to 1972	25 × 25 cm core, 1.0-mm mesh sieve	26.0-31.0		Sediment ranged from coarse sand (>0ϕ) to fine sand (<2ϕ)	Maurer (unpubl.)
Small bays Rehoboth and Indian River (F)	Transects; 146 samples, transects; 127 samples; both summer, winter 1968-70	0.07-m² Petersen grab, 1.0-mm mesh sieve	20.1-30.8 7.5-31.9	0.6-5.8 0.5-6.7	Clean sand, sediment near creek mouths, silty-sand; coarse sand at bay mouth, silty sand increase towards river	Maurer (in press)
Coastal: Bethany Beach (G)	Transects; 144 samples; July, Oct. 1973, Jan., Apr. 1974	0.1-m² Petersen grab, 1.0-mm mesh sieve	28.5-30.7	9.0-12.0	Sediment ranged from silt sand (3.5ϕ) to gravelly sand (−0.5ϕ) finest sediment contained 30-33% silt-clay	Maurer et al. (see text footnote 8)
Hen and Chickens Shoal (H)	Transects; 144 samples; July, Oct. 1973, Jan., Apr. 1974	0.1-m² Petersen grab; 1.0-mm mesh seive	27.2-29.8	3.0-24.0	Coarse sand (>2ϕ) in deepest areas, medium sand (2-3ϕ) off shoals, well sorted sand on shoal	Maurer et al. (see text footnote 8)
Off Delaware Bay mouth (I)	Random spacing; 27 samples; 27 samples, July 1972	0.1-m² Van Veen grab, oyster dredge, 1.0-mm mesh sieve	28.2-32.5	15.2-42.5	Medium sand (2-3ϕ) with silt in depressions	Watling et al. (1974)
Offshore (J)	Random spacing; 160 samples; May, Nov. 1973, Mar. 1974	0.4-m² Shipek grab, all sediment examined or 0.25-mm mesh sieve	31.0-40.0	30.0-57.0	Medium sand, some sediment with >25% gravel	Maurer et al. (1976) Watling et al. (1974)

sects, medium sands (1.5-3.0ϕ) were restricted to the ship channel, grading rapidly into finer sediments (7.0ϕ) away from the channel.

At the interidal site (E) just inside Cape Henlopen (Figure 1), salinity ranged from 26.0 to 31.0‰, but it became higher in trapped shallow ponds during the summer. Sediment consisted of a fine sand (<2.0ϕ) at the northwest end of the flat and a coarse sand (>0ϕ) at the ocean end. Environmental data, including sediment distribution, surface and bottom temperature, salinity, and dissolved oxygen, are discussed more extensively by Maurer et al. (1971), Maurer et al.,[7] Kinner et al. (1974), and Watling and Maurer (see footnote 6).

Small Bays

Delaware has several small bays (F), which have received considerable attention in recent years (Logan and Maurer 1975; Watling 1975; Brenum 1976; Maurer in press; Jones et al.[8]). In Rehoboth Bay, salinity varied seasonally from 20.1 to 30.8‰ and the average silt-clay in the sediment was 40.3%. Salinities in Indian River Bay ranged from 27.7 to 31.9‰ at the mouth of the bay and 7.5 to 19.3‰ near the Indian River. Sediment was similar to that in Rehoboth Bay, except that the bay mouth contained coarse sand and shell fragments.

Coastal Areas

In coastal waters, collections were concentrated at three sites (Figure 1; G, H, I). The annual mean range of salinity was 28.5-30.7‰ and 27.2-29.8‰ at Bethany Beach (G) and Hen and Chickens Shoal (H), respectively. Sediment at the two sites can be characterized as medium sand. Occasional depressions and holes trapped finer grained sediment. The deeper areas of Hen and Chickens Shoal

[7]Maurer, D., R. Biggs, W. Leathem, P. Kinner, W. Treasure, M. Otley, L. Watling, and V. Klemas. 1974. Effect of spoil disposal on benthic communities near the mouth of Delaware Bay. Univ. Del., Coll. Mar. Stud. Publ., 200 p.

[8]Jones, R. D., L. D. Jensen, and R. W. Koss. 1974. Environmental responses to thermal discharges from the Indian River station, Indian River, Delaware. Rep. 12, Cooling Water Studies for Electric Power Research Institute, Res. Proj. (RP-49).

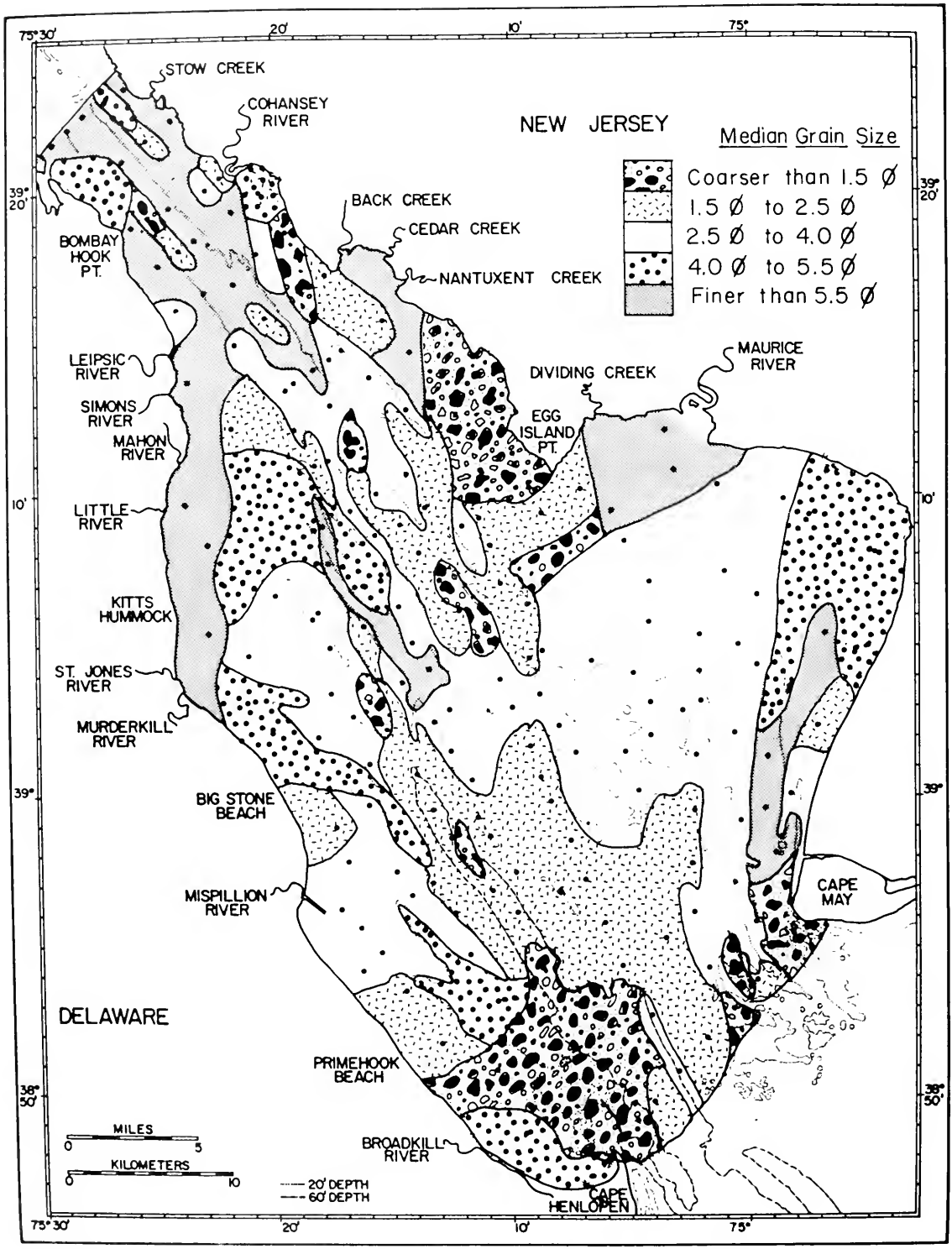

FIGURE 2.—Mean grain size for surface sediment in Delaware Bay. Dots represent the baywide (A) sampling stations.

also contained large rocks, small boulders, and mussel beds. A detailed account of these areas can be found in Maurer et al.[9] Although Area I was about 20 km off the Delaware Bay mouth, the western portion of this area appeared to be influenced by the hydrography of Delaware Bay. Salinity ranged from 28.2 to 32.5‰ and the sediment varied from silty-sand to gravelly sand. However, a few sediment samples contained black mud (30-33% silt-clay and 2.63-3.64% organic content) (Watling et al. 1974).

Offshore

The oceanic or offshore area, termed midshelf site (Figure 1, J), has been the subject of several studies. An extensive review of the hydrography and geology was presented by Bumpus et al.[10] and Milliman.[11] Salinity was 31-40.0‰ and the sediment was dominated by clean sand with some pebbles and dead shells at the collecting site. Ridge and swale microtopography influences sediment composition. Crests of the ridges contained clean sand and swales or troughs consisted of shell and flocculent material (Maurer et al. 1976).

Results and Discussion

A total of 125 species of polychaetes, representing 34 families and 88 genera, were identified from all the sampling areas. Eighty-three species and 25 families were collected within Delaware Bay proper (Table 2, columns A-E). The Delaware Bay samples usually showed less than 10 species and 250 individuals/m^2. However, the most species (95) were collected in the offshore samples. The number of individuals per sample was much higher at stations in the midshelf area. This was also the only collection where the polychaetes dominated the fauna. Infaunal samples in both the bay and in the nearshore areas are otherwise dominated by members of the Mollusca (Maurer et al. see footnote 7; Watling et al. 1974).

[9]Maurer, D., J. Tinsman, W. Leathem, and P. Kinner. 1974. Baseline study of Sussex County, Delaware ocean outfalls. Rep. Sussex County Engineer, Sussex County Delaware. Univ. Del., Coll. Mar. Stud., 287 p.

[10]Bumpus, D. F., R. E. Lynde, and D. M. Shaw. 1973. Physical oceanography. *In* S. B. Saila (editor), Coastal and offshore environmental inventory Cape Hatteras to Nantucket Shoals, 72 p. Univ. R.I., Mar. Publ. Ser. 2.

[11]Milliman, J. D. 1974. Marine geology. *In* S. B. Saila (editor), Coastal and offshore environmental inventory Cape Hatteras to Nantucket Shoals. Univ. R.I., Mar. Publ. Ser 3.

Delaware Bay

Intertidal—Cape Henlopen (E)

Eight core samples (25 cm diameter × 25 cm height) were taken each month for 25 mo on Cape Henlopen near the mouth of the bay, from 1970 to 1972 (Figure 1). The study area was on the bay side of the spit on a tidal flat with swash bars. Eighteen species of polychaetes were collected in the sampling area (Table 2, column E). The number of species decreased gradually from fine to coarse sand (Maurer unpubl. data). Large tube-building polychaetes (*Diopatra cuprea*) and burrowing infaunal species (*Lumbrineris tenuis* and *Scoloplos fragilis*) occurred in highest densities in the fine sand, whereas spionids and nephtyids were better represented where sediment grain size increased towards the ocean. Two species (*S. fragilis* and *Spio setosa*) were particularly abundant from the low to the high tide line. *Scoloplos fragilis* was most common just above the reducing layer in the sediment. *Pista palmata* was collected only in the sand flat area.

Baywide (A)

The polychaete fauna in the upper bay (5-15‰) was dominated by the deposit feeders *Heteromastus filiformis* and *Scolecolepides viridis* (Table 2, column A). *Glycera dibranchiata* was also present at a number of stations. Sediments in this area ranged from M 4.2 to 7.9ϕ (median grain size), with generally poor sorting (σ = 2.4-3.9ϕ). At all stations the numbers of individuals were very small, with four individuals being the most recorded at one time. This paucity of individuals was also evident in other groups of the benthic fauna.

Farther down the bay where salinities were 15-25‰, there was an increase in number of species and individuals. Thirty-two species were collected, including all the six species recorded in the area of 5-15‰ (Table 1). The sediment showed a much wider range of particle size (M 1.0-7.0ϕ) than in the previous zone, with a tendency toward better sorting in the larger sediment classes. *Heteromastus filiformis* was still the dominant polychaete in fine sediments, with *G. dibranchiata* important in coarser material. Deposit-feeding polychaetes predominated, particularly on the sides of the estuary in the finer sediment (Figure 2). The coarser sediments in the middle of the

TABLE 2.—Polychaete species in the Delaware Bay region (maximum number per square meter) and their zoogeographic distribution on the northeast coast of the United States.

[A = Baywide, B = Bay mouth, C = Midbay, D = Oyster beds, E = Intertidal—Cape Henlopen, F = Small bays, G = Bethany Beach, H = Hen and Chickens Shoal, I = Off Delaware Bay mouth, J = Midshelf site; 1 = NE United States (<200 m), 2 = Offshore (>200 m), 3 = Chesapeake Bay, 4 = North Carolina; * = species at the southern extension of their range; ** = species at the northern extension of their range.]

Polychaete species	A	B	C	D	E	F	G	H	I	J	1	2	3	4
Ampharetidae:														
Ampharete arctica Malmgren		10	20				110	10		100	x	x		
Asabellides oculata (Webster)	80	20	1,770				50	190	10	50	x		x	
Hypaniola florida (Hartman)				x		243					x		x	x
Melinna maculata Webster	40												x	x**
Amphictenidae (= Pectinariidae):														
Cistena gouldii (Verrill)	10		150	x	x	1,273					x		x	x
Aphroditidae														
Aphrodita hastata Moore									10		x			
Arabellidae:														
Arabella iricolor (Montagu)	20					14		10	10	25	x		x	x
Drilonerls longa Webster	40		20				10		10	25	x		x	x
D magna Webster and Benedict	10		30					10	10	25	x			x
Capitellidae:														
Capitella capitata (Fabricius)	20		150			458	10	40			x		x	x
Heteromastus filiformis (Claparède)	490	220	900	x	1,659	114	10	20			x	x	x	x
Mediomastus ambiseta (Hartman)			1,500							25	x*			
Chaetopteridae														
Spiochaetopterus oculatus Webster				x		29					x		x	x
Cirratulidae:														
Caulleriella spp.	560		40				10	130		150				
Chaetozone setosa Malmgren			30					10	10	275	x	x		x
Chaetozone spp.	10		30				20			325				
Cirratulus grandis Verrill	10							20	20	25	x		x	x
Cirriformia filigera (Delle Chiaje)						129								x
Tharyx acutus Webster and Benedict	10		30				80	960		180	x			
Tharyx sp.	180		30		x			60	20	525				
Dorvilleidae:														
Protodorvillea gaspeensis Pettibone										25	x*			
Schistomeringos caeca (Webster and Benedict)			10				40			50	x			x
S rudolphi (Delle Chiaje)			30				160	100		50	x		x	x
Eunicidae:														
Marphysa belli (Audouin and Milne-Edwards)									10	50	x			
M sanguinea (Montagu)	230		180			43					x		x	x
Flabelligeridae:														
Pherusa affinis (Leidy)			60				20	160	10	25	x		x	
Glyceridae														
Glycera americana Leidy	40	10	30		x	157	10	70			x	x	x	x
G capitata Oersted	50		100			200	270	50		125	x			x
G dibranchiata Ehlers	80	20	50	x	42	43	100	40	40	175	x		x	x
Goniadidae:														
Glycinde solitaria (Webster)	40	20	270			257	80	10			x		x	x
Goniadella gracilis (Verrill)			40				10		110	3,950	x			x
Hesionidae:														
Gyptis vittata Webster and Benedict						29					x		x	x
Microphthalmus schzelkowii Mecznikow	10						10	10			x*			
Podarke obscura Verrill			100			72					x		x	x
Lumbrineridae:														
Lumbrinerides acuta (Verrill)	10		10				20	10	20	925	x			x
Lumbrineris coccinea (Renier)										25	x			x
L. fragilis (O F. Müller)					x		10	10	150	75	x	x		x
L. impatiens (Claparède)										150	x			
L latrielli (Audouin and Milne-Edwards)										425	x		x	x
L. tenuis Verrill	50	x	10		x	1,530		40	110	100	x		x	x
Magelonidae														
Magelona sp. A	10						10			25				
Magelona sp. B (near *riojai*)	10		10				30	10			x			x
Maldanidae:														
Asychis elongata (Verrill)	10					129					x		x	x
Clymenella mucosa (Andrews)										25				x**
Clymenella spp.			30							475				
C torquata (Leidy)	60		10			114				200	x		x	x
C zonalis (Verrill)										250	x		x	x
Clymenura borealis (Arwidsson)										25	x	x		
Praxillella sp.										150				
Nephtyidae:														
Aglaophamus circinata Verrill										825	x			x
Nephtys bucera Ehlers	10		30		x	229	80	20	30	50	x		x	x
N incisa Malmgren			40						100	75	x		x	x
N picta Ehlers	60	40	150		x		270	40	110	250	x		x	x

TABLE 2.—(Continued).

Polychaete species	A	B	C	D	E	F	G	H	I	J	1	2	3	4
Nereidae:														
Nereis grayi Pettibone							11			125	x		x	x
N. succinea (Frey and Leuckart)	130	30	450	x	63	672	20	900		25	x		x	x
Onuphidae:														
Diopatra cuprea (Bosc)		10	10		x	29			10		x		x	x
Onuphis opalina (Verrill)							10			10	x			
Opheliidae:														
Ophelia bicornis Savigny	10	180					30	40		25	x		x	
O. denticulata Verrill							20		10	25	x			x
Ophelina cylindricaudata Hansen										25		x		x
Travisia carnea Verrill	30		10				380	10		75	x		x	
Orbiniidae:														
Orbinia ornata (Verrill)	20							10		25	x		x	x
O. swani Pettibone										25	x*			
Scoloplos armiger (O.F. Müller)	30		20				20			50	x			x
S. fragilis (Verrill)	60	30	130	x	3,024	858	10			25	x		x	x
S. robustus (Verrill)	40		40				10				x		x	x
Oweniidae:														
Myriowenia sp. A										25				
Owenia fusiformis Delle Chiaje				x		14					x		x	x
Paraonidae														
Aricidea catherinae Laubier	40		90				240	180	60	350	x		x	x
A. suecica Eliason										125	x	x		x
A. wassi Pettibone										250	x		x	
Cirrophorus branchiatus Ehlers										25		x		x
Paradoneis lyra (Southern)	10						130	10		125	x	x		
Phyllodocidae:														
Eteone flava (Fabricius)										25	x*			
E. heteropoda Hartman	10		30	x				10		25	x		x	x
E. lactea Claparède	10			x		558		30		25	x		x	x
E. longa (Fabricius)	60		60								x			
E. trilineata (Webster and Benedict)										25	x*			
Eulalia bilineata (Johnston)										50	x			
Eumida sanguinea (Oersted)	40		1,240	x		143					x		x	x
Paranaitis kosteriensis (Malmgren)	10							10			x			
P. speciosa (Webster)			20			14				50	x		x	x
Phyllodoce arenae Webster	20		60			14	30	50		75	x		x	x
P. maculata Linnaeus			50				10	10		25	x*			
P. mucosa Oersted								20		25	x		x	x
Pisionidae:														
Pisione remota (Southern)							10		80					x
Polynoidae:														
Harmothoe extenuata (Grube)	240	10	790	x			30	380	20	25	x			x
Lepidametria commensalis Webster			10			72					x		x	x
Lepidonotus squamatus (Linnaeus)	20		270				10	50	10		x		x	
L. sublevis Verrill	10	30	270	x	x						x		x	x
Sabellariidae:														
Sabellaria vulgaris Verrill	70	150	2,310	x		57	720	120			x		x	x
Sabellidae:														
Chone spp.										400				
Euchone spp.										100				
Potamilla neglecta Sars										50	x		x	
P. reniformis (Leuckart)										50	x			x
Sabella microphthalma Verrill					x	14				25	x		x	x
Scalibregmidae:														
Scalibregma inflatum Rathke										150	x	x		x
Serpulidae:														
Hydroides dianthus (Verrill)	1,930	40	8,160	x	21	43	10	40		150	x		x	x
Sigalionidae														
Pholoe minuta (Fabricius)										25	x			x
Sigalion arenicola Verrill							40	10	50	75	x			x
Sthenelais limicola (Ehlers)		10	10				20	10		50	x		x	x
S. boa (Johnston)			60				10	10		75	x		x	x
Spionidae:														
Dispio uncinata Hartman	10		10				20	10			x			x
Parapionspio pinnata (Ehlers)		10	10				10				x		x	x
Polydora caulleryi Mesnil			10				10			50	x			
P. concharum Verrill			10							75	x*			
P. ligni Webster	1,050	10	330	x		2,131		80			x		x	x
P. socialis (Schmarda)	10		440				10	200	10	25	x			x
P. websteri Hartman	20			x							x		x	x
Prionospio cristata Foster										25				x**
P. steenstrupi Malmgren										100	x	x		x
Scolecolepides viridis (Verrill)	40	20									x		x	x
Scolelepis squamata (O.F. Müller)	10	10	20		21		40	30		25	x			x
Spio setosa Verrill	10		5,450		42		150	40	40	50	x		x	x
Spiophanes bombyx (Claparède)	70		110				320	70	160	2,550	x		x	x
Streblospio benedicti Webster	160	10	590	x		86	10	120			x		x	x

TABLE 2.—(Continued).

Polychaete species	A	B	C	D	E	F	G	H	I	J	1	2	3	4
Syllidae:														
Brania clavata (Claparède)						x					x		x	x
Exogone dispar Webster										25	x	x	x	x
E. hebes (Webster and Benedict)										850	x*			
E. verugera (Claparede)	20									1,425	x			x
Parapionosyllis longicirrata (Webster and Benedict)	10						20			1,125	x		x	x
Proceraea cornuta (Agassiz)	220		30							175	x		x	x
Sphaerosyllis erinaceus Claparède										50	x			
S. hystrix Claparède										125	x*			
Streptosyllis arenae Webster and Benedict										175	x			x
S. varians Webster and Benedict										75	x*			
Syllis cornuta Rathke									40	50	x			x
S. gracilis Grube			50								x			x
Syllides sp.							40		20	100				
Terebellidae:														
Amphitrite ornata (Leidy)			40					40			x		x	x
Pista cristata (O.F. Müller)							10				x		x	x
P. palmata (Verrill)					x						x		x	x
Polycirrus eximius (Leidy)	190		1,140					830		100	x		x	x

estuary contained larger densities of carnivores and omnivores. One station on the most southerly transect in this salinity range had the coarest sediment found to this point (M 1.0ϕ) and the most diverse fauna. Eleven species were present representing both sedentary (e.g., *H. filiformis*, *Streblospio benedicti*, and *Asabellides oculata*) and errant types (e.g., *Glycera dibranchiata*, *G. americana*, *Eteone heteropoda*, and *E. longa*). Since all species mentioned occurred at both higher and lower salinities, species richness may be a response to the sediment type.

Fifty-one species were collected in the estuary in salinities >25‰. The six species found in the upper bay all occurred here. Nineteen species collected in the midbay area were also found in the high-salinity samples. Twenty-six additional species found in the lower estuary were not found in salinities <25‰. They were equally divided between sedentary and errant types. The sedentary deposit-feeding species are mainly sand-dweller types, such as *Paradoneis lyra*, *Scolelepis squamata*, and *Spio setosa*, while the errant species consisted of phyllodocids, nephtyids, and polynoids.

Delaware Bay Temporal Studies

To examine more closely the temporal changes in assemblages in different Delaware Bay sediments, a program of quarterly sampling was undertaken in Area C (Figure 1). Three sandy shoals, three muddy sand bottoms, a polymodal sediment, and a calcareous serpulid assemblage were the selected sites (Watling and Maurer see footnote 6). At all of the stations the salinity was >25‰. In addition to the quarterly samples, 20 replicate grabs and 20 replicate dredge hauls were taken at a station representing each substrate to obtain a more accurate count of species abundances.

SANDY SHOALS.—Two of the shoal stations were located in the middle of the bay on Brown Shoal and Lower Middle Shoal. Sediments were medium-well sorted (M 1.9-2.9ϕ, σ = 0.30ϕ) sand constantly subjected to strong tidal currents. The fauna was restricted to a few species of polychaetes throughout the year: *Nephtys picta*, *N. bucera*, *Magelona* sp. 2 (near *riojai*), and *Spiophanes bombyx*. The species were always present in densities of <10 individuals/0.1 m^2. The third shoal station on Old Bare Shoal was slightly different in faunal and sedimentary characteristics. The sediment was finer (M 2.8-2.9ϕ, σ = 0.30ϕ), with sorting the same as the other shoals. The polychaete fauna was dominated throughout the year by *Glycera capitata*, *G. dibranchiata*, *Scoloplos robustus*, *S. fragilis*, and *Spiophanes bombyx*. The 20 replicate grabs taken at this station in the summer indicated that *G. capitata* had a density of 4.1 individuals/0.1 m^2. *Glycera dibranchiata* occurred in a density of 1.8/0.1 m^2. The dredge hauls indicated the same dominant species with the addition of *Asabellides oculata*.

MUDDY SAND BOTTOM.—The three muddy sand stations were similar in sediment composition (M 3.2-4.7ϕ, σ = 1.50ϕ) and also in polychaete distribution. One of the stations was dominated by the bivalve, *Nucula proxima*, to the exclusion of other species. *Asabellides oculata* and *Capitella capitata* were the dominant polychaetes according to the quarterly studies; however, their densities were very low all year. The 20 grab sam-

ples produced 13 specimens of *Nephtys picta*. No other species was represented by more than one or two individuals. In the 20 dredge hauls taken at the same location, *N. incisa* was present in almost all samples in densities great enough to be considered a dominant organism in the community. Sanders (1958) described a muddy sand community from Buzzards Bay as a *Nucula proxima-Nephtys incisa* group. The sampling in Delaware Bay indicated that *N. incisa* was not sufficiently dominant to be a characteristic species for this community. The other two muddy sand stations contained *N. incisa, A. oculata, Scoloplos robustus, S. fragilis, Spio setosa,* and *Glycinde solitaria* as important polychaete species throughout the year.

EPIFAUNAL-INFAUNAL ASSEMBLAGES.—The epifaunal-infaunal assemblages include a calcareous serpulid assemblage; a polymodal sediment, which contained a mussel community; and the oyster community. These epifaunal-infaunal assemblages are pooled here because certain infaunal species occurred only in samples containing the epifaunal assemblages. The latter also contributed to the formation of the sediment containing particular species of infauna.

Blue Mussel Assemblage.—The blue mussel, *Mytilus edulis*, was the primary species in an epifaunal-infaunal assemblage in lower Delaware Bay (C). The assemblage was transitory and depended on the life cycle of the mussels and physical disturbances such as storms. The substratum beneath the *Mytilus* beds consisted of a poorly sorted polymodal sediment. The mussels were first collected as juveniles in May. Their growth over the summer was accompanied by an increase in the number of species of polychaetes as well as the number of specimens. Mussels were almost absent in November samples, with a corresponding decrease in numbers of species and individuals of polychaetes. There was a reappearance of the mussel beds the following May. A total of 49 species of polychaetes were collected in the *Mytilus* beds, ranging from 5 to 22 species/sample. The most common species living on the mussels and among the byssal threads included *Harmothoe extenuata* and *Nereis succinea*. Other important members of the epifauna were *Lepidonotus squamatus, L. sublevis, Eumida sanguinea, Polydora ligni, Polycirrus eximius,* and *Eteone heteropoda*. The infaunal species were dominated by *Mediomastus ambiseta, Spio setosa* (which occurred in 60% of the samples), and *Asabellides oculata. Aricidea catherinae, Streblospio benedicti, Tharyx* spp., and *Chaetozone* spp. also contributed significantly to the infaunal community. During the winter there was a reduction in the density and number of epifaunal species. In the spring, when the young mussels were still small, *Spio setosa* composed as much as 70% of the individuals of the samples, with over 5,000 individuals/m^2. This type of opportunism by the infaunal species was observed the preceding spring to a lesser degree, when *S. setosa* made up as much as 40% of the specimens collected. Steimle and Stone (1973) described a similar *Mytilus* aggregation from off Long Island, N.Y. where *H. imbricata, H. extenuata, L. squamatus,* and *N. succinea* were the dominant polychaetes.

Serpulid Assemblage.—A second major epifaunal-infaunal assemblage in Delaware Bay was a serpulid assemblage. Geological descriptions of serpulid reefs have been reported from England (Garwood 1931; Bosence 1973). Descriptions of the biology of such assemblages formed by *Hydroides dianthus* from the east coast of the United States are unknown to us. *Hydroides dianthus* forms calcareous tubes encrusting shells and rocks, with the distal part of the tube erect, away from the substrate. *Hydroides* larvae then settle on the adult tubes forming heads of tubes. This assemblage does not form a continuous structure, but a series of heads occurring over an area of 1 km^2. Similar assemblages have also been observed in Indian River Bay and Little Assawoman Bay, but have not been studied to date.

In addition to *H. dianthus*, the dominant polychaetes of this assemblage were *Sabellaria vulgaris, Eumida sanguinea, Mediomastus ambiseta, Asabellides oculata,* and *Polydora ligni. Sabellaria vulgaris*, which forms reefs of its own in other areas of the bay (Curtis 1975), attached its sandy tubes on the *H. dianthus* tubes. *Polydora ligni* builds its muddy tubes in the crevices between the calcareous structures and in empty *H. dianthus* tubes. *Polycirrus eximius* also exploited the vacant tubes, while *Harmothoe extenuata, L. squamata,* and *L. sublevis* primarily were found wedged between the tubes. *Marphysa sanguinea*, which was collected only rarely on the *Mytilus* beds and nowhere else in the bay, was an important member of the serpulid community. *Asabellides oculata, Glycinde solitaria, Mediomastus*

ambiseta, and *Heteromastus filiformis* were the dominant organisms in the silt-fine sands around and beneath the serpulid tubes. Other polychaetes, such as *Cistena gouldii* and *Streblospio benedicti*, inhabited the surrounding sediment.

Two seasonal changes were noted in the polychaete distributions of the *Hydroides dianthus* assemblage. Adult *Polydora ligni* were not found in the August grab samples; however, when dredge hauls were sieved through a 250-mm mesh screen, juveniles down to the eight or nine setiger stages were collected. *Harmothoe extenuata* was totally absent from the fall collections, but reappeared the following spring.

Oyster Assemblage (D)

The oyster assemblage (Figure 1) was the first of the epifaunal-infaunal communities to be sampled. Since this study was described in detail in Maurer and Watling (1973), it will only be briefly described here for purposes of comparison with the other epifaunal-infaunal groups. Twenty species of polychaetes were collected on oyster bars in Delaware Bay and in the Broadkill, Mispillion, Murderkill, St. Jones, and Leipsic Rivers. Four of the species, *Hydroides dianthus, Polydora websteri, P. ligni*, and *S. vulgaris*, were associated directly with the shell substratum. *Polydora websteri* is known to burrow into oyster shells and dissolve the shell to form U-shaped cavities lined with detritus (Zottoli and Carriker 1974). *Polydora ligni* forms silty mucous tubes which may be present in very high densities on the external surface of the oysters.

Five species of polychaetes, *Harmothoe extenuata, L. sublevis, Eteone heteropoda, E. lactea*, and *Eumida sanguinea*, were found to inhabit the mud and debris associated with the epifaunal organisms. Other species such as *Scoloplos fragilis, Spiochaetopterus oculatus, Cistena gouldii*, and *Streblospio benedicti*, were found on nearby soft bottoms. *Nereis succinea* was collected in all types of sediment.

Small Bays (F)

From 1968 to 1970, 273 samples were taken in Rehoboth and Indian River Bays (Figure 1) during summer and winter, with emphasis on the former. Seventeen polychaete species were collected in Indian River Bay in summer 1968, 14 in winter 1969, 15 in summer 1969, and 17 in winter 1970. During the same time periods, 28, 13, 20, and 14 polychaete species, respectively, were collected in Rehoboth Bay. Based on density and frequency of occurrence, the following five species of polychaetes emerged as dominants: *Capitella capitata, Glycera americana, Lumbrineris tenuis, Scoloplos fragilis*, and *Glycinde solitaria*. *Capitella capitata* was found in both bays in high numbers in the summer samples only. Only three of the dominant organisms, *L. tenuis, S. fragilis*, and *Glycera americana*, were present during all sampling periods. *Nereis succinea* was another important species. Logan and Maurer (1975) found that *N. succinea* and *Heteromastus filiformis* dominated monthly samples throughout the year in the upper Indian River Bay; *N. succinea* was postulated to be an indicator organism for thermal pollution.

Watling (1975) reported that *Streblospio benedicti* and *C. capitata* were the dominant benthic species in a deposit-feeding community in a small cove of Rehoboth Bay. Other species, such as *Polydora ligni* and *H. filiformis*, were also important. His study further indicated that *S. benedicti* and *C. capitata* showed opportunism and rapidly recolonized the area after a summer die-off, presumably taking advantage of available food resources. *Brania clavata, Exogone dispar*, and *H. filiformis* gradually increased in numbers as the community stabilized.

Coastal Fauna (G, H, I)

The Hen and Chickens Shoal (area H), immediately adjacent to the bay mouth, showed the greatest resemblance to the estuarine fauna. Bethany Beach (area G) and the northeast stations off the mouth of Delaware Bay (area I) appeared more like the offshore assemblages (Figure 1). The southeastern portion of area I was also estuarine in character (Watling et al. 1974). *Tharyx acutus* and *Harmothoe extenuata* were the dominant polychaetes in area H. *Tharyx acutus* occasionally occurred in the bay and frequently offshore, but never in the densities recorded in area H. *Tharyx acutus* was particularly important during January through April, when it reached densities of 960/m^2. *Harmothoe extenuata* was present in large numbers in Delaware Bay, but very rarely offshore. Pettibone (1963a) stated that *H. extenuata* is a highly adaptable species which occurs intertidally and at great depth on all types of

bottoms. The highest density of *H. extenuata* in our studies always occurred in the epifaunal-infaunal assemblages, mentioned above. Other species that were present in significant numbers in area H, and also important in the bay but not normally found in offshore assemblages, include: *Polydora ligni, P. socialis, Asabellides oculata, Nereis succinea,* and *Sabellaria vulgaris*.

A number of species, including *Glycinde solitaria, Spio setosa,* and *Diopatra cuprea*, occurred in areas G and I, but not farther offshore. *Glycinde solitaria* was found primarily in muddy sands, both in the bay and nearshore areas, which agrees with the findings of Pettibone (1963a). The lack of mud on the inner shelf may be the primary reason why they were not found at the offshore sites. *Diopatra cuprea* and *S. setosa* were found extensively on the intertidal sand flats of Cape Henlopen. Only a few individuals of *D. cuprea* were found in lower Delaware Bay and in areas G and I. *Spio setosa* was most prevalent subtidally in the epifaunal-infaunal assemblages.

In addition to estuarine species, members of the offshore assemblages were found in areas G and I. *Lumbrinerides acuta* (an offshore dominant) and *L. fragilis* were present in sand stations in both areas. *Spiophane bombyx*, which was found occasionally in sandy sediment in the bay, was an important species in the nearshore marine areas and a dominant in offshore assemblages. The increase in density of *S. bombyx* seaward appears to be a response to increased areas of fine sand, rather than salinity, as *S. bombyx* was found in estuarine waters of 15‰.

Midcontinental Shelf Fauna (J)

Polychaetes represented 35.7% of the total individuals in samples collected in May and 54.4% in November, making them the dominant (by number of individuals) benthic group offshore (Maurer et al. 1976). In May, *Goniadella gracilis* and *Lumbrinerides acuta* were codominants among all benthic organisms. *Clymenella* spp. and *Aricidea catherinae* were also abundant. In November there was a shift in dominance, with the exception of *G. gracilis*, when *Exogone verugera* and *Spiophanes bombyx* were established as dominant forms. *Parapionosyllis longicirrata* was present in a few samples in large numbers, but was not as widely distributed as the other dominant species. The following March, *Aglaophamus circinata* became the dominant species based on the large number of juveniles collected. *Spiophanes bombyx* was the second-most important species; *Exogone hebes* and *E. verugera* were also collected extensively. The March samples contained a large number of individuals of *Euchone* spp. and *Chone* spp. This represented the first time in our offshore sampling that a suspension feeding polychaete group contributed more than an occasional rare individual, although these small sabellid species are probably not typical suspension-feeding polychaetes (M.H. Pettibone pers. commun.). *Euchone* spp. were present in 13 samples, and species of *Chone* spp. were dominant in two of the five samples in which they were collected.

Goniadella gracilis was a dominant form in all the offshore stations and in all sampling periods. It was present in more than 65% of the samples in May and November, with average occurrences of 297 individuals/m^2 and 693 individuals/m^2, respectively. In the May samples, it was reduced to 32% of the samples with fewer numbers of individuals. However, it still remained the second-most important polychaete species.

Members of the family Sigalionidae occurred more frequently and in higher densities in the offshore samples than in the bay and nearshore areas. *Sthenelais boa* and *S. limicola* occurred in Delaware Bay in salinities >25‰, as well as in the nearshore and offshore communities. *Pholoe minuta* and *Sigalion arenicola* were present only in the coastal and offshore stations. *Sigalion arenicola* occurred in 12% of the November offshore samples, with many individuals being juveniles. None of these scale worms were ever found in large numbers in any sample. The increase in sigalionids offshore was not matched by the other major scale worm family, the Polynoidae. Polynoids were extremely numerous in the bay, particularly in the epifaunal-infaunal communities. In the offshore marine areas, only *Harmothoe extenuata* was present. The absence of collections from hard substrate offshore may affect the average numbers of offshore polynoids. The Sigalionidae typically are burrowing forms and may find the fine sandy substrate more suitable than do the polynoids.

Maldanids were important in the three seasonal offshore sampling periods. Most of the individuals collected were juveniles, and thus difficult to identify. Most adult specimens were *Clymenella zonalis, C. torquata,* and *C. mucosa*.

ANIMAL-SEDIMENT RELATIONSHIPS

To describe some of the sediment associations of the dominant species of Delaware Bay, correlations were made with median grain size and percentage of silt-clay using Spearman's ρ ($\alpha = 0.05$). *Nephtys picta* was collected in sediments with an unweighted mean grain size of 2.1ϕ and in 1-10% silt-clay ($\bar{x} = 4.7\%$). Increasing abundance of *N. picta* was associated with increasing amounts of silt-clay within the range in which it occurred. *Glycera dibranchiata* was found in sediment with up to 50% silt-clay ($\bar{x} = 13.3\%$), and a mean size ranging from 0.8 to 6.6ϕ ($\bar{x} = 2.7$). There was a positive association between numbers of individuals and increasing silt-clay content. No other associations were significant.

Two of the dominant species were found primarily in muddier sands. *Heteromastus filiformis* has been described as a member of soft sediment communities in Delaware Bay (Kinner et al. 1974) as well as elsewhere (Dean and Haskin 1964). The species inhabited a wide range of sediments, M 0.08-6.5ϕ ($\bar{x} = 3.7$), and was positively correlated with increasing silt-clay and increasing median and mean grain size. *Streblospio benedicti* occurred in sediments with a wide range of silt-clay (2.5-59.0%). The distribution of the species was not correlated with median grain size, silt-clay, or mean grain size. *Streblospio* showed an even greater affinity for the areas along the Delaware and New Jersey shoreline than did *H. filiformis*.

Correlations were also made between measures of sediment and five of the dominant polychaetes of the offshore assemblages. *Lumbrinerides acuta* (0.76-2.40ϕ) and *Goniadella gracilis* (0.76-2.49ϕ) were negatively associated ($\alpha = 0.05$) with increases in median ϕ and positively correlated with an increase in the percentage of sediment >1 mm in diameter. Both species showed correlations of high density with more poorly sorted sediments. Nichols (1970) has postulated that although sorting is not well understood biologically, positive correlations with well sorted sediments may indicate niche specificity, while poor sorting suits a wider variety of needs. The larger sediment sizes probably facilitate burrowing.

Aricidea catherinae (0.34-2.64ϕ) was negatively associated with an increase in the size of the median ϕ. This deposit-feeding species builds a flexible mucous tube and is far less mobile than *L. acuta* and *G. gracilis*. Sediments containing particles >1 mm may be difficult for this fragile species. *Aglaophamus circinata* was not significantly associated with any sediment parameters. However, it was found in a range of sediment (0.34-2.64ϕ) similar to that of the other species. Sediments which contained the greatest densities of *Spiophanes bombyx* were generally well sorted (σ = 0.21-0.57ϕ) with between 25% and 50% of the sediment >0ϕ. There was a negative association ($\alpha = 0.05$) between *S. bombyx* and sediment >1 mm. This species was also negatively associated with an increase in the standard deviation of ϕ indicating its preference for a well-sorted sediment.

GENUS-SPECIES RELATIONSHIPS

A comparison was made of the genus to species ratios for each of the estuarine coastal and offshore areas to obtain information on diversity and speciation. The midshelf station had the highest ratio of 1.0:1.6 with the Serpulidae and *Mytilus* assemblages second (1.0:1.4). Coastal areas were next with Hen and Chickens Shoal and Bethany Beach 1.3 and off the bay mouth 1.2. The areas within Delaware Bay and the small bays were as follows: baywide (1.3), intertidal (1.3), bay mouth (1.0), oyster beds (1.2), and small bays (1.1). The epifaunal-infaunal speciation ratio does not reflect the stability of the habitat, but rather the greater number of niches due to a mixed substratum. Winter reductions in species diversity in the *Mytilus* assemblage due to storms and mussel mortality emphasize the fragile nature of the environmental stability.

TAXONOMIC NOTES

Revisions and synonymies that appear in polychaete taxonomic literature are often not included in ecological publications for a long time. Based on suggestions from Marian Pettibone, we have included a section describing some of the systematic changes that affect the east coast of the United States. We formally acknowledge her for providing us with much of the information included in this section.

Ampharetidae
Hypaniola florida (Hartman)

In a recent paper Pettibone (1977) has presented the synonomy and distribution of the estuarine species, *Hypaniola florida* (Hartman). The

species was reported as *Amphicteis gunneri floridus* by Hartman in 1951 from Florida and as *Hypaniola grayi* by Pettibone (1953) from Massachusetts and by Kinner et al. (1974) from Delaware Bay. Wass (1972) listed the species as *Lysipiddes grayi* from Chesapeake Bay and Zottoli (1974) used the name *Amphicteis floridus* from New Hampshire. Pettibone stated that this species is distributed in estuaries from Maine to Florida and the Gulf of Mexico.

Amphictenidae (= Pectinariidae)

Lucus and Holthuis (1975) showed that the type-species of the well known generic name *Pectinaria* Lamarck was confused and had to be replaced by *Cistena* Leach. Since the genus *Pectinaria* is no longer valid, the widely used family name Amphictenidae is now preferred to Pectinariidae. The single east coast representative should now be referred to as *Cistena gouldii* (Verrill) new combination.

Capitellidae

Mediomastus ambiseta (Hartman) was a dominant species in the mussel and serpulid assemblages. Hartman (1947) described the species as *Capitata ambiseta* from intertidal flats in California. Hartman-Schröder (1962) later synonymized *Capitata* with *Mediomastus*, and Hobson (1971) reported it for the east coast of the United States. The species has been reported as a dominant species in Newport Bay, Calif., and Baja California by Reish (1959, 1963) and in Florida by Dauer and Simon (1975, 1976a, b). *Mediomastus californiensis* has been reported from North Carolina (Day 1973), but it differs from *M. ambiseta* in a number of characteristics. *Mediomastus californiensis* lacks a caudal process, and spinous setae in posterior segments that are represented in *M. ambiseta,* and has a different positioning of the distal teeth of the hooked setae.

Dorvilleidae

According to a recent revision of the genera of the family Dorvilleidae by Jumars (1974), the new generic name *Schistomeringos* replaces *Staurocnereis* as used by Pettibone (1963a) and Wass (1972) and *Dorvillea* as used by Day (1973) for the species *Schistomeringos caeca* and *S. rudolphi.*

Protodorvillea gaspeensis, described originally by Pettibone (1961) from the Gulf of St. Lawrence, was reported from Massachusetts by Hobson (1971) and now from the midcontinental shelf off Delaware.

Magelonidae

Two species of Magelonidae have been recorded from Delaware and designated as *Magelona* sp. A and *Magelona* sp. B. Meredith Jones is currently revising this group and he informs us that *Magelona* sp. B is near *M. riojai* (Jones 1963).

Maldanidae

In a revision of three species of Maldanidae from the east coast of the United States, Mangum (1962) included three species under *Clymenella: C. torquata* (Leidy), *C. zonalis* (Verrill), and *C. mucosa* (Andrews). Day (1973) maintained the genus *Axiothella* for *C. mucosa*; however, Mangum has pointed out that this separation, based on the position of segmental collars, is not warranted because of the presence of collars scattered throughout the family. *Clymenella zonalis* was reported by Day (1973) as *Macroclymene zonalis*. The genus, *Macroclymene*, was originally erected as a subgenus by Verrill for a specimen which had a much larger number of segments than his type. The subgenus was raised to generic status by Hartman (1951) for a fragment found in the Gulf of Mexico. Mangum pointed to the great variation in segmental number even within populations and thus rejected *Maroclymene*. It has also been our experience that numbers of segments vary. We have found that juveniles particularly do not fit the characteristic segmental numbers, and as a result, have used *Clymenella* spp. and *Praxillella* sp.

Light (1974), in a comparison of Maldanidae specimens from San Francisco Bay and the east coast of the United States, followed Ardwidsson and referred Verrill's species *Maldane elongata* to *Asychis* (including the synonymy). The species has been reported from Chesapeake Bay by Wass (1972) as *Maldanopsis* and from North Carolina by Hartman (1945) and Day (1973) as *Branchioasychis americana* Hartman.

Orbiniidae

In a study involving various growth stages of *Scoloplos armiger*, Curtis (1970) has shown *S. acutus* to be a juvenile form of *S. armiger*. The

characters which were used to separate these two species were the specialized thoracic hooks and the abdominal papillae. Curtis documented the appearance of first hooks, then papillae, with the increasing size of the animals. He also observed various intermediate stages with the population.

Paraonidae

In a revision of the family Paraonidae by Strelzov (1973), McIntosh's species of *Scolecolepides* (?) *jeffreysii* was shown to be an indeterminable *Aricidea* sp. The records of *A. jeffreysii* from New England (Pettibone 1963a) and from the Chesapeake Bay (Wass 1972) were referred to *A. catherinae* Laubier by Strelzov (1973:91). The record by Day (1973) of *A. cerruti* (not Laubier) from North Carolina should also be referred to *A. catherinae*. Strelzov (1973:108) also has referred *Cirrophorus lyriformis* (Annekova) to *C. branchiatus* Ehlers. The species collected in our mid-shelf collection thus was referred to *C. branchiatus*. Both species were recorded by Day (1973) from North Carolina. These specimens probably require further examination.

Sabellidae

Banse (1970, 1972) revised the generic descriptions of both *Chone* spp. and *Euchone* spp. emphasizing the branchial crown, setae, and anterior abdominal segments (*Euchone*).

There were many specimens of *Euchone* spp. and *Chone* spp. on the continental shelf off Delaware. We experienced difficulty in distinguishing the species because many of our specimens were juvenile forms. Our specimens of *Euchone* spp. appear to have more variability than those reported by Banse. In addition, many specimens were damaged or lacked branchial crowns so the number of radioles and the palmate membrane could not be observed. The specimens of *Euchone* compared most favorably with *E. incolor* and *E. elegans*, and the specimens of *Chone* spp. were most like *C. duneri*.

ZOOGEOGRAPHY

Some 125 species of polychaetes (and 8 other species identified only to genus) were collected in the Delaware Bay area. Based on the literature, 116 species have been collected in areas off New England (Table 2, column 1). Sixty-seven species were cited from Chesapeake Bay (Wass 1972; Table 2, column 3). The number of species common to the Chesapeake and Delaware Bay areas is lower than expected, considering their proximity. This was mainly because many of the offshore species encountered in our work were not included in Wass's list. However, work in progress on the mid-Atlantic shelf is expected to change this (D. Boesch, pers. commun.). Ninety-one of the species were common to North Carolina (Hartman 1945; Day 1973; Gardiner 1975; Table 2, column 4).

Examination of the local species revealed that for 11 of them, this was the southern extent of their range; i.e., they were reported for New England, but not from Chesapeake Bay or North Carolina (Table 2). Only three species were found to be at the northern limit of their range in the Delaware Bay area, having been found in Chesapeake Bay or North Carolina, but not New England. It appears that the polychaete fauna from the Delaware Bay area is more closely related to the northern than the southern fauna. Two of the species with their northern range in this area, *Prionospio cristata* and *Clymenella mucosa*, were offshore species. The probability of larvae being carried north into the area by the Gulf Stream is great, as Lear and Pesch[12] have shown the intrusion of this water from offshore during the winter and summer months.

Data from Hartman (1965) and Hartman and Fauchald (1971) showed that 14 species, which were collected in depths >200 m, were also found in our samples (Table 2, column 2). Seven of these species were recorded only in our offshore samples (J). The remaining seven species, *Brania clavata, Paradoneis lyra, Lumbrineris fragilis, Ampharete arctica, Heteromastus filiformis, Chaetozone setosa,* and *Glycera americana*, were also found in the estuary. It was interesting to note that of these seven species, *H. filiformis* and *C. setosa* belong to particularly difficult families taxonomically. In our work, *H. filiformis* was found in salinities as low as 5‰. The species was reported in depths of >1,000 m by Hartman (1965) and Hartman and Fauchald (1971). *Lumbrineris fragilis, L. latrielli, Aricidea suecica, Prionospio steenstrupi*, and *Exogone dispar* are other species given wide distributions in the literature (M. Pettibone pers. commun.). The distribution of species over such a

[12]Lear, D. W., and G. G. Pesch. 1975. Effects of ocean disposal activities on the mid-continental shelf environment off Delaware and Maryland. EPA Reg. III Rep., 78 p.

wide salinity and depth range appears to be highly doubtful and emphasizes the need for more definitive taxonomic work in some of the errant, and in particular, the sedentary polychaete families.

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TROPHIC ONTOGENY OF THE LEOPARD SEAROBIN, *PRIONOTUS SCITULUS* (PISCES: TRIGLIDAE)

STEPHEN T. ROSS[1]

ABSTRACT

Ontogenetic feeding changes of the leopard searobin, *Prionotus scitulus,* from Tampa Bay, Fla., showed a shift from planktonic and epifaunal prey in small fish to infaunal prey in larger fish. Smaller fish utilized larval crustaceans, natantians, brachyurans, cumaceans, copepods, and gammarid amphipods while larger fish showed increasing reliance on the lancelet, *Branchiostoma floridae.*

Biomass and linear dimensions of prey increased exponentially with fish size for larger fish, but were relatively constant for small fish. Relative prey biomass was lowest for intermediate-sized *P. scitulus* (65-95 mm) and increased for both large and small predators so that small individuals were most similar to very large fish in terms of relative prey size.

The switch to larger prey was preceded by rapid increases in mouth size and intestinal length, and was followed by attainment of minimum reproductive size and greater body weight per unit length.

Spatial and trophic partitioning appear quite efficient in reducing potential intraspecific competition.

Our present understanding of energy resource partitioning among metazoans is based primarily on food analyses. However, the study of trophic relationships among fishes is frequently complicated by indeterminate growth and the cooccurrence of several size classes of a species at a single locality.

A significant degree of prey variability of fishes may be due to size related changes. For instance, Darnell (1958) and Carr and Adams (1973) demonstrated changes in food habits with increasing size for numerous juvenile marine fishes, and Northcote (1954), Ivlev (1961), Keast and Webb (1966), Wong and Ward (1972), and others have shown a close relationship between morphology (in particular mouth size and shape) and prey kind or size. Such results indicate that inter- and intraspecific partitioning of energy resources in fish biofacies vary with fish size.

This study examines ontogenetic changes in trophic biology of the leopard searobin, *Prionotus scitulus* Jordan and Gilbert, a common nearshore benthic fish in the eastern Gulf of Mexico. Morphological and developmental attributes of jaw size, intestinal length, growth, reproduction, and distribution are evaluated in relationship to trophic changes and to intraspecific resource partitioning.

MATERIALS AND METHODS

I collected *P. scitulus* from three locations in Tampa Bay, Fla. (Figure 1). Numbers of fish collected and inclusive dates for each station were: Station 1, 489 specimens, July 1972-July 1973; Station 2, 838 specimens, August 1972-July 1973; Station 3, 690 specimens, April 1972-July 1973.

I examined stomachs from 650 specimens of *P. scitulus* from Station 3, collected monthly from April 1972 to May 1973. I also identified stomach contents of fish from August 1972 collections from

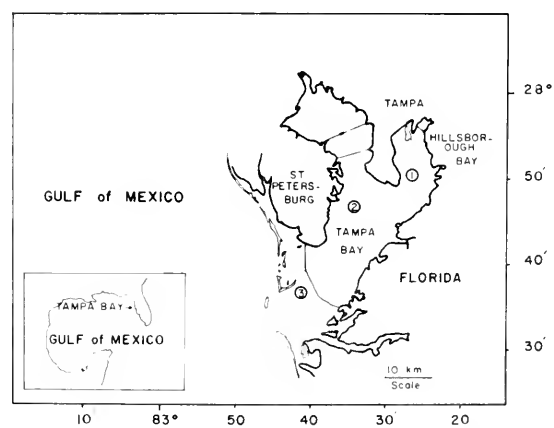

FIGURE 1.—Collection localities of *Prionotus scitulus* in Tampa Bay, Fla., 1972-73.

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Station 2 (N = 22) and November and July collections from Station 1 (N = 122). A total of 469 stomachs (72%) from all stations contained food items. April and May collections at Station 3 were made during the day; all other collections were from 1 to 5 h after sunset which was near the end of the greatest diel feeding activity. Ross (1977) demonstrated that searobins from the West Florida Shelf, including *P. scitulus*, had their greatest feeding activity during the day, but retained full stomachs through midnight.

Collection depths averaged 5, 5, and 7 m, respectively, for Stations 1-3. Sampling gear was a 3.6-m otter trawl with 2.5-cm stretched mesh and a 0.5-cm cod end liner. Upon capture I injected all specimens intraperitoneally with 10% Formalin.[2] Fish were fixed for 2 wk in 10% Formalin and then washed and transferred to 40% isopropanol for storage.

I sorted prey by taxa from each 10-mm size class of fish and measured a random sample ($n \leq 25$) of each prey kind to the nearest 0.1 mm along the axis of greatest dimension. The level of prey identification used in comparisons of size groups was the lowest taxon which was regularly identifiable for each prey kind. Since polychaetes were generally fragmented, they were not measured. Mean number of prey per fish was based only on fish which contained food items.

I used a volume displacement technique to measure food items >0.05 cm^3 and a squash technique, modified from Hellawell and Abel (1971), to measure volume of food items <0.05 cm^3 (Ross 1974). To establish minimum sample sizes for description of the ration I used the criterion t, obtained by plotting cumulative trophic diversity (H_k) against cumulative stomachs examined (k). Actual numbers of stomachs (k) varied between samples but had a lower limit of 17. The value of k was greater when specimens varied more in date or location of capture. Trophic diversity was determined by the Brillouin information function (H) according to Pielou (1966) and Hurtubia (1973). A horizontal asymptote, beginning at t, indicated a sufficient sample size so that examination of stomachs in excess of t would not yield an increase in trophic diversity.

To compare trophic differences of size groups of *P. scitulus* I used an unweighted pair group, arithmetic average (UPGMA) cluster analysis (Sneath and Sokal 1973) based on a Czechanowski similarity matrix (Bray and Curtis 1957). All linear regressions were based on the Berkson case of a model I regression (Sokal and Rohlf 1969).

All fish lengths reported are standard length (SL), measured to the nearest 0.1 mm. Mouth width was measured externally between the posterior maxillary processes with the mouth fully closed. Internal mouth width was not routinely measured because of difficulty in working with preserved specimens. However, there was no difference between external mouth width with the mouth fully closed and internal mouth width with the mouth fully opened on 36 specimens favorable to such a comparison (two-tailed paired t = 1.88; $P > 0.05$). Measurement of mouth length followed Hubbs and Lagler (1958).

To measure intestinal length I cut the hindgut distally at the anus and freed the intestine from the investing mesentery. Length (to the nearest millimeter) was measured from the stomach with the intestine fully extended, but not stretched.

Wet weights of *P. scitulus* were taken to the nearest 0.1 g after removing stomach contents and blotting the specimens with absorbent paper. Ovaries and testes were removed, blotted, and weighed to the nearest 0.001 g. To compare levels of gonadal activity I used a gonadosomatic index (GSI = (gonad weight/somatic weight) $\times$ 100).

RESULTS

Food Habits

The dominant prey of *P. scitulus* based on percent occurrence and percent volume was the lancelet, *Branchiostoma floridae*, which composed 61% of the food volume and occurred in 60% of the fish examined (Table 1). Numerically, cumaceans were dominant, making up 40% of the total number of prey. On the basis of percent number, volume, and occurrence, the ration of *P. scitulus* was composed primarily of lancelets, polychaetes, natantians, brachyurans, gammarid amphipods, cumaceans, pelecypods, copepods, and larval crustaceans. Ninety percent of the number of prey items and volume of prey items were accounted for by 6 and 7, respectively, of the 22 major food categories.

I examined seasonal feeding patterns of *P. scitulus* from Station 3, using fish 100 mm or larger to eliminate effects of fish size. *Branchiostoma floridae* occurred in over 50% of the fish in 8 of the

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

TABLE 1.—Food items utilized by *Prionotus scitulus* collected between April 1972 and May 1973 at three stations in Tampa Bay, Fla. Based on 469 specimens containing food items.

Prey category	Percent occurrence	Number no.	Number %	Volume cm³	Volume %
Teleostei:					
Sciaenidae	0.2	1	0.01	0.06	0.09
Prionotus scitulus	0.4	2	0.01	0.15	0.23
All fishes	2.3	11	0.06	0.81	1.24
Amphioxi:					
Branchiostoma floridae	59.5	1,171	6.50	39.77	60.49
Hemichordata:					
Enteropneusta	0.6	3	0.01	0.02	0.03
Echinodermata					
Ophiurae	0.4	2	0.01	0.06	0.09
Brachyura:					
Portunidae	3.0	25	0.01	0.40	0.61
Xanthidae	3.6	42	0.20	1.27	1.93
Grapsidae	0.9	35	0.20	0.58	0.88
Pinnotheridae	7.4	127	0.70	0.75	1.14
Oxyrhyncha	0.2	1	0.01	0.01	0.02
Unidentified crabs	13.9	138	0.80	1.56	2.37
Brachyuran megalops	8.4	140	0.80	0.11	0.17
All crabs	44.6	507	2.82	4.70	7.13
Anomura					
Euceramus praelongus	9.4	71	0.40	0.58	0.88
Paguridae	0.4	2	0.01	0.12	0.18
Natantia:					
Leptochela serratorbita	4.9	45	0.20	0.79	1.21
Palaemonidae	2.4	11	0.06	0.05	0.08
Alpheidae	0.6	11	0.06	0.21	0.32
Processidae	1.7	8	0.04	0.43	0.65
Hippolytidae	0.4	4	0.02	0.02	0.03
Penaeidae	8.4	99	0.50	2.42	3.68
Lucifer faxoni	1.3	13	0.07	0.02	0.03
Unidentified shrimp	17.4	111	0.60	1.18	1.80
Natantian larvae	0.4	2	0.01	(1)	
All shrimps	42.4	304	1.70	5.12	7.79
Amphipoda:					
Gammaridea	56.1	4,615	25.6	2.44	3.71
Caprellidea	3.9	67	0.04	0.02	0.03
Isopoda	13.1	87	0.50	0.19	0.29
Cumacea	38.3	7,287	40.40	1.45	2.21
Mysidacea	7.7	119	0.70	0.14	0.21
Leptostraca					
Nebalia	0.8	4	0.02	0.08	0.12
Copepoda	12.8	2,882	16.00	0.12	0.18
Ostracoda	8.8	83	0.50	0.07	0.11
Unidentified crustacea	5.1	363	2.00	0.03	0.05
Acarina:					
Hydracarina	0.4	2	0.01	(1)	
Pycnogonida	0.2	1	0.01	(1)	
Annelida:					
Polychaeta	36.2	(2)		9.11	13.86
Mullusca:					
Pelecypoda	22.1	356	2.00	0.78	1.19
Gastropoda	4.9	52	0.30	0.13	0.20
Brachiopoda	0.2	1	0.01	0.01	0.02
Cnidaria	0.9	6	0.03	0.02	0.03
Totals		17,992		65.75	

[1]Only a trace amount of food present.
[2]An accurate count of individuals was not possible.

13 mo examined, dropping between 30 and 40% in September, January, and May. Number, volume, and percent occurrence for *B. floridae* all showed major peaks in utilization between June and August, and October and December 1972. Polychaetes were irregular in percent occurrence, but the data suggest a peak in spring and summer, while natantians and brachyurans showed increases in percent occurrence in the spring and fall. Amphipods, cumaceans, mysids, and pelecypods showed strong spring peaks in importance.

Nine size groups of *P. scitulus* (21-40, 41-60, 61-80, 81-90, 91-100, 101-110, 111-120, 121-130, 131-140) reached stabilized horizontal asymptotes of cumulative trophic diversity versus cumulative stomachs examined. The analyses of size changes in feeding are based on these groups.

The percent occurrence of lancelets and polychaetes increased with increasing fish size, while gammarid amphipods decreased (Table 2). Brachyurans, cumaceans, copepods, larval crustaceans, pelecypods, and ostracods increased in percent occurrence for searobins up to 80-100 mm,

TABLE 2.—Percentage of prey occurrence for size groups (millimeters standard length) of *Prionotus scitulus* from Tampa Bay, Fla., 1972-73. Only prey categories with an overall occurrence of 1% or greater were included.

Prey category	21-40	41-60	61-80	81-90	91-100	101-110	111-120	121-130	131-140
Teleostei	0	5.3	4.6	5.9	0	3.7	2.9	0	3.7
Branchiostoma floridae	4.0	21.1	22.7	29.4	63.0	69.1	64.5	70.6	70.3
Brachyura	8.0	20.1	45.5	64.7	25.9	37.0	30.4	29.4	22.2
Natantia	20.0	26.3	13.6	17.6	11.1	29.6	34.1	32.4	48.2
Anomura	4.0	5.3	0	5.9	11.1	11.1	10.9	9.8	7.4
Gammaridea	88.0	89.5	54.5	52.9	48.1	51.9	59.4	48.0	48.2
Caprellidea	8.0	0	4.6	0	0	2.5	8.7	2.0	3.7
Isopoda	0	15.8	9.1	5.9	18.5	8.6	17.4	8.8	25.9
Cumacea	36.0	78.9	72.7	52.9	74.1	51.9	25.4	21.6	25.9
Mysidacea	8.0	10.3	0	0	25.9	17.3	5.8	1.0	7.4
Copepoda	8.0	26.3	63.6	41.2	37.0	9.9	3.6	4.9	7.4
Ostracoda	16.0	20.1	22.7	41.2	14.8	7.4	3.6	2.9	7.4
Crustacean larvae	4.0	21.1	54.6	23.5	3.7	2.5	0	0	0
Polychaeta	0	5.3	9.1	23.5	25.9	30.9	47.1	44.1	62.9
Pelecypoda	4.0	0	45.5	29.4	25.9	21.0	21.7	23.5	22.2
Gastropoda	0	0	18.2	11.8	7.4	2.5	5.8	2.0	7.4
No. of fish examined	25	19	22	25	27	81	138	102	27

and then decreased for larger fish. Other prey categories either did not show regular trends or remained relatively constant in occurrence between size classes. The percent number of prey showed similar trends with increasing fish size. Crustacean larvae, copepods, gammarid amphipods, and cumaceans were of greater importance to small fish, while larger fish (100-140 mm) utilized more lancelets and pelecypods.

The volumetric importance of *Branchiostoma* to the 41- to 60-mm size group resulted from one fish capturing a single large lancelet. Volumetrically, the diet of *P. scitulus* 80 mm and larger was dominated by lancelets and polychaetes, while cumaceans, copepods, and natantians (especially larval forms) were of greater importance to small fish (Figure 2). Brachyurans showed a more uniform pattern of distribution among size groups.

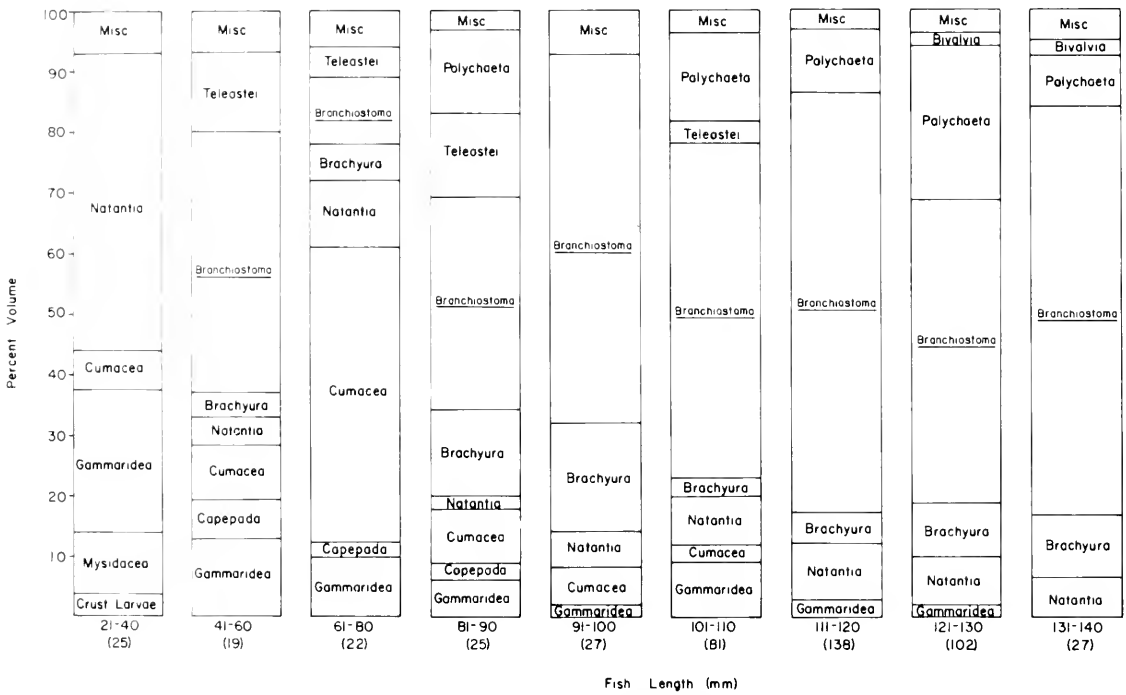
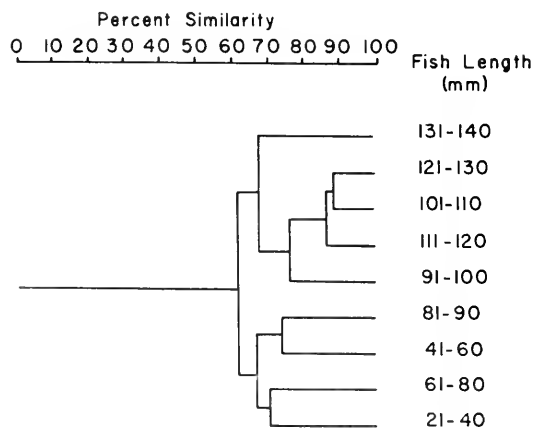


FIGURE 2.—Changes in the percent volume of major prey categories for size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73.



Trophic relationships among size groups were summarized by cluster analysis based on the percent occurrence of prey (Figure 3). Fish smaller than 81-90 mm and larger than 91-100 mm formed two major divisions, linking at 77% similarity. The lower similarity between size classes of smaller searobins compared with larger size classes is indicative of the more rapid changes in trophic ontogeny occurring between small individuals.

FIGURE 3.—Cluster analysis (UPGMA; unweighted pair group, arithmetic average) of prey similarity between size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73. Similarity was determined from percent occurrence of prey categories.

The total amount of food ingested, as shown by the mean volume of stomach contents, increased rapidly with increasing fish size; log transformed values of total prey volume varied linearly with fish size over most size classes (Figure 4). The total number of prey per fish also increased rapidly with increasing fish size up to the 60- to 80-mm size class, but then declined markedly for larger size groups (Figure 4). The decline in number of prey ingested occurred somewhat prior to a detectable increase in mean prey size (cf. Figure 5). Searobins smaller than the 90- to 100-mm size group showed an asymptotic relationship of fish length and linear prey size, while prey sizes increased rapidly over the larger size groups. Since linear prey measurements may be misleading, I also examined the average volume (cubic centimeters) of prey items eaten by size classes of *P. scitulus*. Prey volume was calculated from the total sorted food volume from each 10- or 20-mm size class, divided by the total prey number for each size class. Mean prey volume did not increase over small size classes of searobins, but at 90-100 mm it initiated a rapid increase (Figure 6). Consequently, the rapid rise in total stomach volume of the leopard searobin occurred initally through the capture of increasing numbers of small prey, followed (after 90-100 mm) by the capture of fewer, but progressively larger, prey.

Relative prey biomass (mean prey volume/mean wet weight) was initially very high but then decreased with fish size to the 61- to 70-mm size class, followed by an increase for fish larger than the 90- to 100-mm size class (Figure 6).

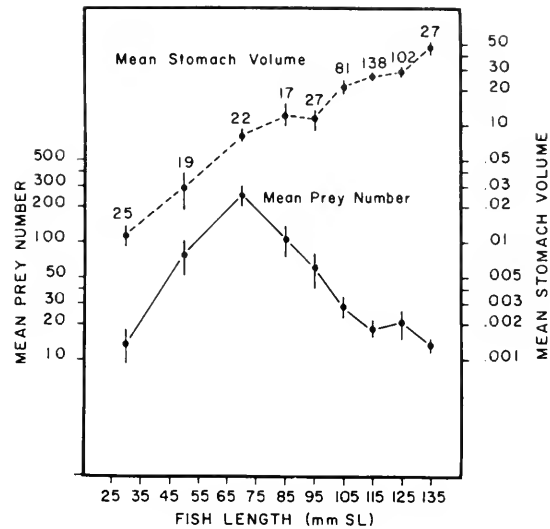


FIGURE 4.—The relationship of mean volume of stomach contents (cubic centimeters) and mean prey number (logarithmic scales) to fish length for *Prionotus scitulus*, Tampa Bay, Fla., 1972-73. The vertical lines indicate 1 SE on either side of the mean, sample sizes are shown above the upper graph.

Increases in prey size with increasing predator size might occur through shifts in the utilization of progressively larger prey kinds, or through the

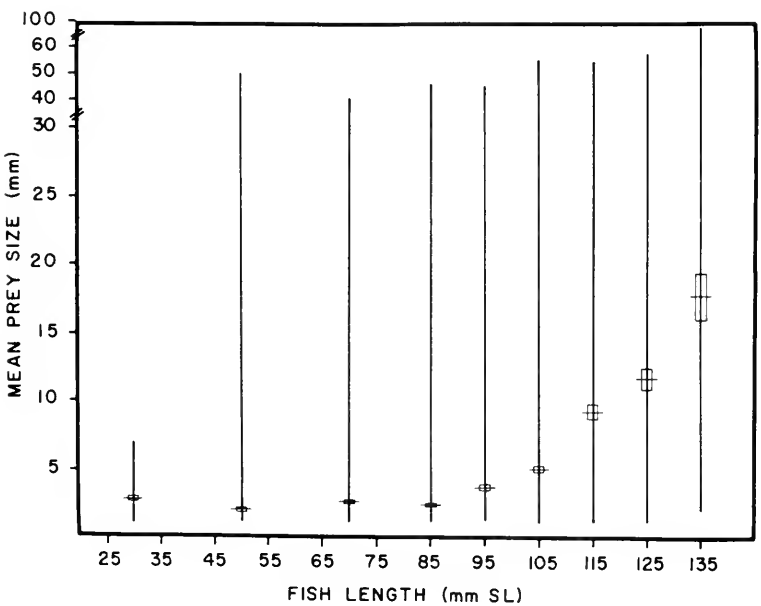


FIGURE 5.—Mean prey length versus standard length groups of *Prionotus scitulus* from Tampa Bay, Fla. Vertical lines are ranges; cross-bars and open rectangles are $\bar{x} \pm 2$ SE.

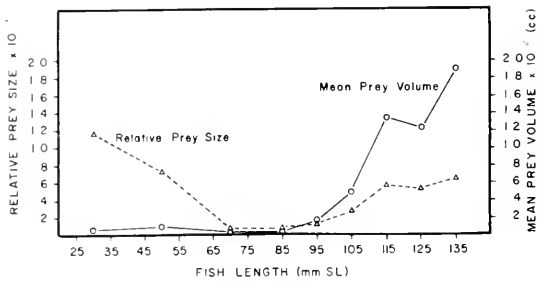


FIGURE 6.—Mean prey volume (cubic centimeters) and relative prey size ($\bar{x}$ prey volume/$\bar{x}$ wet fish weight) for size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73.

selection of larger sized individuals within a single prey kind. Only one prey item, *B. floridae*, exhibited a broad enough size range to meaningfully test for differences between fish sizes. The mean size of lancelets, however, did increase with increasing fish size ($P<0.001$) (Figure 7), but the rate of increase was quite low compared with the overall increase in mean prey size (cf. Figure 5).

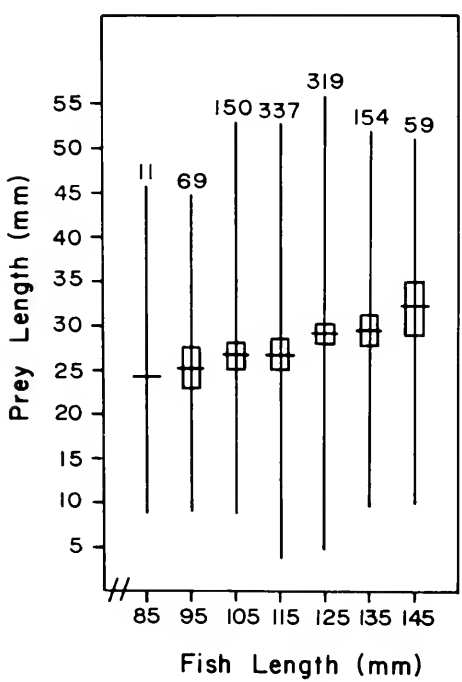


FIGURE 7.—The relationship between lengths of the dominant prey, *Branchiostoma floridae*, and its predator, *Prionotus scitulus*. See Figure 5 for explanation of symbols.

Morphology and Growth

Trophic changes showed a critical size interval between approximately 60 and 100 mm, within which the mean prey number decreased, and after which the mean prey volume, length, and relative volume increased. These trophic changes suggested the presence of certain morphological or developmental correlates, of which I examined jaw size, intestinal length, and growth.

Ontogenetic changes in mouth size were expressed by relative jaw width and relative jaw length. Juvenile leopard searobins showed proportionately greater mouth widths and lengths compared with adults, but plots of both relative jaw length and relative jaw width versus SL showed considerably lower slopes by approximately 75 mm (Figure 8). Proportionate mouth length continued to decrease with increasing fish size for fish >75 mm; however, proportionate mouth width remained constant for fish >75 mm. Mouth size thus increased rapidly with increasing fish size for early juvenile *P. scitulus*, but by 75 mm the relationship between mouth size and fish length was essentially fixed.

Intestinal length increased rapidly between the 45- and 65-mm size classes. Fish <50 mm had mean intestinal lengths of 70% SL, while fish >60 mm had mean intestinal lengths of 102% SL.

Log transformed length-weight values of leopard searobins showed an increase in the slope of the regression line between approximately 55 and 75 mm (Figure 9). The fish were divided into two size groups, <75 mm and >75 mm, and sepa-

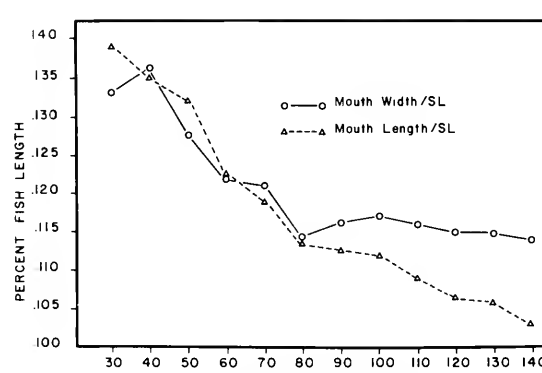


FIGURE 8.—Relative mouth width and relative mouth length versus fish length for *Prionotus scitulus*, Tampa Bay, Fla. Each data point is based on the mean of 20 individuals.

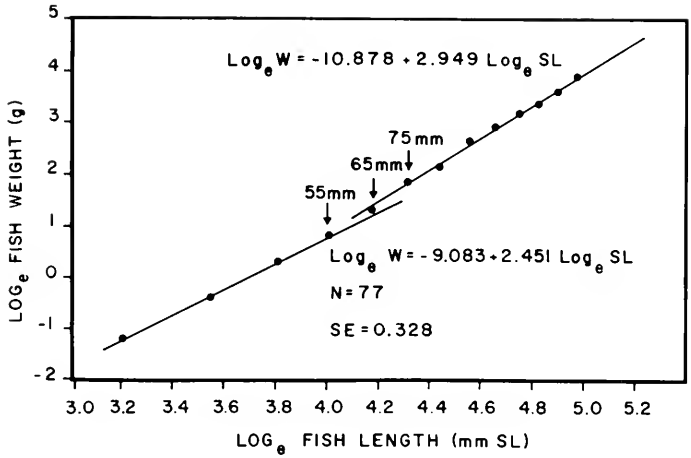


FIGURE 9.—Length-weight relationships for size classes of *Prionotus scitulus*, Tampa Bay, Fla.

rate length-weight regressions were calculated. The 75-mm size was chosen because of its association with changes in relative mouth size. The growth data showed that *P. scitulus* >75 mm were gaining weight much more rapidly than smaller fish, even after allowing for the expected exponential rate of increase by using the log transformation.

Reproduction and Distribution

Mean female GSI's remained below 0.4 for *P. scitulus* between 20 and 90 mm and these fish did not contain mature ova. Leopard searobins 100 mm and larger had mean GSI values between 3 and 6 and were sexually mature. Ross (1974, in press) showed that mean female GSI values during spring to summer spawning were 5 to 10. The GSI values reported here are lower because the fish were combined from all months of the study to avoid possible bias due to differences of spawning times of different size groups. Male searobins showed the same size-related pattern.

Spatial separation between immature and mature *P. scitulus* was quite pronounced (Figure 10). Juvenile searobins consistently had high relative abundances at Station 1 in Old Tampa Bay (5 m deep), while mature fish had high relative abundances near the mouth of Tampa Bay at Station 3 (7 m deep). Overlap between immature and mature searobins was greatest during summer and fall 1972 at Station 2 (5 m). The percent occurrence of juvenile fish in combined collections was highest between March and May (60-75%) and lowest between June and November (25-47%).

Annual mean salinities varied significantly between stations ($P<0.05$); respective means for Stations 1-3 were 25.7, 28.1, and 33.2‰. Consequently, small leopard searobins were occupying somewhat less saline water. Annual mean temperatures did not vary between stations (range = 13°-32°C).

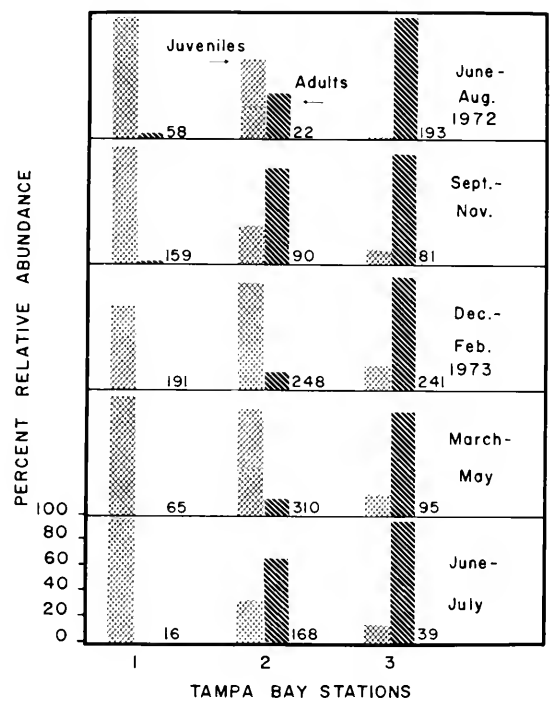


FIGURE 10.—Spatial distribution of juvenile (<100 mm SL), and adult (>100 mm SL) *Prionotus scitulus* at three stations in Tampa Bay, Fla., 1972-73. Percent relative abundance is based on each sample site and date; numbers indicate sample sizes. Adults are indicated by hatching; juveniles by cross-hatching.

DISCUSSION

Ontogenetic changes in prey utilization by *P. scitulus* showed an early dependence on planktonic or epifaunal prey such as crustacean larvae, copepods, mysids, cumaceans, and gammarid amphipods. Larger *P. scitulus* (>90 mm) ate more infaunal organisms such as lancelets and polychaetes. Separation by prey kind was greatest at 90 mm which corresponded to the transition size between immature and mature fishes.

The greatest percent occurrence of juvenile fish (March-May) coincided with periods of higher utilization of brachyurans, natantians, cumaceans, amphipods, mysids, pelecypods, and polychaetes by adult fish, although lancelets remained the dominant prey. Consequently, size differences in food habits were not biased by seasonal unavailability of certain prey to adults or juveniles. Also, Ross (1974) demonstrated that changes in food habits with increasing fish size were generally consistent between stations.

Other studies on food habits of *P. scitulus* have indicated that small crustaceans and polychaetes were important prey (Reid 1954; Springer and Woodburn 1960; Ross 1977, in press). Ross (1977, in press) found that *P. scitulus* from offshore of Tampa Bay utilized principally brachyurans, polychaetes, cumaceans, gammarid amphipods, natantians, and lancelets.

Total food consumption showed an accelerating rate of increase with fish length, but initially this occurred through a rapid rise in the number of prey consumed, rather than through an increase in prey size. Prey size did not increase with increasing fish size for searobins <90 mm. Although numerous studies have demonstrated positive correlations between prey and predator sizes (e.g., Northcote 1954; Hartman 1958; Wong and Ward 1972; Hespenheide 1973), Schoener (1969, 1971) predicted that prey size would decrease with decreasing predator sizes to a lower horizontal asymptote. Essentially, the energy gained from progressively smaller prey gradually approaches the energy expended in obtaining and digesting prey. Data on prey size-predator size relationships supporting this prediction were reviewed by Schoener (1971), but did not include fishes as examples.

Prey size (both length and volume) was positively correlated with fish size for searobins 90 mm and larger. The increase in mean prey size relative to predator size occurred primarily through a progressive shift to different, larger prey taxa, and only secondarily by size selection within a single prey taxon.

The transition from numerous small prey to fewer large prey was preceded by rapid growth of jaw size relative to body size and by an increase in intestinal length. Since intestinal absorption may be increased through the development of folds and an increase in length or both (Siankowa 1966), the relative increase in intestinal length of *P. scitulus* is perhaps a response to increased energy demands of larger fish or to their utilization of larger prey items.

Growth in fishes may occur as a series of stanzas which are entered by ecological and physiological size thresholds (Parker and Larkin 1959). Growth stanzas may be recognized by changes in weight-length relationships (Ricker 1975). The shift from small to large prey in *P. scitulus* was accompanied by a change in the weight-length relationship indicating the presence of two growth stanzas. Growth efficiency, measured as weight gained per ration weight per unit time, varies extensively with prey kind (Paloheimo and Dickie 1966). For instance, growth efficiency of trout increased as the ration progressed from hatchery mash to gammarid amphipods to minnows. The two growth stanzas in *P. scitulus* may thus reflect an increase in the proportion of food energy available for growth as small crustaceans are replaced by larger lancelets and polychaetes in the diet.

Relative prey size showed a parabolic relationship with fish size. Consequently, small *P. scitulus* were, in effect, predators of large prey. Prey size distributions have been shown to follow a lognormal relationship in various communities (Whittaker 1952; Schoener and Janzen 1968; Griffiths 1975), so juvenile leopard searobins were utilizing an apparently abundant energy source. However, since mean prey size did not increase with increasing fish size for searobins <90 mm, with growth, searobins tended toward being "small" predators due to the continued use of the same-sized prey items. Although prey availability was not monitored, *P. scitulus* between 20 and 90 mm were likely operating as number maximizers (cf. Griffiths 1975). Griffiths presented evidence that juvenile stages of several kinds of vertebrates pass through such a stage during which prey items are utilized in close proportion to their actual occurrence.

Searobins >90 mm showed an increase in relative prey size, thus tending again towards being

predators of large prey. The data suggest a switch in feeding strategy to an energy maximizer (cf. Griffiths 1975) in which predators feed in such a manner as to maximize their energy intake. In *P. scitulus* this is perhaps accomplished by a switch in feeding behavior after achieving a critical size threshold requisite for capturing partially buried infaunal prey.

The shift to utilization of large prey occurs slightly before the onset of reproduction. Increased energy demands, or a decrease in foraging time, brought about by gonadal development and breeding activity or both, might be critical factors in selecting for the change in the feeding strategy of *P. scitulus*.

Mature and immature *P. scitulus* were effectively segregated along both spatial and trophic dimensions in Tampa Bay. Spatial segregation might occur through the ability of juvenile searobins to occupy shallower water or to withstand lower salinity, a characteristic of many juvenile marine fishes (Gunter 1961). Trophic overlap in prey kind between immature and mature size groups was closely comparable with trophic overlap between adult individuals of different species of searobins on the West Florida Shelf (Ross 1977). Consequently, *P. scitulus* in Tampa Bay were effectively reducing the potential for intraspecific competition.

ACKNOWLEDGMENTS

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DESCRIPTION OF LARVAE OF THE HUMPY SHRIMP, *PANDALUS GONIURUS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

EVAN HAYNES[1]

ABSTRACT

Except for Stage I, identification of larval stages of *Pandalus goniurus* has not been verified by rearing the larvae from known parentage. Larvae of *P. goniurus* were reared in situ in Kachemak Bay, Alaska, from the first zoea (Stage I) through the first juvenile stage (Stage VII). Each of the seven stages is described and illustrated. The descriptions are compared with descriptions of larval stages of *P. goniurus* given by other authors.

Studies on the early life history of pandalid shrimp in Alaskan waters were begun in 1972 by the National Marine Fisheries Service with the initial objective of describing pandalid shrimp larvae reared in the laboratory from known parentage. I have reported on larvae of coonstripe shrimp, *Pandalus hypsinotus* Brandt, reared in the laboratory (Haynes 1976). In the present report I describe and illustrate larvae of humpy shrimp, *P. goniurus* Stimpson, reared in situ in Kachemak Bay, Alaska. A third report will describe larvae of pink shrimp, *P. borealis* Krøyer, and compare the larvae of *P. borealis* with larvae of other local pandalid species, including *P. goniurus*.

MATERIALS AND METHODS

The laboratory technique used successfully for rearing larvae of *P. hypsinotus* (Haynes 1976) proved unsuitable for rearing *P. goniurus* beyond Stage II. Beginning with Stage III, molting frequency and number of larval stages of *P. goniurus* reared in the laboratory were inconsistent, mortality was high, and the larvae of a given stage were not always morphologically identical. Rearing *P. goniurus* in situ reduced mortalities and yielded larvae essentially identical morphologically within each stage.

Larvae were reared in situ from the first zoea (Stage I) through the megalopa and first juvenile (Stages VI and VII) in the following manner. Stage I zoeae of known parentage were obtained using the laboratory technique described by Haynes (1976). The Stage I zoeae were then transported to sea and placed in 500-ml flasks containing seawater of about 35‰ salinity and 4°C obtained from about 6 m depth with a plastic hand pump and hose. Subsurface seawater was used to avoid the lower salinity (about 28‰) of surface waters derived from local runoff which, as I had found during previous rearing studies, adversely affects larval development by resulting in delayed molting and variable numbers of stages. One larva was placed in each flask. The mouths of the flasks were then covered with nylon screening of #0 mesh (0.571 mm); the flasks were placed in holding containers and suspended upright at 15-20 m depth in water about 40 m deep. The #0 mesh size allowed plankton to collect in the flasks for food but prevented the larvae from escaping. Each flask was numbered and a record kept of the molting history of each larva in each flask. Flasks were checked at least every other day for cast skins and refilled with fresh subsurface seawater. When a larva molted, the cast skin was removed from the flask with a large-bore pipette and preserved in 5% formaldehyde for subsequent examination ashore.

Identification of larval sequence and stage was verified using larvae obtained from plankton with a net of #0 mesh towed near the bottom at about 2 kn in water 60 m deep. The plankton sample was immediately placed in a glass receptacle containing several liters of subsurface seawater. Stage I zoeae of *P. goniurus* were removed from the glass receptacle using a large-bore pipette, placed in 500-ml flasks, one zoea to a flask, and reared to

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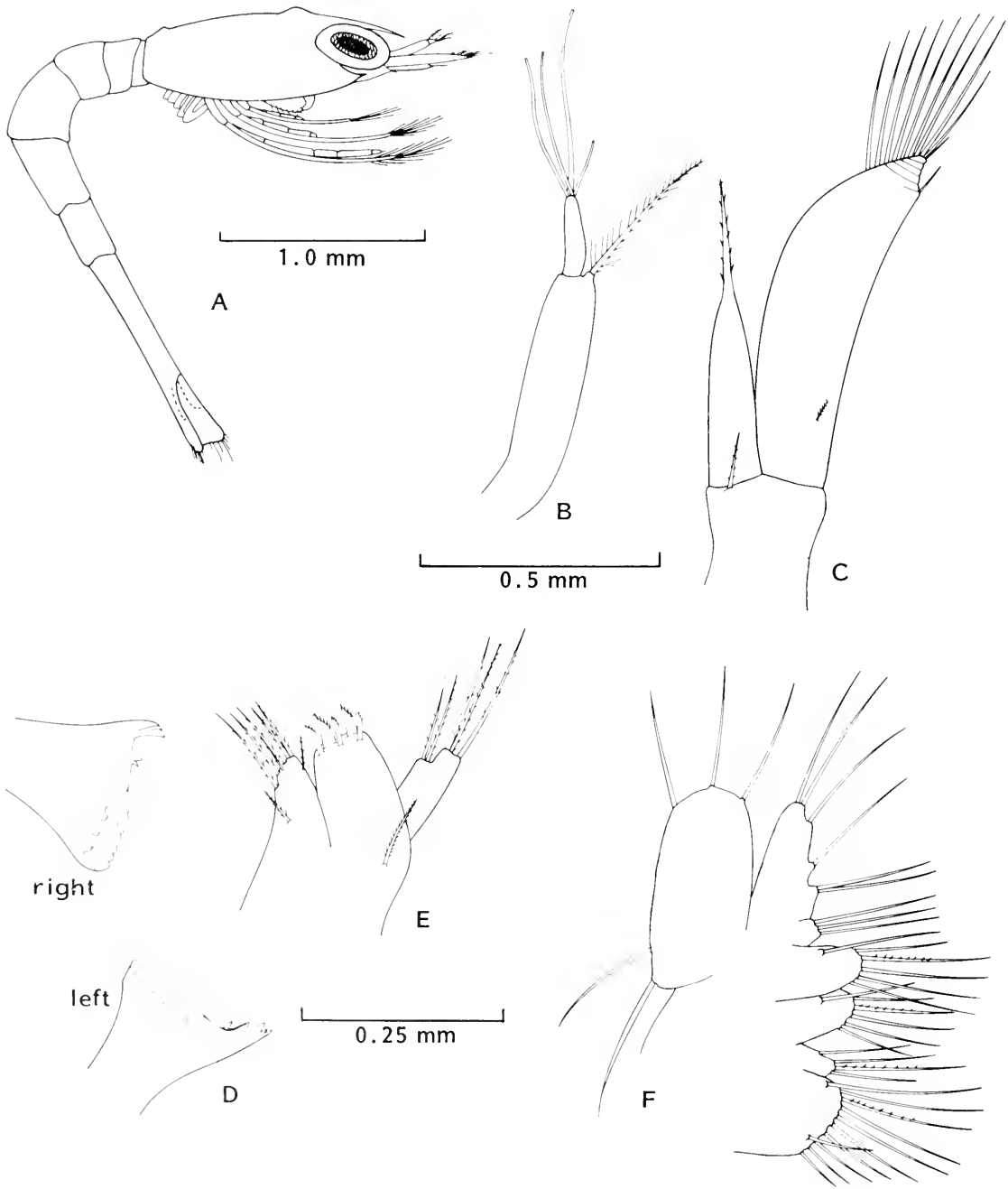
postlarvae in the same manner as the Stage I zoeae obtained in the laboratory.

To verify the validity of the sequence of the larval stages obtained from flasks, larvae of each stage were obtained from plankton and reared in flasks in the same manner for one molt. They were then removed from the flasks along with their cast skins, preserved, and replaced with a larva of the same stage. Thus, a Stage II zoea that had molted to Stage III in a flask was replaced with a Stage III zoea from plankton, the Stage III zoea being replaced in like manner when it had molted to Stage



IV. This procedure was done for each stage including the megalopa (Stage VI). In addition to the larvae and cast skins obtained from rearing in flasks, molting sequence and stage were verified by monitoring the sequence of larval stages from local collections, obtained at least weekly in areas where larvae were abundant, and by examining larvae caught while in the process of molting.

Only those morphological characteristics useful for readily identifying each stage are given.

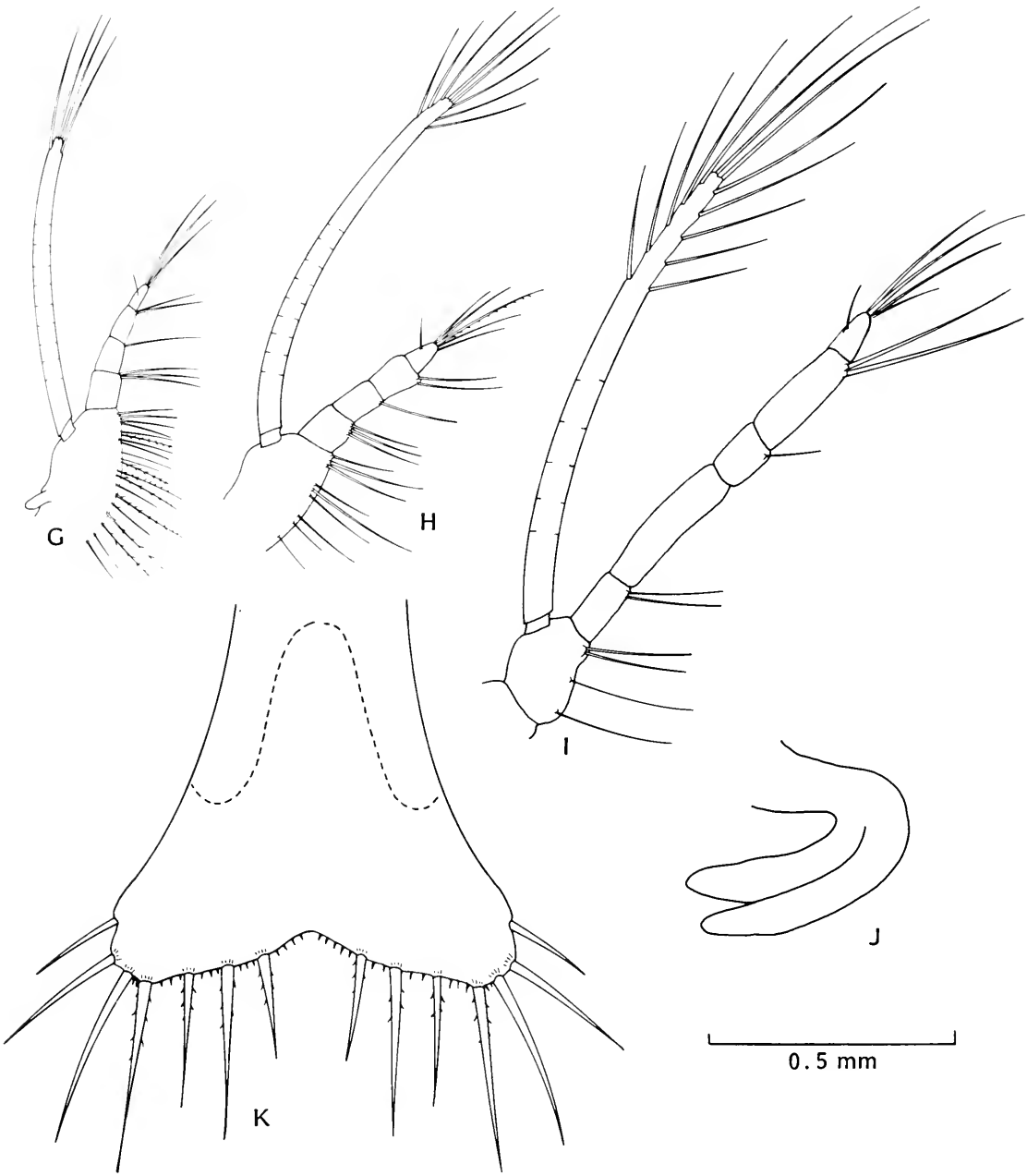


FIGURE 1.—Stage I zoea of *Pandalus goniurus:* A, whole animal; B, antennule; C, antenna; D, mandibles (right and left); E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, second pereopod; K, telson.

Stages I and II are described in greatest detail because these stages are the most difficult to identify. 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 each pair of appendages the left member is figured except for the mandibles, which are drawn in pairs and figured from the right side. For clarity, setules on setae are usually omitted but spinulose setae are shown.

STAGE I ZOEA

Total length of Stage I (Figure 1A) 4.0 mm (range 3.7-4.2 mm; 10 specimens). Live specimens translucent with isolated areas of color: mouthparts orange with a bright yellow chromatophore at base; internal thoracic organs greenish, especially heart area; base of maxillipeds greenish orange; distinct yellow chromatophore at anus. Rostrum slender, spiniform, without teeth, about one-third length of carapace, and projects horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and a smaller rounded prominence near posterior edge. These two prominences occur in all zoeal stages. Pterygostomian spines present but usually hidden by sessile eyes. Three to four minute 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 a simple unsegmented tubular basal portion with a heavily plumose seta terminally and a distal conical projection bearing four aesthetascs: one long, one short, and two of intermediate length.

ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, and tipped by a spinulose spine. Antennal scale distally divided into five joints (the proximal joint incomplete) and fringed with nine heavily plumose setae. Two simple setae occur on outer margin, one terminal and adjacent to plumose setae and the other near base of terminal segments. A small plumose seta usually occurs proximally near lateral margin in all zoeal stages. Protopodite bears spinous seta at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 1D).—Without palps in all zoeal stages. Incisor process of left mandible bears four teeth in contrast to triserrate incisor process of right mandible. Left mandible bears a movable premolar denticle (lacinia mobilis) whereas right mandible bears two immobile premolar denticles. Truncated molar process of left mandible bears a subterminal tooth that occurs throughout all zoeal stages.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) bears stout seta near base, and seven spinulose spines terminally. Median lobe (basipodite) bears five stout spinulose spines on terminal margin, two of them especially thick with projecting teeth, and a large setose seta proximally. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal setae; two of the setae are especially spinulose.

MAXILLA (Figure 1F).—Bears platelike exopodite (scaphognathite) with four long plumose setae along distal and outer margins, and one slightly longer and thicker seta at proximal end. Endopodite gives indication of four partly fused segments and bears nine large plumose setae. Basipodite bilobed; each lobe bears six setae. Bilobed coxopodite bears 15 setae, 4 on distal lobe and 11 on proximal lobe. Four setae, one on each lobe of basipodite and coxopodite, bear a row of little spines along entire length.

FIRST MAXILLIPED (Figure 1G).—Most heavily setose of natatory appendages. Protopodite not segmented; bears 17-20 setae, several of them especially spinulose. Endopodite distinctly four-segmented; setation formula 4, 2, 1, 3. Exopodite a long slender ramus segmented at base; has two terminal and two lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite not segmented; bears nine sparsely plumose setae. Endopodite distinctly four-segmented; setation formula 6, 2, 1, 3. Exopodite with two terminal, six lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite bears four setae. Endopodite distinctly five-segmented; nearly as long as exopodite; setation formula 5, 2, 1, 0, 2. Exopodite with 2 terminal, 10 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, directed under body somewhat anteriorly. First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3.

PLEOPODS.—Not evident.

TELSON (Figure 1K).—Not segmented from sixth abdominal somite; slightly emarginate distally; bears seven pairs of densely plumose setae. Fourth pair of setae longest, length about one-half width of telson. Minute spinules at base of each seta except possibly last pair. Larger spinules along terminal margin between bases of four inner pairs and on setae themselves. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II (Figure 2A) 4.9 mm (range 4.5-5.3 mm; 10 specimens). Chromatophore color and pattern essentially identical to Stage I except chromatophores larger and color more pronounced, especially in mouth parts. From this stage on, zoeae become increasingly more orange and color pattern is not useful as an aid to specific identification. Rostrum still without teeth but not curved downward as strongly as in Stage I. Carapace has prominent supraorbital spine; antennal and pterygostomian spines clearly visible. These spines persist throughout all zoeal stages. Epipodite still not bilobed; pleurobranchiae not yet present.

ANTENNULE (Figure 2B).—Three-segmented; bears on terminal margin a large outer and a smaller inner flagellum. Inner flagellum not segmented, conical, and bears one long spine terminally. Outer flagellum bears two groups of aesthetascs, one group terminally consisting of seven aesthetascs, two of them larger than remaining five, and a second group of two aesthetascs on inner margin. A small budlike projection (not shown in Figure 2B) originates at base of the two flagella and bears three simple setae. Joint of proximal segment faint and may not be complete; bears about five dorsally projecting small plumose setae. Second segment has one lateral plumose seta and about five dorsally projecting plumose setae ringing terminal margin. Third segment has five lateral plumose setae.

ANTENNA (Figure 2C).—Flagellum unsegmented, still shorter than scale, styliform, and tipped by a short spine. Antennal scale fringed with 19 long, thin, plumose setae along terminal and inner margins; small seta on outer margin near base of terminal segments; has four joints distally but only the three most distal joints are complete. Protopodite bears minute spine at base of scale in addition to spine at base of flagellum.

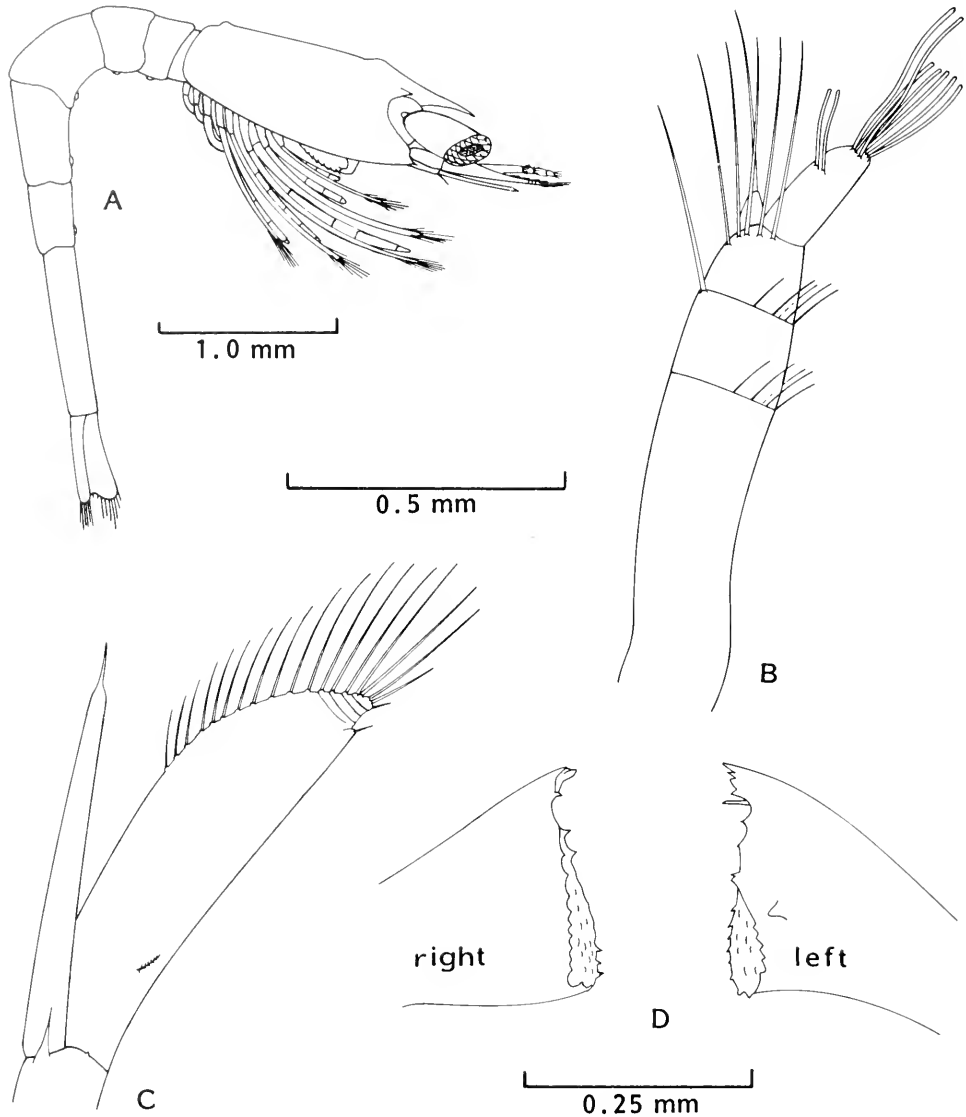
MANDIBLES (Figure 2D).—More massive than in Stage I. Both mandibles bear additional denticles and molar processes more developed. Curved lip of truncated end of molar process of right mandible more developed.

MAXILLULE.—Unchanged from Stage I except basipodite now bears two additional spinulose spines.

MAXILLA.—Shape similar to Stage I except exopodite slightly longer proximally and now bears nine marginal plumose setae in addition to plumose seta at proximal end. No change in number of setae on basipodite or coxopodite.

MAXILLIPEDS.—Essentially identical to Stage I but bear additional setae as follows. First maxilliped bears 17-20 setae on protopodite; exopodite bears 6 natatory setae rather than 4 as in Stage I; no change in epipodite. Second maxilliped bears 7 setae on protopodite; exopodite bears 10 lateral natatory setae in addition to the 2 terminal setae; endopodite five-segmented, setation formula 5, 2, 1, 1, 3. Third maxilliped bears 2 setae on protopodite; exopodite bears 10 lateral natatory setae in addition to the 2 terminal setae; segments of endopodite may or may not bear an additional seta or 2, setation formula usually 5, 4, 0, 1, 2.

FIRST PEREOPOD (Figure 2E).—Endopodite functionally developed; five-segmented and terminating in a simple conical dactylopodite; setation formula 4, 2, 1, 0, 0. Protopodite bears no setae. Exopodite, longest among pereopods, has 2 terminal and 10 lateral natatory setae.



SECOND PEREOPOD (Figure 2F).—Similar to first pereopod except endopodite shorter, setation formula 3, 2, 0, 0, 1. Protopodite bears no setae. Exopodite with two terminal and six lateral natatory setae.

THIRD PEREOPOD (Figure 2G).—Endopodite five-segmented; one-fourth to one-third longer than exopodite. Dactylopodite slightly longer than in first two pereopods; bears two setae terminally. Propodite bears two setae; remaining segments without setae. Exopodite noticeably shorter than exopodites of first two pereopods; bears six lateral natatory setae in addition to two terminal natatory setae.

FOURTH AND FIFTH PEREOPODS.—Unsegmented except at base; without exopodite or setae; directed under body somewhat anteriorly as in Stage I (Figure 2A).

PLEOPODS (Figure 2A).—Present as minute buds.

TELSON (Figure 2H).—Similar in shape to Stage I but distinctly segmented from sixth abdominal

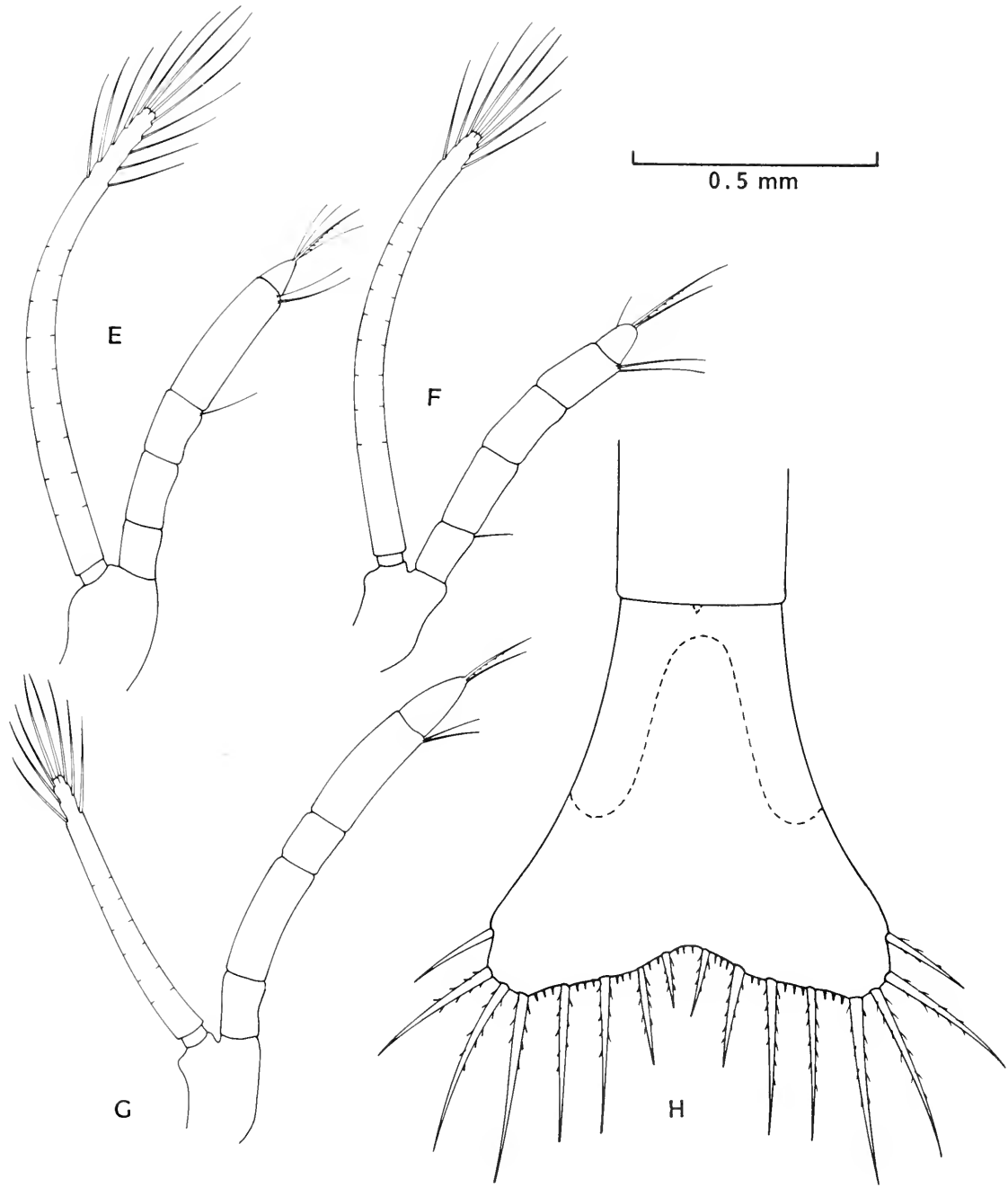


FIGURE 2.—Stage II zoea of *Pandalus goniurus:* A, whole animal; B, antennule; C, antenna; D, mandibles (right and left); E, first pereopod; F, second pereopod; G, third pereopod; H, telson.

somite; bears eight pairs of densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

Total length of Stage III 6.2 mm (range 6.0-6.6 mm; 10 specimens). Rostrum (Figure 3A) projects horizontally but curves slightly downward at tip; bears the beginning of a tooth at base. Epipodite of first maxilliped minutely bilobed; pleurobranchiae present as minute buds.

ANTENNULE (Figure 3B).—Inner flagellum unsegmented; about one-half to two-thirds length of outer flagellum. Outer flagellum unsegmented; bears three long and three shorter aesthetascs terminally and one group of two aesthetascs proximally. Each segment bears additionally one or two long plumose setae. Large spine projects ventrally from proximal segment.

ANTENNA (Figure 3C).—Flagellum three-segmented; about two-thirds length of scale and tipped by remnant terminal spine. Antennal scale slightly narrower than in Stage II and fringed with 21 plumose setae; two complete joints at tip. Spine on protopodite at base of scale somewhat larger than in Stage II.

FIRST PEREOPOD (Figure 3D).—Has begun to acquire adult shape, particularly in widened propodite and carpopodite segments. Exopodite bears 12 natatory setae in addition to terminal pair.

SECOND PEREOPOD (Figure 3E).—Endopodite bears a few additional setae and dactylopodite slightly more conical than in Stage II. Propodite not yet projected anteriorly. Exopodite of second pereopod bears 9-10 natatory setae in addition to terminal pair.

THIRD PEREOPOD.—Essentially identical to third pereopod of Stage II except each segment of endopodite bears an additional seta or two.

FOURTH (Figure 3F) AND FIFTH PEREOPODS.—Have begun to acquire adult shape, especially in lengthened dactylopodite and slightly widened propodite.

PLEOPODS (Figure 3G).—Bilobed, unsegmented, and without setae.

TELSON (Figure 3H).—Uropods free. Endopodite undeveloped; about one-third length of exopodite and bearing two simple setae terminally. Anal spine clearly visible.

STAGE IV ZOEA

Total length of Stage IV 7.7 mm (range 6.8-8.3 mm; 10 specimens). Rostrum (Figure 4A) bears two teeth dorsally, no teeth ventrally; tip not yet bifid. Epipodite of first maxilliped fully bilobed; pleurobranchiae small but readily visible, project anteriorly. Epipodite on second maxilliped present as a small bud. No mastigobranchiae.

ANTENNULE.—Shaped as in adult. Neither inner nor outer flagellum segmented. Outer flagellum bears an additional group of three aesthetascs proximally.

ANTENNA (Figure 4B).—Flagellum six-segmented; longer than scale but does not extend past terminal setae of scale. Antennal scale without joints at tip. Other than increase in size, changes in antennal scale from Stage IV onward are negligible.

FIRST PEREOPOD.—Essentially no change from Stage III except exopodite may have an additional pair of natatory setae.

SECOND PEREOPOD (Figure 4C).—Distal joint of propodite projects slightly anteriorly. Exopodite has 10-12 natatory setae in addition to terminal pair.

THIRD PEREOPOD.—Shaped as in adult; exopodite with five pairs of natatory setae in addition to terminal pair.

FOURTH AND FIFTH PEREOPODS.—Shaped as in adult.

PLEOPODS (Figure 4D).—Still unsegmented; length of second pleopod about one-third height of second abdominal segment. Neither setae nor appendix internae present.

TELSON (Figure 4E).—Endopodite of uropod nearly as long as exopodite and fringed with about 20 setae. Lateral margins of telson nearly parallel but slightly wider posteriorly and bear two spines each. Terminal margin still slightly emarginate;

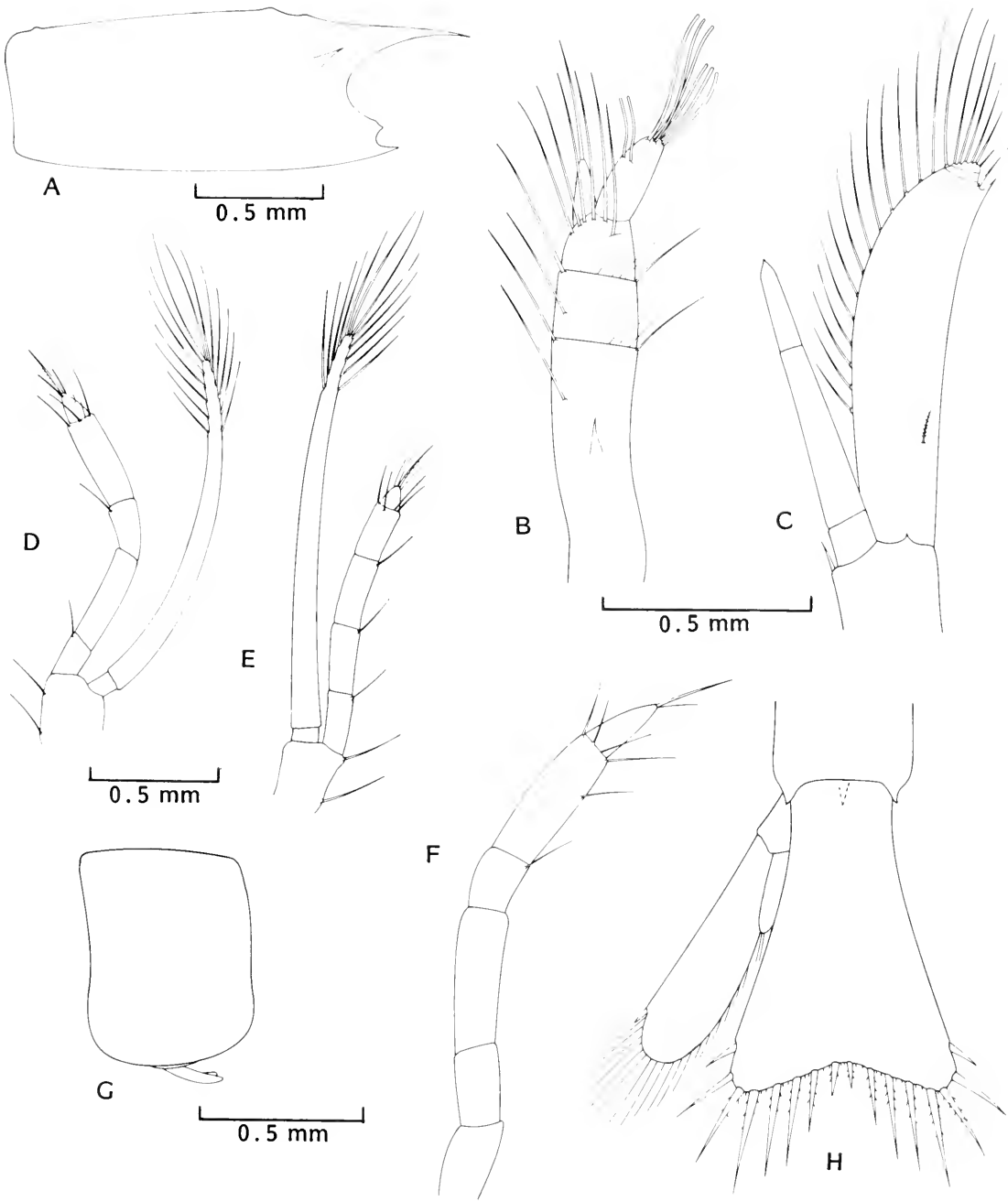


FIGURE 3.—Stage III zoea of *Pandalus goniurus:* A, carapace; B, antennule; C, antenna; D, first pereopod; E, second pereopod; F, fourth pereopod; G, second abdominal segment and pleopod; H, telson.

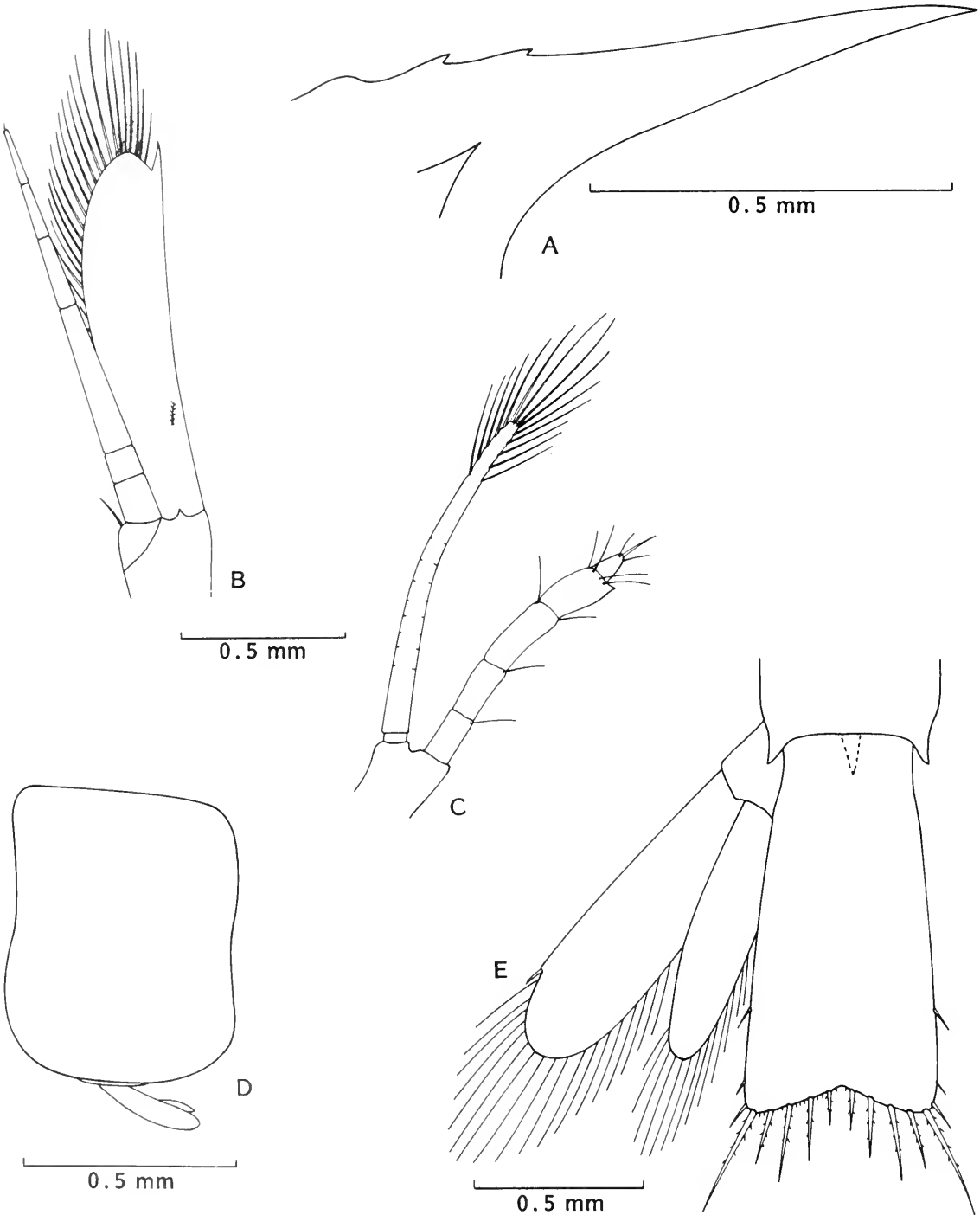


FIGURE 4.—Stage IV zoea of *Pandalus goniurus:* A, rostrum; B, antenna; C, second pereopod; D, second abdominal segment and pleopod; E, telson.

bears six pairs of spines, the outermost (sixth) pair usually without spinules.

STAGE V ZOEA

Total length of Stage V 10.3 mm (range 8.2-11.3 mm; 10 specimens). Rostrum (Figure 5A) with five or six dorsal teeth and no ventral teeth; tip smooth but may bear small hump indicating future location of bifid tooth. Epipodite of second maxilliped lobed. Mastigobranchiae occur as minute buds on third maxilliped and pereopods 1-3.

ANTENNULE.—Inner flagellum usually four-segmented; still bears terminal spine. Outer flagellum three-segmented; bears four groups of three aesthetascs each in addition to terminal aesthetascs.

ANTENNA (Figure 5B).—Flagellum about 1.7 times length of scale; 11-12 segments.

FIRST PEREOPOD (Figure 5C).—Propodite projects anteriorly but not as much as in second pereopod; projection bears small spine terminally. Neither dactylopodite nor propodite projection bear subterminal spines.

SECOND PEREOPOD (Figure 5D).—Chela well formed. Dactylopodite bears two spines subterminally, and propodite projection one spine subterminally. Carpopodite not segmented.

PLEOPODS (Figure 5E).—Segmented; length about two-thirds height of second abdominal segment. Flagella tipped with several simple setae, except first pair of pleopods bears setae only on outer flagellum.

TELSON (Figure 5F).—Uropods similar in shape to adult; telson margins somewhat parallel, bear two spines each. Terminal margin straight or only slightly emarginated, bears six pairs of spines. No evidence of transverse hinge of exopodite of uropod.

STAGES VI AND VII (MEGALOPA AND FIRST JUVENILE)

Total length of Stage VI (megalopa) 13.8 mm (11.1-15.8 mm; 6 specimens). Carapace without supraorbital spine. Rostrum (Figure 6A) shaped as in adult; posterior dorsoventral width not as pronounced nor ventral teeth as fully developed as in Stage VII; bears eight or nine teeth dorsally in addition to distinct bifid tip and four or five teeth ventrally. Usually one or two setae occur between several of the posterior dorsal teeth. Exopodites on third maxilliped and pereopods reduced. Mastigobranchiae larger but still not evident on fourth pereopod. Pleurobranchiae clearly lobulated. Inner flagellum of antennule five- or six-segmented and outer flagellum four-segmented. Inner flagellum lacks terminal spine. Outer flagellum bears subterminally six groups of three aesthetascs each; terminal segment lengthened, without aesthetascs. Mouthparts shaped as in adult; mandibular palp present, two-segmented, without setae. Chelae of first and second pereopods shaped as in adult; carpal joints of left and right second pereopods 20 to 25 and 7 to 9, respectively. Meropodite of left second pereopod three-segmented. Pleopodal setae extend along entire lateral margins of both flagella; tips of appendix internae bear several distinct cincinnuli. Telson (Figure 6B) shows, for first time, shape and spination similar to adult; lateral margins narrow posteriorly but widen slightly at terminal margin. Typically three pairs of spines on lateral margins of telson but often a spine, rarely two, lacking. Terminal margin of telson rounded but not as much as in Stage VII; bears three pairs of stout spines. Transverse hinge of uropod exopodite complete.

Total length of Stage VII (first juvenile) 14.9 mm (range 13.7-15.8 mm; 3 specimens). Rostrum (Figure 7A) typically adult; posterior dorsoventral width slightly greater than in Stage VI; ventral teeth fully formed and one or two setae between most, if not all, teeth including bifid tip. No exopodite on third maxilliped or pereopods. Mastigobranchia evident on fourth pereopod. Flagella of antennules lengthened as in adult; outer flagellum nine-segmented, bears nine groups of three aesthetascs each; inner flagellum six-segmented. Mandibular palp three-segmented, with spinous setae. Carpal joints of left and right second pereopods 29 and 11, respectively. Meropodite of left second pereopod 11-segmented. Telson (Figure 7B) adult in shape, typically bears four pairs of lateral spines although often lacks a single lateral spine.

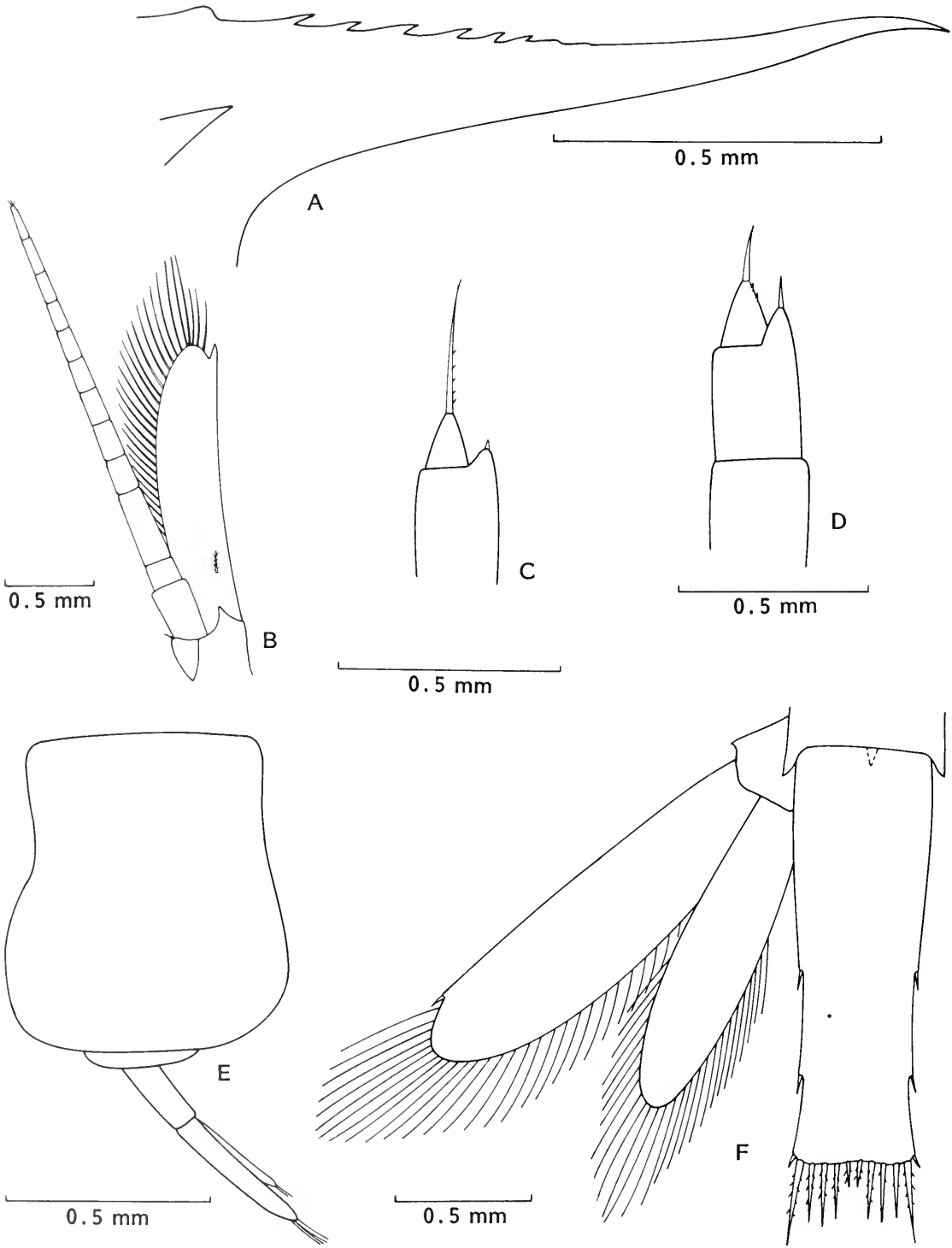


FIGURE 5.—Stage V zoea of *Pandalus goniurus:* A, rostrum; B, antenna; C, first pereopod (terminal segments only); D, second pereopod (terminal segments only); E, second abdominal segment and pleopod; F, telson.

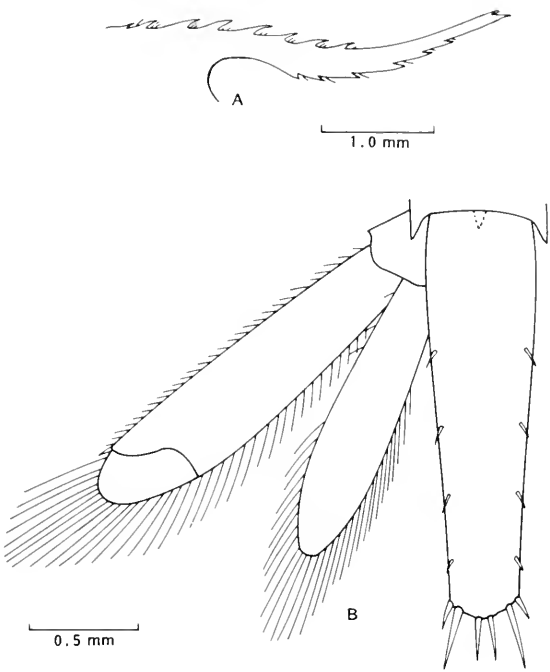


FIGURE 6.—Stage VI (megalopa) of *Pandalus goniurus:* A, rostrum; B, telson.

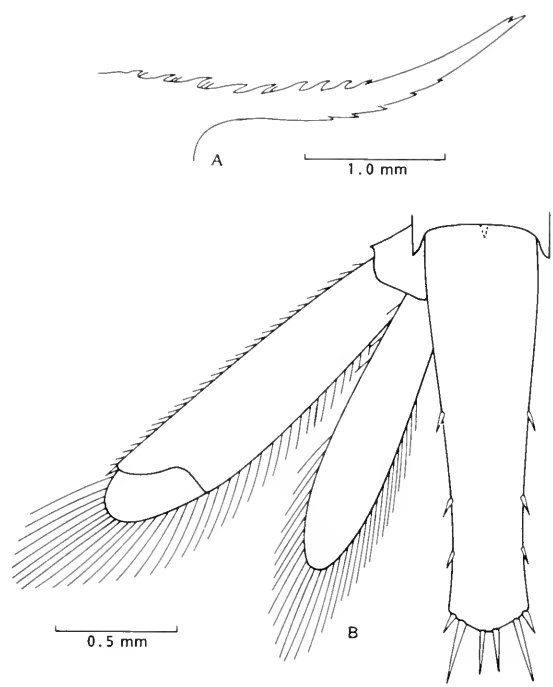


FIGURE 7.—Stage VII (first juvenile) of *Pandalus goniurus:* A, rostrum; B, telson.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Ivanov (1965) described and illustrated the first stage zoeae of *P. goniurus* that he reared in the laboratory from known parentage. His descriptions agree in all aspects with mine except for the third maxillipeds: Ivanov's zoeae had 9 natatory setae on the exopodite compared with 12 natatory setae in my zoeae.

The only other description of *P. goniurus* larvae known to me is that of Makarov (1967) who constructed a series of zoeal stages from plankton of the western Kamchatka coast based on Ivanov's description of Stage I. Makarov's descriptions of each stage are brief and include primarily development of the rostrum, antennal flagellum, dactylopodite of the second pereopod, pleopods, and telson. Makarov's zoeae are essentially identical to mine through Stage V but Makarov's Stages VI and VII possess mostly zoeal characteristics, rather than postzoeal as mine do. For instance, in Stage VI the rostrum of Makarov's specimens is not bifid and does not bear ventral teeth, and the telson still bears six pairs of spines terminally. In my Stage VI specimens, the rostrum is bifid, bears five or six distinct ventral teeth, and the telson bears only four pairs of spines terminally. In Stage VII, the rostrum of Makarov's specimens is bifid but bears only three or four poorly developed teeth ventrally and the telson still bears six pairs of spines terminally. In my Stage VII specimens both the rostrum and telson are essentially fully developed as in the adult. Apparently *P. goniurus* from the western Kamchatka coast has at least two more zoeal stages than *P. goniurus* from Kachemak Bay.

The morphological differences between larval Stages VI and VII of *P. goniurus* from the western Kamchatka coast and from Kachemak Bay, Alaska, may reflect variation in number of molts in response to environmental conditions. Variability in number of molts required to reach a specific point in development in the Crustacea is well known. In a review of the literature, Costlow (1965) showed that variability in number of molts occurs in the Cirripedia, Euphausiacea, Natantia, Reptantia, Anomura, and Brachyura regardless of whether the larvae are reared in the laboratory or

from the natural environment. Regarding the Pandalidae, Pike and Williamson (1964) have shown variability in number of molts required to reach the megalopa stage in the plankton for *Pandalina brevirostris* (Rathke) and *Pandalus propinquus* G. O. Sars, and that larvae of *Dichelopandalus bonnieri* (Caullery) and *Pandalus montagui* Leach reared in the laboratory have more larval stages than specimens from plankton. Berkeley (1931) mentioned the possibility of variation in number of molts in larvae of *Pandalus danae* Stimpson. Kurata (1964) speculated that larvae of *P. borealis* Krøyer in Japanese waters may have six or seven stages.

I have observed that both *P. borealis* and *P. goniurus* reared in the laboratory are capable of prolonging their normal interval between zoeal moltings (about 10-15 days) to as much as 5 wk, and that *P. borealis* may have as many as 11 zoeal stages before reaching the megalopa stage. Although the causes of molt retardation and morphological variation in pandalid larvae have not been established, the potential for variability exists not only in *P. goniurus* but in other pandalids as well. Variability in larval development from different geographical areas, therefore, is to be expected.

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IMMIGRATION OF FISHES THROUGH THE SUEZ CANAL[1]

ADAM BEN-TUVIA[2]

ABSTRACT

The number of Red Sea fishes found in the eastern Mediterranean amounts to 36 species. Twelve immigrants, namely: *Spratelloides delicatulus, Herklotsichthys punctatus, Tylosurus choram, Sebastapistes nuchalis, Epinephelus tauvina, Autisthes puta, Pelates quadrilineatus, Silago sihama, Rhonsicus stridens, Crenidens crenidens, Rastrelliger kanagurta, Scomberomorus commerson*, were found in the last 12 yr. The southward migration, from the Mediterranean to the Red Sea is almost negligible. Only *Liza aurata, Dicentrarchus punctatus*, and perhaps *Carcharhinus plumbeus* can be regarded as Mediterranean immigrants.

In studying the immigration of fishes through the Suez Canal, three zooecological areas must be taken into consideration: 1) the northern Red Sea; 2) the eastern Mediterranean; and 3) the Suez Canal itself in which many marine animals from the two neighboring areas have found a permanent habitat (Steinitz 1968).

The prevailing hydrographic conditions differ in these three areas, although the salinities and summer temperatures are to some extent similar (Morcos 1967, 1970; El-Saby 1968; Oren 1970; Oren and Hornung 1972). Temperature and salinity are the main abiotic factors influencing the distribution of organisms over large zoogeographical areas. Often they also have a decisive influence on the ecological distribution of species in various biotopes of an area.

The process of immigration is highly selective. Common species of the home seas are not necessarily successful immigrants in a new region. Similar effects have been shown to occur in many forms of colonization (MacArthur and Wilson 1967). The adaptation of a species to a new area requires adjustment of its reproductive processes, especially with regard to the correct timing of spawning in order to ensure suitable physical and ecological conditions for the development and survival of the young stages.

It is evident that the direction of immigration is mainly from the Red Sea into the Mediterranean (Figure 1). The possible causes of such one way immigration have been discussed elsewhere (Aron and Smith 1971; Ben-Tuvia 1971a, 1973; Por 1971a, b).

Thirty-six Red Sea or cosmopolitan species can be regarded as Suez Canal immigrants. Twelve of them were found within the last 12 yr. Evidently, immigration is a continuous process, and over time the probability of suitable species of fishes entering the Suez Canal and colonizing the new region increases. Time also plays an essential role in the biological processes of adaptation of the species to the modified conditions of life. More resistant species, endowed with greater plasticity of genetic characters, can form local "races" within a few generations by natural selection in the new environment (Kosswig 1974). But first they need a firm foothold on the other side of the Canal, geographically close to the parental stock and in places where conditions are not drastically different from their normal habitat.

Recently I had an opportunity to collect samples from the Gulf of Suez (Ben-Tuvia and Grofit 1973), Suez Canal (Steinitz and Ben-Tuvia 1972), and Bardawil Lagoon (Ben-Tuvia 1975a) which revealed interesting data on the distribution of immigrants. Many of the species which have successfully colonized the eastern Mediterranean, such as *Saurida undosquamis, Leiognathus klunzingeri, Upeneus moluccensis*, and *U. asymmetricus*, and which are abundant there, are also dominant species on the trawling grounds of the Gulf of Suez.

High percentage of Red Sea fishes found in the hypersaline Bardawil Lagoon on the northern coast of Sinai indicates that it may serve as a stepping stone in the immigration of Red Sea fishes into the Mediterranean, especially if we regard it as a part of the system of lakes and lagoons of the Isthmus of Suez (Por 1971a). Among 55

[1]This paper was read at the 17th International Zoological Congress in Monte Carlo, 25-30 September 1972; some changes were introduced to include more recent information on immigrants.

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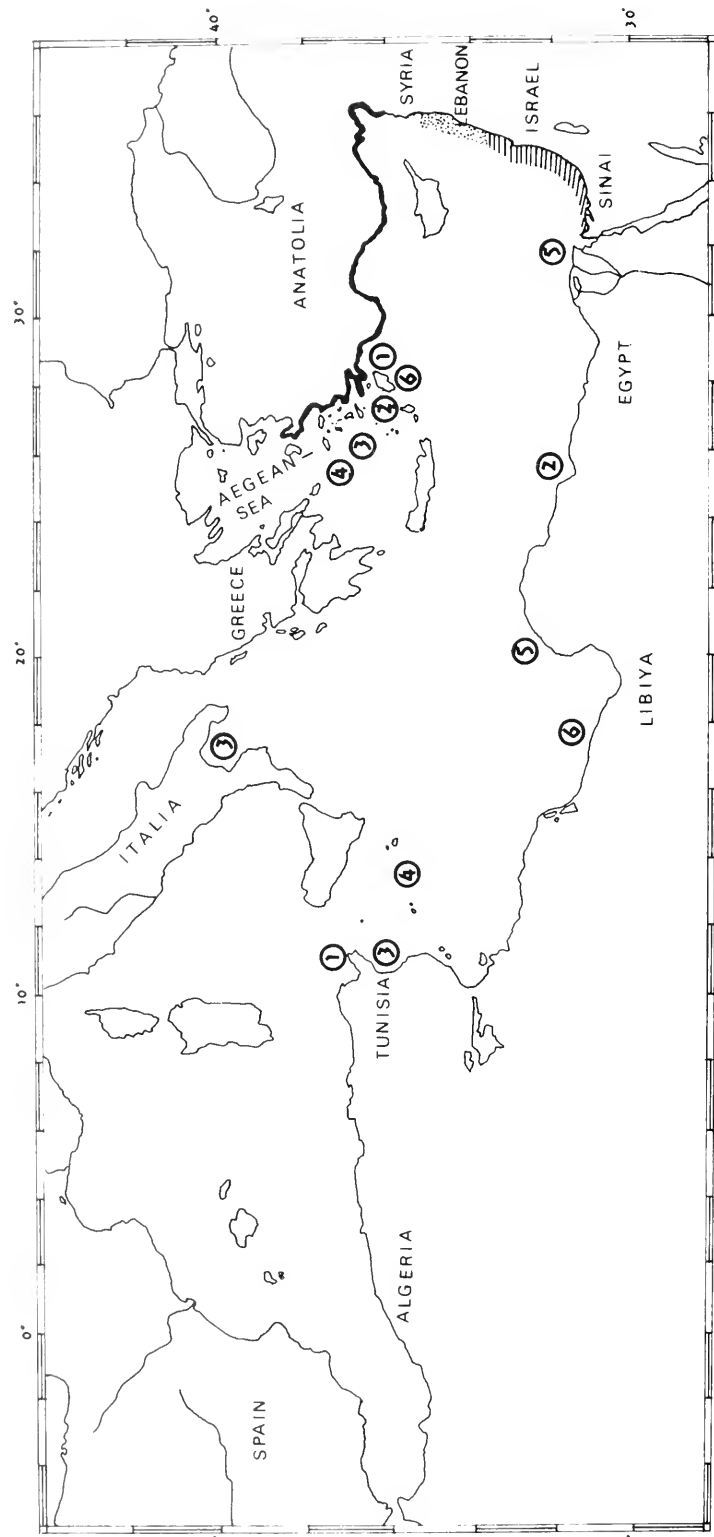

FIGURE 1.—Distribution of Red Sea fishes in the Mediterranean Sea: coast of Israel and Sinai with 34 species; coast of Lebanon with 27 species; Aegean Sea with 9 species. Numbers in circles refer to the following fishes: 1. *Signaus luridus*, 2. *S. rivulatus*, 3. *Stephanolepis diaspros*, 4. *Leiognathus klunzingeri*, 5. *Pranesus pinguis*, and 6. *Parexocetus mento*.

species collected in Bardawil Lagoon, 14 species (25.5%) are Red Sea immigrants in comparison with about 11% estimated for all the fishes collected in the eastern Mediterranean (Ben-Tuvia 1971b).

The following Red Sea immigrants were collected in Bardawil Lagoon: *Hemiramphus far, Aphanius dispar, Atule djeddaba, Pelates quadrilineatus, Leiognathus klunzingeri, Upeneus moluccensis, Crenidens crenidens, Liza carinata, Pranesus pinguis, Siganus luridus, S. rivulatus, Sphaeroides spadiceus,* and recently *Herklotsichthys punctatus* and *Autisthes puta.*

In addition to the Red Sea immigrants, four cosmopolitan species were also found in Bardawil Lagoon: namely, *Sardinella aurita, Lobotes surinamensis, Mugil cephalus,* and *Echeneis naucrates.*

RED SEA FISHES IN THE MEDITERRANEAN SEA

In my previous summary of the immigration of Red Sea fishes into the Mediterranean (Ben-Tuvia 1966), 24 species were listed; 12 additional immigrants were since found, most of them are rare fishes at this time. Their names, distribution, and the maximum size observed in the Mediterranean Sea are given in Table 1. As yet, only one specimen of *Tylosurus choram* (Collette and Parin 1970), *Rastrelliger kanagurta* (Collette 1970), *Sebastapistes nuchalis* (Froiland 1972), and *Silago sihama* (Mouneimne 1977) have been reported from the eastern Mediterranean.

Froiland (1972), who studied scorpaenids from Cyprus in the collection of the Hebrew University Zoological Museum, reported one specimen of *Sebastapistes nuchalis* (Günther) 58 mm long. This species is known from the Indo-Pacific, including East Africa, but no records are available from the Red Sea, Suez Canal, and other localities in the eastern Mediterranean besides Cyprus. Froiland assumed that this scorpaenid "migrated through the Suez Canal."

Epinephelus tauvina (Ben-Tuvia and Lourie 1969), *Pelates quadrilineatus* (Lourie and Ben-Tuvia 1971), and *Scomberomorus commerson* (George and Athanassiou 1965) were collected on several occasions and do not seem to be very rare. *Herklotsichthys punctatus* and *Rhonciscus stridens* have been found recently in the eastern Mediterranean at several localities (Ben-Tuvia 1967, 1977; Mouneimne 1977). One specimen of *Spratelloides delicatulus* (Bennet) 51 mm long was collected with rotenone on 4 June 1973 in a shallow bay about 3 km south of Atlit (Ben-Tuvia, unpubl. data). The occurrence of *Crenidens crenidens* and *Autisthes puta* is restricted to the hypersaline Bardawil Lagoon.

It is of interest to note that some of the Red Sea immigrants have been found in recent years in new localities west of Levant (Figure 1); *Stephanolepis diaspros* in the Gulf of Taranto, south Italy and Gulf of Gabes, Tunisia (Tortonese 1967); *Siganus rivulatus* off Tobrouk, Libya (Tortonese 1970).

With the exception of perhaps two fishes, *Saurida undosquamis* and *Siganus luridus,* very little information is available on the rate of increase of the immigrant population and the ecological influence of their appearance in the new region. The first Mediterranean specimen of *Saurida undosquamis,* 145 mm standard length, was collected in Haifa Bay, by a trawler, in December 1952. Additional specimens (160-171 mm) were collected in Haifa in February 1953. According to my observations in August 1953, taken on the deck of a commercial trawler, this fish was fairly common in the Gaza-El'Arish area, and 10-20 specimens were usually caught in each haul. There is also some information on the trawling activities in the Gulf of Iskenderun and Mersin on the Anatolian coast of Turkey. In August 1952, I participated in a commercial trawling cruise to the Gulf of Mersin between Karadash-Burnuun and Bagase, during which no *Saurida undosquamis* were collected. But in 1956, this fish was common on the same trawling grounds and fished in commercial quantities. According to catch data, *S. undosquamis* started to appear in commercial quantities in the year 1955, first on the southern fishing grounds (El'Arish to Tel Aviv) and towards the end of the same year and especially during 1956 also on the northern fishing grounds such as Haifa Bay, and even in the Gulf of Iskendrun and Mersin (Ben-Yami 1955; Oren 1957).

It is worthwhile noticing that no specimens of *S. undosquamis* were found before December 1952, although Mediterranean fishes were collected in Israel during earlier years by the staff of the Sea Fisheries Research Station, Haifa, and by scientists of the Hebrew University, Jerusalem.

No less interesting is the sudden appearance of *Siganus luridus* (Ben-Tuvia 1964). Not a single specimen was found before February 1955, in spite of extensive collecting activities in Israel during

TABLE 1.—Data on Red Sea fishes found in the Mediterranean.

Species	Occurrence in eastern Mediterranean	Ecological distribution	SL[1] (mm)	Geographical distribution: Indo-Pacific	Red Sea	Suez Canal	Mediterranean[2]
Carcharhinus brevipinna	Common	Inshore-pelagic	1,200	+	+	–	Israel
Himantura uarnak	Common	Demersal	[3]1,200	+	+	+	Anatolia
Dussumieria acuta	Very common	Inshore-pelagic	155	+	+	+	Anatolia
Herklotsichthys punctatus	Rare	Inshore-pelagic	76	+	+	+	Lebanon
Etrumeus teres	Single record	Inshore-pelagic	170	+	+	–	Israel
Spratelloides delicatulus	Single record	Inshore-pelagic	51	+	+	+	Israel
Saurida undosquamis	Very common	Demersal	335	+	+	+	Anatolia
Paraexocoetus mento	Common	Pelagic	111	+	+	–	Aegean Sea; Gulf of Sidra
Hemiramphus far	Common	Inshore-pelagic	340	+	+	+	Aegean Sea
Tylosurus choram	Single record	Inshore-pelagic	—	+	+	+	Lebanon
Aphanius dispar	Common	Sublittoral	46	+[4]	+	+	Israel
Pranesus pinguis	Very common	Inshore-pelagic	120	+	+	+	Anatolia; Libya
Holocentrus ruber	Common	Inshore-pelagic	177	+	+	–	Aegean Sea
Sebastapistes nuchalis	Single record	Sublittoral	58	+	–	–	Cyprus
Platycephalus indicus	Rare	Demersal	550	+	+	+	Lebanon
Epinephelus tauvina	Rare	Demersal	790	+	+	+	Israel
Autisthes puta	Rare	Sublittoral	133	+	+	–	Bardawil Lagoon
Pelates quadrilineatus	Rare	Demersal	116	+	+	–	Lebanon
Apogonichthyoides nigripinnis	Common	Sublittoral	77	+	+	+	Lebanon
Silago sihama	Single record	Sublittoral	115	+	+	–	Lebanon
Atule djeddaba	Very common	Inshore-pelagic	230	+	+	+	Lebanon
Leiognathus klunzingeri	Very common	Demersal	77	+	+	+	Aegean Sea; Lampedusa
Rhonciscus stridens	Rare	Demersal	128	+	+	+	Lebanon
Upeneus asymmetricus	Common	Demersal	140	+	+	+	Anatolia
Upeneus moluccensis	Very common	Demersal	170	+	+	+	Aegean Sea
Crenidens crenidens	Rare	Demersal	150	+	+	+	Bardawil Lagoon
Liza carinata	Rare	Inshore-pelagic	128	+	+	+	Egypt; Israel
Sphyraena chrysotaenia	Very common	Inshore-pelagic	225	+	+	+	Anatolia
Callionymus filamentosus	Common	Demersal	110	+	+	+	Lebanon
Siganus luridus	Common	Sublittoral	215	–	+	–	Aegean Sea; Tunisia
Siganus rivulatus	Very common	Sublittoral	223	+	+	+	Aegean Sea; Libya
Rastrelliger kanagurta	Single record	Pelagic	215	+	+	–	Israel
Scomberomorus commerson	Rare	Pelagic	460	+	+	–	Lebanon
Dollfusichthys sinusarabici	Common	Demersal	110	–	+	+	Lebanon
Stephanolepis diaspros	Common	Demersal	124	+[5]	+	+	Aegean Sea; south Italy; Tunisia
Sphaeroides spadiceus	Rare	Demersal	245	+	+	+	Aegean Sea

[1]Maximum length observed in Mediterranean.
[2]Farthest point of distribution.
[3]Length of disc.
[4]Indian Ocean only
[5]Persian Gulf only

the preceding years. Then the fish suddenly appeared to be fairly common along the whole Mediterranean coast of Israel, although it remained inferior in numbers to a previous Red Sea immigrant, *S. rivulatus*. Recent observations and reports show that *S. luridus* spread rapidly in the Mediterranean towards the west and north. It is common in Lebanon (George and Athanassiou 1967), Cyprus, Rhodes, and has even reached Tunisia (Ktari-Chakroun and Bouhlal 1971), a distance of more than 1,000 n.mi. from the Suez Canal.

It is a common feature of invading organisms that after an initial period of successful adaptation to the new and basically favorable environment, they may suddenly increase in number and spread to adjacent areas (Elton 1958). Various factors such as decrease in salinities of the Bitter Lakes and cessation of the Nile flood after the completion of the Aswan Dam may facilitate the passage or dispersion of Red Sea species. There is speculation that this immigration was also favored by a series of warm years (Oren 1956; Ben-Yami and Glaser 1974).

MEDITERRANEAN FISHES IN THE RED SEA

The occurrence in the Red Sea of the two Atlanto-Mediterranean and one cosmopolitan species (Table 2) is assumed to be the result of Suez Canal migration. The discovery of *Dicentrarchus punctatus* in the lagoon of El Bilaiyim, situated about 180 km south of the entrance to the Suez Canal (Ben-Tuvia 1971a), is one of the few indisputable evidences of the immigration of a Mediterranean fish into the Gulf of Suez. However, we have to bear in mind that the conditions of El Bilaiyim differ considerably from those of the Gulf proper. Salinities are much higher (50-60‰ according to measurements taken in June 1968) and most probably the seasonal and diurnal fluctuations are greater than those of surrounding waters. In this particular biotope, less competition is expected than in the open coastal waters. *Dicentrarchus punctatus* is known to inhabit the Bardawil Lagoon on the northern (Mediterranean) coast of Sinai, where salinities may reach 80‰. It was noted already by Tillier (1902) that this fish was common in the Suez Canal and reached its southern entrance. Evidently, it settled in the Canal soon after its opening.

A taxonomic study of Red Sea mugilids (Ben-Tuvia 1975b) revealed that another Mediterranean immigrant, *Liza aurata* is common in the northern Red Sea. An earlier record of its presence was made by Al-Hussaini (1947) who examined the intestine of this mullet that was captured off Ghardaqa. *Liza aurata* is known to be euryhaline and could cross the Suez Canal or an earlier freshwater connection that was established by the ancient Egyptian pharaohs and Persian kings between the Mediterranean and the Red Sea using an arm of the River Nile. This fish was reported in the Suez Canal by Tillier (1902). I found it to be common in Great Bitter Lake (Ben-Tuvia 1975a).

Recently two specimens of a sandbar shark, *Carcharhinus plumbeus,* were found in the Red Sea. One specimen, a male, 1,600 mm total length was collected on 6 August 1971 in Dahab, Gulf of Aqaba; the second specimen, a gravid female, 1,764 mm was collected on October 1975 in Ras Muhammad at the entrance to the Gulf of Suez (Baranes and Ben-Tuvia in press). Five additional specimens varying in length between 1,500 and 1,800 mm have been found very recently in the same region (unpubl. data). *Carcharhinus plumbeus* (known also under the name of *C. milberti*) is common on both sides of the Atlantic and is well known in the Mediterranean Sea (Tortonese 1956; Ben-Tuvia 1971b; Compagno 1973). The recent appearance of the sandbar shark in the northern Red Sea could be due to immigration through the Suez Canal although the possibility of penetration from the western Indian Ocean should not be excluded.

Special consideration should be given to *Serranus cabrilla,* which is common in all parts of the Mediterranean, in the Suez Canal, and also in the Red Sea. However, it cannot be regarded as an example of Suez Canal immigration, since a 17-cm long specimen was collected by Hemprich and Ehrenberg in the Red Sea before the completion of the Canal (Klunzinger 1884). According to my observations in September 1970, *S. cabrilla* is common in the northern part of the Gulf of Suez. Individuals were easily observed on sandy patches between coral heads and rocks in the shallow coastal waters off Ras Masalla and Ras Sudar. A total of 10 specimens, 52-100 mm, were collected from the Gulf of Suez plus 1 specimen, 70 mm standard length, from the Gulf of Aqaba. The abundance of *S. cabrilla* in the northern section of the Gulf of Suez indicates the possibility that the present distribution might be related to the proximity of the Suez Canal. However, further taxonomic and behavioral studies will be needed to ascertain the relationships between the Red Sea and the Mediterranean populations.

Serranus cabrilla in the Mediterranean shows great plasticity and adaptability to various ecological conditions. This fish is found in shallow coastal waters on sandy beaches and among rocks. It is

TABLE 2.—Data on Mediterranean fishes found in the Red Sea.

Scientific name	Occurrence in Red Sea	Ecological distribution	SL[1] (mm)	Geographical distribution: West Atlantic	East Atlantic	Suez Canal	Red Sea record
Carcharhinus plumbeus	Rare	Pelagic	1,764	+	+	–	Gulf of Aqaba Gulf of Suez
Dicentrarchus punctatus	Rare	Demersal	245	–	+	+	Gulf of Suez
Liza aurata	Very common	Inshore pelagic	320	–	+	+	Gulf of Aqaba Gulf of Suez

[1]Maximum length observed in Red Sea.

also occasionally found on trawling grounds in various depths, at least up to 100 m. It is common throughout the Mediterranean but rare in the Black Sea. In the eastern Atlantic, it occurs from the English Channel to Angola. Smith (1961) quoted its presence in South Africa (Natal), but it seems not to have been recorded from any other part of the Indian Ocean. Gruvel and Chabanaud (1937) reported that this fish is common throughout the Suez Canal.

CONCLUSIONS

The occurrence of large numbers of circumtropical-cosmopolitan species in the eastern Mediterranean deserves special attention. They demonstrate the distinct faunistic character of the fish population in this area. Of the 290 species of marine fishes identified from the Mediterranean coast of Israel and its immediate neighborhood, 40 species are circumtropical-cosmopolitan. Many of them are found also in the Indo-Pacific and Red Sea regions. Thus, summing up the Red Sea and cosmopolitan fishes in the eastern Mediterranean, there are 76 species which constitute about one-quarter of all fishes identified from this region. The remaining species belong to the Atlanto-Mediterranean fauna.

The Red Sea element in the eastern Mediterranean is particularly pronounced among demersal fishes. This is evident by the large number of demersal immigrants and by their common occurrence. About 17 species are bottom-living fishes, and at least 6 of them are of commercial value. I estimate that they constitute about 21% (by weight) of the Israeli trawl catches and 8% of the inshore fishery (Ben-Tuvia 1973). George and Athanassiou (1967) in their analysis of beach-seine catches of St. George Bay, Lebanon, found that among 26 commercially important fishes, 5 (19%) were Red Sea immigrants.

For a better understanding of Suez Canal immigration, additional taxonomic and biological investigations are required. Comparison of racial characteristics of immigrant fishes could help to clarify the question of the origin and relationship between the Red Sea and the Mediterranean populations. It is suspected that in some cases, exchange of fauna may have taken place before the opening of the Suez Canal as a result of the elevation of sea level and undulation of the Isthmus during the Pleistocene.

Knowledge of the comparative life histories of the immigrant fishes in the two areas is essential for understanding the selective mechanisms controlling passage through the Suez Canal and evaluating extensive ecological changes that the invading species may produce in the new areas of their distribution.

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FOOD AND HABITAT OF THREE SWITCH-FEEDING FISHES IN THE KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Diets and habitat distributions were compared among the blue rockfish, *Sebastes mystinus,* kelp bass, *Paralabrax clathratus*, and olive rockfish, *Sebastes serranoides*, all of which cooccur in areas of reef and giant kelp off Santa Barbara, Calif. The three species make up a feeding guild of large-mouthed predatory fishes that commonly switch among planktonic prey, nektonic prey (fish and squid), and substrate-oriented prey (invertebrates that live on or about reef and plant surfaces). At the semi-isolated study site, blue rockfish, which are somewhat better adapted than the others to ingest and retain small particles, ate relatively more plankton than did individuals of the other species, while olive rockfish ate more fish. Kelp bass had both the broadest diet and habitat distribution. All three species ate more plankton during winter-spring, yet had smaller dietary overlaps then. Olive rockfish ate more fish and less plankton at the heavily foliaged study site than they did over a deeper kelpless reef farther offshore. The three species tend toward deeper and calmer areas of the reef; kelp bass and olive rockfish prefer clear-water areas of dense kelp; kelp bass often concentrate near the outer kelp-bed margin; and both rockfishes prefer areas of high-relief rocky bottom. The morphologically similar kelp bass and olive rockfish may segregate spatially, perhaps reducing mutual interference. As inferred from other studies and our own, areal variation in feeding habits of the three species may reflect their environmental tolerances, range limits, numbers of competitors, food supplies, habitat structures, or predator densities. The closely related rockfishes show least dietary overlap between themselves and most overlap with the more distantly related kelp bass.

Kelp-bed fishes that have similar diets and habitat requirements form feeding guilds. For example, Bray and Ebeling (1975) described how three species of small picker-type microcarnivorous fishes share substrate-oriented prey and plankton in the kelp forests off Santa Barbara, Calif. Also occupying the midwater zone between kelp canopy and reef bottom is a feeding guild of larger, predatory fishes. These include two members of the scorpaeniform family Scorpaenidae, the blue rockfish, *Sebastes mystinus,* and olive rockfish, *S. serranoides,* and one member of the perciform family Serranidae, the kelp bass, *Paralabrax clathratus.* All have fusiform bodies, head spines reduced or absent, large flexible fins, large mouths, and numerous well-developed and closely set gill rakers. Blue rockfish are ovate with blue-gray bodies stippled darkly above the flanks; olive rockfish and kelp bass are more elongate with brownish bodies and characteristic arrays of white blotches along their backs. The three species are similar enough in general appearance to be grouped by most Santa Barbara fishermen simply as bass: blue, Johnny, and calico basses, respectively. They form the nucleus of a shallow-water sport fishery at the edges of the Santa Barbara kelp forests.

Our primary interest was how the three species share food and space over a single, semi-isolated area of reef and kelp (Naples Reef) near Santa Barbara. We emphasized the most common size range of fishes sighted, large juveniles to small adults. Previous studies indicated that the species are generalized carnivores, occurring throughout the water column and eating a wide variety of large and small prey of all major categories (Limbaugh 1955; Young 1963; Gotshall et al. 1965; Quast 1968a-d; Turner et al. 1969). We wanted to see if the three species can switch (change almost entirely) from eating one prey type to another, and under what circumstances they may do so. Using data from other studies, we also investigated food habits of olive rockfish from a deeper, offshore population living in an environment quite unlike that of the kelp bed, and we investigated the spatial distributions of all three species at Naples Reef and in an adjacent island environment.

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METHODS

Food

For interspecific comparisons, collections were made over a single isolated reef, where the three species probably exploit a common forage base. Naples Reef is a large rocky outcrop surrounded on all sides by sand flats and forested by lush stands of giant kelp, *Macrocystis*. It is located about 1.6 km offshore, 24 km west of Santa Barbara (lat. 34°25′N, long. 119°57′W). Covering an area of about 2.2 ha, the reef averages 8-10 m in depth, although its rocky crest projects to within 5 m of the surface. It is separated from similar habitats by sand and cobble flats at 16-20 m (Ebeling and Bray 1976).

We tried to collect fish as randomly as possible. One of us (Ebeling) using a pole spear shot fish as they were encountered, with two exceptions: he ignored small juveniles and often missed large kelp bass (>300 mm SL, standard length), which were consequently underrepresented in the collections. Thus the samples probably reflect the usual size distribution of fish between ca. 100 and 300 mm SL over the reef (Table 1). In this way, 324 specimens were collected between 0900 and 1500 h during all seasons from March 1971 to June 1972. Of these, 80% had food in their stomachs.

We made considerable effort not to bias stomach-content composition. Underwater chumming or disturbing the bottom were never used as ways to attract fish near the collector. Spearing was begun only after it was ascertained that no sport fishing involving chumming with live bait (usually northern anchovy, *Engraulis mordax*) occurred within visual range of the collecting site. An initial practice of securing individual fish in plastic bags or locking their mouths with paper clips was soon discontinued when no individual was seen to regurgitate food. All specimens were placed immediately in an ice chest aboard the diving skiff. In the laboratory, they were measured (nearest millimeter SL), slit open, and their intestines detached and measured (millimeters SL). Other trophic structures (jaw length, gill rakers on first arch, and greatest width between gill rakers) were measured on a few typical specimens of about 225 mm SL. Specimens were then fixed in 10% Formalin[3] and preserved in 50% isopropanol.

To investigate the effect of habitat on the olive rockfish's diet, one of us (Love) collected an additional 110 individuals from One-Mile Reef, an open, rocky reef located 1.6 km offshore of Santa Barbara Harbor, about 20 km east of Naples Reef. Of these, 72 (65.5%) had stomachs containing food (Table 1). Too deep and turbid to support kelp, this reef is made up of a strip of rocky bottom at about 27 m depth, with 1.5-5.0 m high rock piles scattered along its length. From January to October, fish were caught by angling with artificial lures and by gill net. No sport fishing or chumming were seen to occur during collecting. Fish were preserved and processed as before.

Gut fullness was estimated before stomach contents were sorted and identified. Degrees of fullness of stomach and of the first half of the intestine were scored from 1.0 (empty) to 5.0 (full). Stomach contents were sorted taxonomically into 26 food items (Table 2). The volume of each item was measured by liquid displacement. The "nekton" category of items (prey type) included all nonlarval fish and squid prey. The substrate-oriented prey type included all prey (except fish) that live on or about reef and plant surfaces. Such prey are either motile like shrimps, amphipods, and small crabs, or attached like hydroids, bryozoans, and the algae itself. Plant material was identified as either kelp (*Macrocystis*) or other algae, mostly low lying browns and reds. In computing percent volumes and frequencies of occurrence of prey per

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

TABLE 1.—Number, size, and food containment of specimens examined of the three species of kelp-bed fishes (blue rockfish, kelp bass, and olive rockfish) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. See also Figure 1.

Locality and species	Total specimens examined	Total with food	Percent with food	Specimens with food in their stomachs by size groups								
				50-150 mm SL			151-300 mm SL			301-400 mm SL		
				No.	Range	Median	No.	Range	Median	No.	Range	Median
Naples Reef.												
Blue rockfish	122	97	79.5	30	78-149	118.5	67	150-262	193.0	—	—	—
Kelp bass	102	86	84.3	—	—	—	67	167-296	209.0	19	304-400	328.0
Olive rockfish	100	86	86.0	13	82-150	122.5	73	151-274	196.0	—	—	—
One-Mile Reef.												
Olive rockfish	110	72	65.5	—	—	—	72	158-290	222.0	—	—	—

TABLE 2.—Percent total volume and frequency of occurrence of 26 food items in stomachs with food of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Food items are listed by general characteristics and presumed major daytime source. A tr indicates unmeasurable trace; a dash indicates none.

	Naples Reef						One-Mile Reef	
	Blue rockfish		Kelp bass		Olive rockfish		Olive rockfish	
Food item	% vol.	% freq.	% vol.	% freq	% vol.	% freq	% vol.	% freq.
Primarily planktonic (Sum =)	(56.7)		(12.6)		(10.5)		(41.8)	
Small crustaceans (0.5-5 mm long):								
Ostracods	—	—	—	—	—	—	tr	2.9
Cladocerans	—	—	—	—	—	—	0.4	8.6
Zoea larvae	0.6	20.9	0.3	6.0	0.3	15.1	6.5	35.7
Copepods	0.2	22.4	1.5	7.5	0.3	15.1	15.8	34.3
Megalops larvae	0.6	11.9	0.1	3.0	2.6	24.7	7.0	47.0
Large crustaceans (>10 mm):								
Euphausiids	tr	1.5	—	—	0.1	2.7	1.2	2.9
Pleuroncodes	—	—	—	—	—	—	4.4	4.9
Small-medium sized, transparent (1-10 mm):								
Eggs	0.6	1.5	2.5	1.5	—	—	—	—
Chaetognaths	1.9	10.4	—	—	—	—	0.1	2.9
Tunicates (small salps, larvaceans)	51.5	40.3	7.8	16.4	5.4	6.8	1.0	5.7
Large, transparent (>15 mm):								
Siphonophores, medusae, etc.	0.7	4.5	0.4	1.5	—	—	—	—
Fish larvae (5-15 mm)	0.6	10.4	—	—	1.8	16.4	5.4	16.7
Primarily nektonic (20-80 mm) (Sum =)	(15.7)		(55.3)		(85.0)		(55.2)	
Fish	7.4	13.4	51.0	46.3	84.2	54.8	51.0	28.0
Squid	8.3	3.0	4.3	6.0	0.8	4.1	4.2	5.7
Ectoparasites of other fish:								
Parasitic copepods	—	—	—	—	tr	2.7	0.4	12.9
Primarily substrate oriented (Sum =)	(27.5)		(32.3)		(4.5)		(2.6)	
Free moving animals:								
Crabs	—	—	0.8	3.0	—	—	—	—
Shrimps	—	—	0.7	1.5	—	1.4	—	—
Mysids	0.3	6.0	0.5	9.0	0.8	8.2	1.4	14.3
Isopods	0.2	3.0	0.2	1.5	—	—	—	—
Gammaridean amphipods	1.6	17.9	2.2	13.4	0.8	6.8	tr	1.4
Caprellid amphipods	0.1	1.5	7.5	13.4	tr	1.4	tr	1.4
Hyperiid amphipods	0.1	1.5	—	—	—	—	0.1	2.9
Polychaete worms	0.3	1.5	0.4	7.5	2.9	20.5	1.0	14.3
Hydroids	13.1	16.4	8.7	16.4	—	—	—	—
Kelp, etc.:								
Kelp (including encrusting bryozoans)	10.5	25.4	8.8	16.4	—	—	0.1	1.4
Other algae (including encrusting bryozoans)	1.3	9.0	2.5	14.9	—	—	—	—
Total volume of food consumed (ml)	171.2		141.3		85.8		102.9	
Total number of specimens examined		67		67		73		72

species (Table 2), fish with empty guts and of sizes outside the middle range of 151-300 mm SL (Table 1, Figure 1) were excluded.

To test for communal switch feeding and dietary consistency, we examined variation among individuals. We counted fish that contained mostly one food item or prey type and that 1) were of one species collected on the same day, 2) were of all three species collected on the same day (Table 3), and 3) were of all species collected at any time (Table 4).

To examine seasonal variation in diet, stomach contents of each species were pooled by seasonal periods that correspond roughly to different oceanographic regimes off Santa Barbara. Brown (1974) concluded that in the Santa Barbara Channel, cooling of surface water typically proceeds from December to July, first by surface mixing and small-scale upwelling associated with storms from December to April, then by large-scale upwelling from May through July. This precedes gradual surface warming from late June to December, with strongest thermal stratification and clearest water from August to December. Therefore, we delimited seasonal periods as: 1) December-February, a period of winter storms and the beginning of vertical mixing and surface cooling (initial breeding season of many species); 2) March-May, a period of most intense upwelling of deep cold water (high surface productivity, zooplankton blooms, appearance of young-of-the-year fish, etc.); 3) June-August, a period of decreasing upwelling and the beginning of thermal stratification and surface warming (a transitional period);

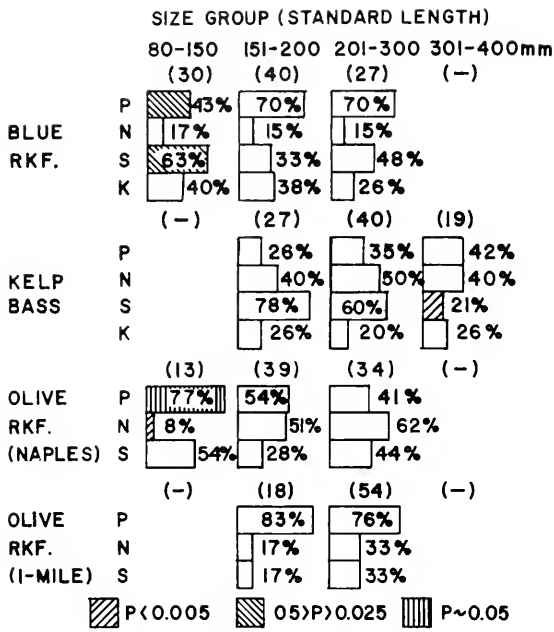

FIGURE 1.—Percentage frequency of prey types (bars and numbers) in stomachs of fish in all size groups of the three species of kelp-bed fishes from Naples Reef (all three species) or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Prey types are designated: P, plankton; N, nekton; S, substrate-oriented prey; and K, kelp and other algae (with encrusting bryozoans), and are represented by any constituent food item under the appropriate prey-type heading in Table 2. Numbers in parenthesis are numbers of fish stomachs examined. Hatching shows significantly different frequencies at the indicated probabilities determined by chi-square tests (see text).

and 4) September-November, a period of warm, clear surface water with little vertical mixing. The 26 food items were ranked for each season by volume, using data from all size groups of fishes to maximize sample size (Table 5). Seasonal variation in diet was also tested by frequencies of occurrence of subsets of items comprising major food categories, using data from the 151- to 300-mm SL size group only (Figure 2).

Habitat

Spatial distributions of the three species were determined from underwater movies taken for another project. Observations were made from 2.5-min Super-8-mm underwater movie strips in color (cinetransects) filmed by scuba divers swimming courses started at random either under the kelp canopy or just over the bottom at study sites near Santa Barbara and across the Santa Barbara Channel along Santa Cruz Island (Bray and Ebeling 1975; Ebeling, R. Larson, and W. Alevizon in prep.). An initial set of cinetransects was filmed in 1970 over a variety of habitats and areas at both localities. Then, during the fall seasons of 1971-74, transects were filmed over permanent study sites at Naples Reef and at Santa Cruz Island west of Prisoner's Harbor. Fish were counted by species as the films were projected in the laboratory. Environmental characteristics were measured or scored either on station or during projection.

Breadth and Overlap

Breadth and overlap of resource use were computed from values of p_i, the proportion of item i used by each species, either at Naples Reef (food and space) or off Santa Cruz Island (space only). For food, p_i is the proportionate volume of any of the 26 different food items included in the species total (S); for space it is the proportionate abundance of the species in any of the 297 cinetransects taken over Naples Reef or 331 cinetransects taken along Santa Cruz Island. Resource breadth, $B = 1/\sum_{i=1}^{S} p_i^2$, can be thought of as the theoretical number of equally used food items (or spaces covered by cinetransects) yielding a value of B equal to the observed. For example, if all items are in equal proportions, B equals S, the total items in the spectrum (see Bray and Ebeling 1975). A Hill's (1973) ratio was used to estimate the degree of concentration of each species among cinetransects (the unevenness of distribution of fish numbers): $HR = \exp(H')/B$, where H' is the Shannon-Weaver measure of diversity, $-\sum_{i=1}^{S} p_i \ln p_i$. Since H' is more sensitive to changes in the small to medium values of proportionate abundances than is B, their ratio is a sample-size independent measure of concentration of observations (Peet 1974). Overlap between two species, $I = 1.0 - [0.5 (\sum_{i=1}^{s} | p_{ij} - p_{ik} |)]$, where p_{ij} is the proportion of item i used by species j and s is the species total of food items eaten (or cinetransects in which recorded), is scaled from zero (complete discordance of item use) to 1.0 (all items used in equal proportions) (e.g., Whittaker 1960; Cody 1974; Ebeling and Bray 1976).

RESULTS

Morphology, Size Groups, Gut Fullness

Of the three species, the blue rockfish appeared best adapted to eat a diverse array of small prey. It has a shorter jaw (ca. 15% of SL) than the olive rockfish and kelp bass (ca. 17%). It has about the same number of gill rakers on the first arch as the others (34-37); but has significantly smaller interraker widths ($\bar{x} = 1.24 \pm 0.088$ mm, 95% confidence limits, $n = 10$) than the others pooled ($\bar{x} = 1.80 \pm 0.076$, $n = 20$). Blue rockfish have a significantly longer intestine (ratio, intestinal length/SL of $\bar{x} = 1.41 \pm 0.147$, $n = 15$) than either kelp bass ($\bar{x} = 1.11 \pm 0.105$, $n = 18$) or olive rockfish ($\bar{x} = 0.807 \pm 0.098$, $n = 19$).

Tests justified comparing diets of fish within the 151- to 300-mm SL size range, which included 82% of all food-containing individuals (Table 1). Within this range, only the median length of olive rockfish from One-Mile Reef differed significantly from the others (Kruskal-Wallace ranks location test, $P < 0.05$ including the One-Mile sample, $P > 0.1$ excluding it). Also (Figure 1), diets as expressed by frequencies of occurrence of prey types were not significantly heterogeneous between subgroups: largest chi-square value determined in tests of the resulting 14 contingency tables of dimension two (presence or absence) by two (subgroups within this size range) = 2.31 ($P > 0.1$).

However, tests showed less justification for increasing sample size by adding individuals from outside the 151- to 300-mm size range (Figure 1). Diets were often significantly heterogeneous between subgroups when either smaller (blue rockfish, olive rockfish) or larger (kelp bass) sizes were included: 5 of 11 chi-square values determined in tests of the resulting 11 contingency tables of dimension two (presence or absence) by three (subgroups both within and without the 151- to 300-mm range) were significant at $P \approx 0.05$ or less.

Scored stomach fullness in 151- to 300-mm Naples Reef fish was about the same for all three species: $\bar{x} = 2.72$-2.75, an equivalent of about 46% full. Intestinal fullness averaged somewhat greater: $\bar{x} = 2.76$ (olive rockfish) to 3.00 (others). Blue rockfish and olive rockfish in the smaller size categories had fuller stomachs: $\bar{x} = 3.81$-3.10, respectively. Olive rockfish from One-Mile Reef had less food in their stomachs ($\bar{x} = 2.15$) but as much food as the others in their intestines ($\bar{x} = 3.05$). Intestinal contents usually resembled stomach contents.

Food

Diets

Blue rockfish ate mostly swimming, drifting, or attached organisms in midwater under and about the kelp canopy (Table 2, Figure 1). Tunicates, hydroids, kelp, fish, and smaller planktonic prey formed most of the fish's diet throughout the year. Recognizable fish prey included juveniles of pipefish, *Syngnathus;* blue rockfish; and C-O soles, *Pleuronichthys coenosus*; and adults of northern anchovy. Fish larvae made up but a small part of the blue rockfish's diet. Pelagic tunicates—the thaliaceans (salps) *Salpa* and *Doliolum* and the larvacean *Oikopleura*—constituted the largest volume of food consumed. Among the relatively large numbers of small plankters eaten, copepods ranked very low in volume, but relatively high in frequency of occurrence. Hydroids (especially *Sertularia*) ranked high in volume consumed. The blue rockfish were probably not merely ingesting hydroids to obtain the caprellid amphipods that live there (Gotshall et al. 1965), because caprellids were found along with hydroids in only 2 of 20 stomachs. Some 73% of the fish that contained kelp and other algae also contained detached hydroids and encrusting bryozoans (*Membranipora*). So most plant material may have once borne epiphytic prey now detached. And like tunicate tunics, algae per se was apparently passed undigested, so fish probably eat plants for the attached animals (Quast 1968d; Bray and Ebeling 1975).

Kelp bass foraged primarily in midwater, but occasionally ate bottom organisms (Table 2, Figure 1). They ate mostly fish, which ranked first in both total volume and frequency of occurrence. Recognizable fish prey included juveniles of rockfishes, pipefish, kelp greenling, *Hexagrammos decagrammus,* topsmelt, *Atherinops affinis,* anchovy, and jack mackerel, *Trachurus symmetricus,* and adults of anchovy and agonids. Kelp bass ate no fish larvae and relatively less plankton than did the other species. Thaliacean tunicates (*Salpa*) contributed the largest volume of plankton consumed; copepods and other small crustaceans occurred at moderate frequency and in fairly large numbers in a few individuals. Bass ate relatively more substrate-oriented prey, with

hydroids (especially *Sertularia*), caprellid amphipods, and kelp ranking highest among such items. Most caprellid amphipods were found in stomachs containing substantial amounts of hydroids and bottom algae, indicating that fish may ingest such turf for the contained animals. About a third of all pieces of kelp bore attached bryozoans (*Membranipora*) or hydroids.

Whether speared from Naples Reef or angled from One-Mile Reef, olive rockfish ate relatively more fish than did the others (Table 2, Figure 1). Recognizable fish prey in Naples Reef individuals included juveniles of blacksmith, *Chromis punctipinnis*, anchovy, pipefish, blue rockfish, other olive rockfish, and adults of topsmelt and anchovy. One-Mile Reef fish had eaten adult anchovies and a young pipefish. Fish larvae made up a relatively large part of the diets of olive rockfish from both localities. One-Mile Reef fish ate more kinds and greater numbers of small zooplankton. Individuals of all sizes ingested and retained such tiny prey as ostracods, cladocerans, and small copepods (e.g., *Coryceus emarginata*). During the winter, copepods and zoea larvae actually outranked fish prey in volumes consumed. Many polychaetes, which occurred commonly in fish from either area, were of the small nereid variety found in the kelp canopy (Quast 1968c) and swarming in the midwater plankton at night (Hobson and Chess 1976). Only olive rockfish contained parasitic copepods among their stomach contents. Although these copepods were identified as *Caligus*, an obligatory ectoparasite, olive rockfish were not observed to clean (i.e., pick such prey from off other host fishes).

Individual Variation

On any given day, individuals of the same species tended to select the same food item. Within particular collections of 2-9 individuals, 67% of a cumulative total of 96 blue rockfish, 60% of 72 kelp bass, and 60.5% of 86 olive rockfish had the same item dominating their stomach contents.

Occasionally, individuals of all three species selected items from the same major prey category, although not necessarily the same item (Table 3). Plankton dominated the stomach contents of most individuals sampled together in a February and in an April collection, while nekton and substrate-oriented prey were favored by those in three May and in one October collections. Yet fish in two November and two January collections showed little communality of diet. And even when they tended to select items from the same prey type, as in the February, April, May, and October collections, they often selected different items. For example, most blue rockfish collected on 22 February 1972 had mostly salps or chaetognaths in their stomachs; kelp bass contained either salps or copepods; and olive rockfish contained larval fish. On the other hand, all blue rockfish and most kelp bass in the 21 January 1972 collection had eaten a single planktonic item, namely salps.

Fish usually selected the same prey type during a particular feeding bout (Table 4). For all species pooled, 76% of the individuals contained more than 95% by volume of items in a single major prey category (prey type), and 39% contained but a single item (20% with relatively small items, 19% with large items). Combinations of prey types varied among the three species: usually plankton and substrate-oriented prey for kelp bass, and plankton and nekton for olive rockfish (Table 4). Of all fish containing kelp, etc. (Figure 1), about 40% also contained relatively large amounts of substrate-oriented prey, about 15% each also contained relatively large amounts of plankton or nekton, and the remainder contained kelp only. About 83% of 81 specimens with recognizable prey in both stomach and intestine had the same prey type dominating the contents of both.

Seasonal Variation

Considering all 26 food items, diets were weakly, though usually significantly concordant among seasons (Table 5). Fish ate relatively greater volumes of plankton during winter-spring periods, and more nekton or substrate-oriented prey during summer-fall. Showing the greatest seasonal variation (least concordance), the blue rockfish's diet included 93% plankton (by volume) in the winter, 75% in the spring, and less than 8% in summer-fall. Tunicates ranked high from December to August, while kelp (with encrusting animals), hydroids, and, later, fish, ranked high from March to November. Similarly, olive rockfish from One-Mile Reef contained 80%, 25%, and $<10\%$ plankton (by volume) in the first three seasonal periods, respectively. Small crustaceans ranked high from December to August, while fish and polychaetes ranked high from March to November. Individuals of both species ate larval fish during late winter and spring when such prey are most abundant. Seasonal trends for the others

TABLE 3.—Numbers of the three kelp-bed fishes that contained more than 50% (by volume) of the indicated food items from the Naples Reef collections (identified by date) that contained all three species: blue rockfish (B), kelp bass (K), and olive rockfish (O).

	21 Jan. 1972			24 Jan. 1972			22 Feb. 1972			26 Apr. 1971			5 May 1972			10 May 1972			23 May 1971			7 Oct 1971			19 Nov 1971			22 Nov 1971			1 Dec. 1971		
Food item	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O
Primarily planktonic:																																	
Zoea larvae				2							1																						
Copepods							1	2																				1					
Megalops larvae																				1													
Chaetognaths				6			2																										
Tunicates:																																	
larvaceans										4																							
salps	7	4					2	4		2															5			6					
Polychaete worms (nighttime planktonic?)																							[1]1								[1]1		[1]1
Larval fish									2			[1]1																					
Primarily nektonic (mostly fish)						3		1			1	2			8			3		8	3		1	3	1	2	4			1		1	
Primarily substrate oriented:																																	
Shrimps									[1]1																								
Mysids				1	1												2							1				1					
Gammarid amphipods		1															1																
Caprellid amphipods											1			1																			
Hydroids		1											3						1			5											
Kelp (incl. encrusting bryozoans)		1		3									2	1		2						3	1			4				2		
"Crustacean pieces"																										2							

[1]Considerable food in the intestine, indicating that the fish may have fed the night before.

TABLE 4.—Numbers of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) that contained more than 95% (by volume) of items composing prey types (plankton, P; nekton, N; or substrate-oriented prey, SOP) listed in Table 2.

Species	P	N	SOP	P + N	SOP + P	SOP + N
Naples Reef						
Blue rockfish	24	3	18	1	13	1
Kelp bass	11	23	23	1	3	6
Olive rockfish	20	28	5	7	3	4
One-Mile Reef						
Olive rockfish	43	15	—	5	3	—
Totals	98	69	46	14	22	11
% of total (279) food-containing specimens	35.1	24.7	16.5	5.0	7.9	3.9

were less clear. Kelp bass ate tunicates from December to May, but fish, kelp, and hydroids were important prey for much of the year. Olive rockfish from Naples Reef ate mostly fish throughout the year.

To test for seasonal differences in diet, the frequencies of prey types were subjected to chi-square tests of homogeneity calculated from contingency tables of dimension two (presence or absence) by four (seasonal periods). Plankton frequencies were significantly heterogeneous, with highest values during winter-spring periods (Figure 2). As fewer kelp bass and olive rockfish ate plankton during the year, more ate nekton, primarily small fish. More blue rockfish and kelp bass ate more algae (with encrusting animals) later in the year.

Species showed greater overlap in diet during periods when their stomachs were fuller of prey (Table 6). For all species, both stomach fullness and food overlap were greater during summer-fall than during winter-spring (Table 6). Fullness may relate to greater exploitation of nekton during summer-fall (Figure 2). For all species, stomachs

TABLE 5.—Seasonal variation in diets of the three species of kelp-bed fishes in all size groups (Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. The first five ranking food items with their percent volume are listed in order for each time period. Sample size is the number of diets (fish) pooled per period; W is Kendall's "W" rank concordance (Tate and Clelland 1957) among seasons for (n) total items.

	December-February		March-May		June-August		September-November		
Species	Item	%	Item	%	Item	%	Item	%	W
Naples Reef:									
Blue rockfish	Sample size	26	Sample size	24	Sample size	18	Sample size	29	
20 total	Tunicates	84.2	Tunicates	70.2	Kelp[1]	43.4	Hydroids	55.2	
items	Chaetognaths	8.1	Kelp[1]	13.6	Fish	23.2	Kelp[1]	31.8	0.37
	Kelp[1]	5.8	Hydroids	9.3	Hydroids	18.4	Fish	11.3	
	Copepods	0.7	Copepods	2.1	Tunicates	3.6	Gammarid amphipods	1.5	
	Gammarid amphipods	0.5	Siphonophores, etc.	1.9	Fish larvae	3.6	Megalops larvae	0.07	
Kelp bass	Sample size	25	Sample size	29	Sample size	17	Sample size	15	
19 total	Kelp[1]	32.9	Fish	57.6	Fish	47.4	Fish	63.4	
items	Tunicates	27.2	Tunicates	18.1	Squid	25.7	Hydroids	17.4	0.41*
	Squid	14.2	Caprellid amphipods	8.5	Kelp[1]	22.1	Kelp[1]	16.1	
	Eggs	8.0	Hydroids	6.3	Caprellid amphipods	1.6	Crabs	1.5	
	Fish	7.3	Kelp[1]	4.1	Shrimps	1.4	Tunicates	1.1	
Olive rockfish	Sample size	8	Sample size	39	Sample size	11	Sample size	28	
14 total	Fish	93.8	Fish	82.4	Fish	86.1	Fish	84.5	
items	Fish larvae	2.5	Fish larvae	4.9	Tunicates	4.8	Tunicates	5.4	0.51**
	Polychaete worms	1.9	Megalops larvae	4.0	Fish larvae	4.4	Polychaete worms	4.1	
	"Crustacean pieces"	0.9	Tunicates	3.5	Isopods	2.9	Mysids	2.5	
	Shrimps	0.5	Squid	1.0	Polychaete worms	0.9	Copepods	0.9	
One-Mile Reef:									
Olive rockfish	Sample size	17	Sample size	40	Sample size	10	Sample size	5	
19 total	Copepods	34.5	Fish	39.0	Fish	88.7	Fish	93.2	
items	Zoea larvae	17.6	Fish larvae	19.9	Megalops larvae	6.9	Fish larvae	3.3	0.44**
	Fish	14.9	Polychaete worms	17.9	Zoea larvae	3.6	Mysids	3.0	
	Pleuroncodes	14.7	Squid	5.6	Mysids	0.7	Copepods	0.1	
	Tunicates	13.9	Tunicates	5.1	Parasitic copepods	0.1	Zoea larvae	0.1	

[1]Including encrusting bryozoans
*Significant at $P = 0.05$
**Significant at $P \leq 0.025$.

TABLE 6.—Seasonal variation in stomach fullness and interspecific dietary overlap in the three species of kelp-bed fishes in all size groups (Figure 1) from Naples Reef off Santa Barbara, Calif. Stomach fullness is mean score, from 1.0 (empty) to 5.0 (full and distended). Food overlap with species in next row down is defined in the text.

	Stomach fullness				Food overlap			
Species	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Blue rockfish	2.59	2.94	3.75	3.26	0.36	0.28	0.49	0.44
Kelp bass	2.22	2.65	3.12	3.08	0.13	0.64	0.48	0.66
Olive rockfish	2.34	2.93	3.01	2.76	0.08	0.08	0.32	0.12
Blue rockfish								
Unweighted mean	2.38	2.84	3.29	3.03	0.19	0.33	0.43	0.41

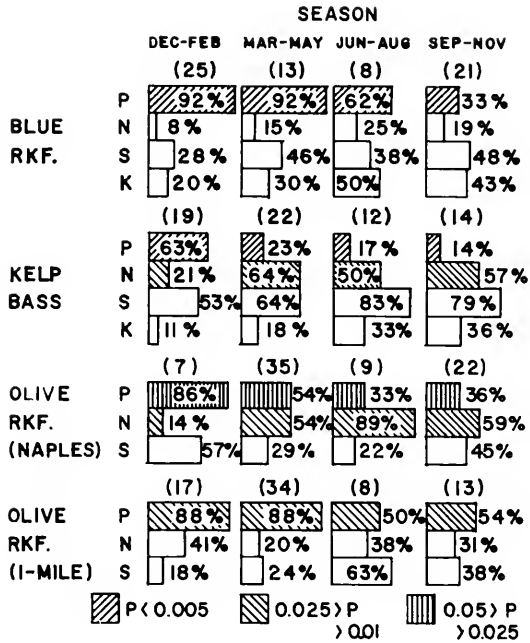

FIGURE 2.—Seasonal variation in percentage frequency of prey types (bars and numbers) in stomachs of fish in the 151- to 300-mm SL size group (Table 1) of the three species of kelp-bed fishes from Naples Reef (all three species) or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Prey types (P-K) are designated in Figure 1; seasonal periods are explained in the text; and numbers in parenthesis are numbers of fish stomachs examined. Hatching shows significant seasonal differences at the indicated probabilities determined by chi-square tests (see text).

containing mostly nekton averaged fuller (weighted means pooled among seasons = 3.12-3.48) than stomachs containing mostly other prey (2.14-2.67).

Habitat

The three species occurred throughout the water column. However, most rockfish (juveniles and subadults) were recorded in canopy cinetransects (Table 7), and younger blue rockfish (reddish phase) usually clustered near the bottom close to shelter. In contrast, kelp bass were more abundant in bottom transects (Table 7). Relatively more blue rockfish and kelp bass were recorded in canopy transects over Naples Reef, where bottom and canopy tend to merge along the reef crest.

One of us (Ebeling) has observed small- to medium-sized fish (ca. 100-250 mm SL) feeding together between middepth and kelp canopy during clear-water days over Naples Reef. Blue rockfish often mingle with blacksmith, a specialized daytime planktivore with small mouth and compressed body. Blacksmith are quicker and more maneuverable than blue rockfish, which pick plankton more slowly and seem to have more difficulty repositioning themselves after feeding lunges. Small numbers of kelp bass and olive rockfish occasionally join the plankton pickers and feed at even lower rates. Although all plankton pickers may cooccur in the same field of view, they usually segregate by species. Larger individuals are usually lower in the water column. But even big kelp bass occasionally pick small particles from near the surface.

All three species were more numerous over greater bottom depths (to about 12 m), where the reef-fish community is generally richer and more abundant (Table 8). Kelp bass and olive rockfish tended toward zones of greater underwater visibility and kelp density, with kelp bass often preferring the outer margin of the kelp bed. Both rockfishes occurred in greater numbers over high-relief rocky bottoms. Olive rockfish (juveniles and subadults) were more numerous higher in the water column.

TABLE 7.—Numbers of the three species of kelp-bed fishes (excluding small juveniles) observed in movie strips (cinetransects) taken at Naples Reef or Santa Cruz Island study sites off Santa Barbara, Calif. Cinetransects are classified as taken either in and about the kelp canopy or reef bottom (see text).

	Naples Reef Cinetransect samples: canopy = 129, bottom = 168			Santa Cruz Island Cinetransect samples: canopy = 146, bottom = 185		
Species	Total fish observed	No. in canopy samples	% in canopy samples	Total fish observed	No. in canopy samples	% in canopy samples
Blue rockfish	3,305	2,953	89.3	919	636	69.2
Kelp bass	861	324	37.6	1,065	318	29.9
Olive rockfish	140	119	85.0	922	843	91.4

TABLE 8.—Correlations between numbers of the three species of kelp-bed fishes and environmental variables observed in an initial set of 175 movie strips (cinetransects) taken over a variety of locations and subtidal habitats along ca. 24-km stretches of coastline at the mainland and Santa Cruz Island off Santa Barbara, Calif. Numbers are Kendall's tau coefficients of rank correlation, significant at $P \leq 0.05$.

Environmental variable	Blue rockfish	Kelp bass	Olive rockfish
Bottom depth	0.26	0.23	0.15
Height in water column (score)	—	—	0.32
Underwater visibility	—	0.18	0.14
Bottom relief (score)	0.19	—	0.10
Kelp density (score)	—	0.18	0.17
Toward outer margin of kelp (score)	—	0.13	—
Total fish numbers	0.19	0.24	0.23
Total fish species	0.40	0.31	0.20

Resource Breadth and Overlap

Olive rockfish from Naples Reef had the smallest food breadth, less than half as large as breadths of the others (Table 9). The Naples Reef fish, which occurred at relatively low density (Tables 7, 10), ate mostly fish. Blue rockfish and kelp bass, whose diets were much more varied (Table 9), supplemented their fare with plankton and substrate-oriented prey. Olive rockfish from One-Mile Reef extended their diet with plankton.

The kelp bass was the most widespread species both at Naples Reef and at Santa Cruz Island (Table 10). Kelp bass tended to aggregate more at Naples Reef, as indicated by a larger Hill's ratio and smaller spatial breadth. Blue rockfish were also more clumped at Naples Reef. Olive rockfish, which were relatively rare at Naples, were more evenly distributed there.

In diet, the kelp bass overlapped the two rockfishes more broadly than either rockfish overlapped the other (Table 11). The kelp bass and olive rockfish overlapped most in diet and overlapped least in space both at Naples Reef and at Santa Cruz Island.

The concordance of food and spatial breadths (Tables 9, 10) indicates that the arithmetic mean of food and spatial overlaps may be a realistic measure of total overlap in resource use (Cody 1974; Pianka 1974; Bray and Ebeling 1975). This is because concordance in breadths suggests that diet and spatial distribution may not vary independently; i.e., certain areas may be best for gathering one prey type, while other areas may be best for another. Total overlap does not vary markedly among the three species pairs because food and spatial overlaps are nearly complementary (Table 11). Even so, total overlap between rockfishes is clearly less than that of either rockfish with the kelp bass.

TABLE 9.—Food breadths of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. The text defines the breadth measure B, which is based on proportionate item volumes. Sample size is the number of fish examined that had food in their stomachs; S is the number of food items eaten; and maximum % volume is of the dominant item (Table 2).

Species	Sample size	S	B	Maximum % volume	Dominant item
Naples Reef:					
Blue rockfish	67	20	3.07	51.5	Tunicates
Kelp bass	67	18	3.44	51.0	Fish
Olive rockfish	73	14	1.40	84.2	Fish
One-Mile Reef:					
Olive rockfish	72	19	3.32	51.0	Fish

TABLE 10.—Spatial breadths of the three species of kelp-bed fishes from Naples Reef or Santa Cruz Island study sites off Santa Barbara, Calif. The text defines the breadth measure B, which is based on proportionate abundances of the species in 297 Naples Reef or 331 Santa Cruz Island movie strips (cinetransects). Sample size is the total fish counted (cf. Table 7); S is the number of cinetransects in which the species was observed; and HR is a measure of concentration (larger values indicate that more individuals are concentrated in fewer of the S cinetransects—see text).

Species	Sample size	S	B	HR
Blue rockfish:				
Naples Reef	3,305	185	42.8	1.66
Santa Cruz Island	919	151	51.0	1.61
Kelp bass:				
Naples Reef	861	218	65.4	1.78
Santa Cruz Island	1,065	217	90.2	1.52
Olive rockfish:				
Naples Reef	140	46	32.6	1.21
Santa Cruz Island	922	144	36.0	1.69

TABLE 11.—Overlap in food and space between members of all pairs of the three species of kelp-bed fishes from Naples Reef or Santa Cruz Island (spatial overlap only) study sites off Santa Barbara, Calif. Thus food overlap, determined from dietary item volumes, and total overlap pertain only to the fish from Naples Reef. Spatial overlap, determined from cinetransect fish counts, is measured separately for Naples and Santa Cruz Island fish.

	Naples Reef		Santa Cruz	Total
Paired species	Food (F)	Spatial (S_n)	Spatial (S_n)	overlap ($F+S_n/2$)
Blue rockfish × Kelp bass	0.43	0 .22	0.26	0.32
Blue rockfish × Olive rockfish	0.17	0.24	0.19	0.20
Kelp bass × Olive rockfish	0.60	0.08	0.16	0.34

DISCUSSION

We first examine possible sources of sampling bias and how they were minimized. Then we argue that within the size range of individuals studied, the three species are indeed able to switch from one prey type to another, and that this ability is not a universal trait of fishes in general. We discuss the circumstances under which the three species may change their diets and why their diets may vary from one place to another. Finally, we discuss coexistence of the three species from an evolutionary viewpoint.

Sampling Bias

Sport fishing activities may bias samples. Fish collected from partyboats often contain anchovies used as chum (Quast 1968d), and the mere pre-

sence of regular sport fishing in particular areas may condition or disturb the fish fauna (Quast 1968b, c). Quast inferred that kelp bass move quickly from bare sites into more heavily foliaged, favored habitats as previous inhabitants are removed by fishing. In the present study, however, the influence of sport fishing was minimal because large partyboats visited Naples Reef infrequently from 1970 to 1973 (due to the erratic state of the Santa Barbara sport fishery then), and we made special effort to avoid the few skiff fishermen.

Nonetheless, our samples may be biased in other ways. Quast (1968b) listed such sport-diving activities as shellfish gathering, which disturbs the bottom, and spearfishing among factors that condition fish behavior. Although we designed our sampling regime to minimize most hazards, we admit that spearing may induce wariness, especially in kelp bass. Hence, our method of spearing fishes as they were encountered may have selected certain individuals by virtue of their size or condition.

Perhaps even more importantly, angling olive rockfish from One-Mile Reef, even with unbaited lures, may have selected hungrier or weakened individuals with empty stomachs. Randall (1967) noted that fish angled in tropical areas often have empty stomachs and some regurgitate their meal during the fight. Our One-Mile Reef specimens did in fact average less stomach fullness than did Naples Reef fish. But since they averaged greater intestinal fullness, they probably had been feeding normally.

Our sampling may reflect some temporal bias. We collected most fish near midday when feeding may slacken. In the tropics, larger generalized carnivores feed mainly at dawn and dusk (e.g., Hobson 1974) or even at night if there is sufficient light (Randall and Brock 1960). In a study of kelp-bed fishes off Santa Catalina Island (ca. 160 km south of Santa Barbara) Hobson and Chess (1976) inferred that juvenile olive rockfish in the 65- to 157-mm SL range feed mostly at night. Quast (1968c) found that only 10-50% of specimens of the three species collected during the day off San Diego contained food. In the present study, however, most specimens contained substantial amounts of food in their stomachs, which were often more packed than their intestines. And individuals were often seen feeding during the day but seldom at night, when they usually sit quietly on the bottom or hide in holes (Ebeling and Bray 1976). Similarly off central California, blue rockfish, at least, are typically active during the day (Gotshall et al. 1965; Miller and Geibel 1973).

Evidence for Switch Feeding

Are the three species indeed switch-feeding predators? They are certainly equipped to switch from large to small prey. All have large mouths for engulfing big items, yet have protrusible jaws and well-developed gill rakers for selecting and keeping small ones.

In general, switch feeders show relatively weak preference for alternative prey and readily take the more abundant or otherwise more available kind (Murdoch et al. 1975). Switching mechanisms may involve avoiding a previous prey or selecting a new one (perhaps by acquiring a search image), spending more time in the area occupied by the new prey, or improving capture technique as the new prey becomes more abundant (Murdoch et al. 1975). Any of these mechanisms should make individual fish specialize. We could not compare diets with prey density, which we did not measure. Indirectly, then, we wanted to see if a relatively large proportion of fish contain mostly one of an array of alternative kinds of prey.

This seems to be the case. A fish usually contained mostly one and not a combination of prey types. Moreover, its stomach and intestinal contents usually matched, implying that it had fed on the particular prey type for a few hours (Windell 1971).

Also, the percentage of fish (76%) containing a single dominant food item is relatively large. It exceeds the estimated percentage (55%) for picker-type microcarnivores—small-bodied fishes with pointed, specialized mouths—which also inhabit the midwaters of the kelp bed (original data from Bray and Ebeling 1975). And it greatly exceeds the small percentage (13%) for demersal microcarnivores—somewhat larger fishes (Embiotocidae) with small mouths and fleshy lips—which usually inhabit the waters just above the reef surface (Ebeling and D. Laur in prep.). With food breadths exceeding 4.0, demersal microcarnivores eat a diverse array of prey, but all of the substrate-oriented type, and seldom one item at a time. Fryer (1959) concluded that in Lake Nyasa (Malawi), Africa, switch feeding is easy for more generalized predatory fishes, but is difficult or impossible for many of the more specialized species.

If switching is a simple functional response (in the sense of Solomon 1949) to more of a particular

prey type, fish may, e.g., switch to plankton when it is particularly dense. This implies that all switch feeders may eat mostly plankton on certain occasions and eat alternative prey on others. There did seem to be a tendency for species to eat mostly plankton during winter-spring when plankton volumes are characteristically large in this area (Smith 1971, 1974) or when other food may be relatively scarce. Yet a fish may spend more energy ingesting many plankters or tiny substrate-oriented prey than a few large prey. Quast (1968c:92) found it ". . . difficult to understand how the effort required to pick caprellids from kelp fronds may be rewarding to a fish as large as 200 mm SL."

Reasons for Switching

In the simple proximate sense, a fish should switch from a dwindling or less accessible type of prey to an increasing or more accessible type (e.g., Murdoch et al. 1975). Yet the factors that ultimately condition fish behavior and control food availability may be many and complex. Quast (1968b) listed predators, hunger, breeding condition, water turbidity, temperature, and neighboring species or conspecific individuals as such factors. Lowe-McConnell (1975) reviewed considerable evidence that generalized predators in tropical freshwaters eat different prey as their environment changes with time, as they occupy different geographic areas and habitats, or simply as they become able to choose among equally abundant food items in a plentiful array. Therefore, we discuss dietary variation with 1) season, 2) geographic areas and faunal mix, 3) habitat, and 4) the presence of large predators.

Unlike wide-ranging, migratory fishes, the three species are limited to the food in their immediate environment. Tagging studies show that even adults have small home ranges. Off central California, juvenile blue rockfish move less than 90 m from their place of settlement unless disturbed by severe winter storms; adults either remain as kelp-bed residents or migrate to deeper water and disperse more widely (Miller and Geibel 1973). Similarly, some 80% of thousands of adult kelp bass tagged off southern California were recovered at or near the release site (Limbaugh 1955; Collyer and Young 1953; Young 1963), and but a small percentage had ventured as far as 8 km (Young 1963). Displaced individuals of *Sebastes flavidus*, a sibling of the olive rockfish, show remarkable homing capabilities (Carlson and Haight 1972).

Feeding habits of kelp-bed residents vary seasonally. All three species eat relatively more plankton on emptier stomachs during the cool-water seasons. Similarly, blue rockfish off central California feed less during winter and more during summer (Gotshall et al. 1965). Unlike Santa Barbara fish, however, their feeding increases during the spring upwelling season when they grow rapidly eating abundant plankton, and decreases during the fall when they grow more slowly eating relatively more substrate-oriented prey and nekton (Miller and Geibel 1973). Like Santa Barbara fish, kelp bass off San Diego feed less during winter, when they are difficult to catch (Limbaugh 1955; Quast 1968c). Quast (1968c) concluded that feeding peaks during fall and late spring may relate to reproductive cycles. Yet in the present study, olive rockfish, which were mostly prereproductive, show the same seasonal feeding cycle as the others. Perhaps here, the seasonal cycle of switching among prey types simply reflects greater availability of larger or more easily accessible prey when fish are most active during warmwater seasons.

Seasonal variation in food overlap corroborates this. Overlap is greatest when stomachs are fullest during summer-fall, and least when stomachs are least full during winter. Zaret and Rand (1971) found that food overlap among sympatric Central American stream fishes was greatest during the food-rich wet season and least during the impoverished dry season when intraspecific competition was presumably greatest. Also, Lowe-McConnell (1975) summarized evidence that diets of species in large African lakes overlap most when food is abundant. Yet we have no direct evidence that smaller overlaps reflect greater competition, because we do not know when, if ever, food is limiting.

Feeding habits vary geographically. Blue rockfish seem to differ markedly in diet, distribution, and behavior between Santa Barbara and San Diego. Quast (1968d) noted that the few blue rockfish sampled from a relatively sparse, marginally distributed population off San Diego (ca. 300 km southeast of Santa Barbara) had eaten little. This prompted him to suggest (1968d:132), "The blue rockfish may be poorly adapted to the environment of this region and the schools may comprise expatriate populations." Off Santa Barbara, a denser population contains a larger size range of

better-fed individuals. Similarly, near Monterey (ca. 300 km north of Santa Barbara), kelp beds abound with all growth stages (Miller and Geibel 1973) eating mostly plankton, but including less attached prey and more nekton as adults (Gotshall et al. 1965).

Kelp bass also show differences. Compared with Santa Barbara fish, relatively more medium-sized bass from off San Diego contained clupeiform fishes (mainly anchovies, reflecting the bias due to sampling from partyboats) and motile substrate-oriented prey, such as crabs, shrimps, and amphipods; but fewer contained plankton, algae, nonclupeiform fishes, and hydroids (Quast 1968c). Other, more cursory results (Limbaugh 1955; Young 1963) agree basically with Quast's. However, Turner et al. (1969), who examined kelp bass speared from about oil platforms and other artificial reefs off southern California, found, as we did, large numbers of pelagic tunicates in some individuals. These researchers saw bass eating chains of salps floating near the reefs. Bass would first bite out and ingest the viscera of large salps, then consume the tunics of the gutted prey; they swallowed small salps whole. Quast (1968c) concluded that larger kelp bass eat larger and more motile prey, especially fish, and ingest more kelp. Although we observed a similar trend, we have no evidence that, as Quast suggested, large bass mistake kelp fragmented by boat propellers for fish prey.

These feeding differences in kelp bass cannot be explained by distributional differences. Like San Diego fish (Limbaugh 1955; Quast 1968b, c), all sizes of Santa Barbara fish are frequently encountered from surface to bottom, and prefer areas of dense kelp at the outer margins of the bed. Quast (1968b) concluded, however, that kelp bass also occupy reefs having little or no kelp.

There is less information on geographic variation in feeding habits of olive rockfish. South of Santa Barbara, olive rockfish and kelp bass reportedly cooccur and even intermingle (Quast 1968d; Turner et al. 1969), eat similar foods (Quast 1968d), and so may compete for the same cover and food (Feder et al. 1974). Off Santa Barbara, however, the two may minimize interference by having a relatively small overlap in spatial distribution. Considering the two species' superficial similarities in body form and color pattern, Limbaugh (1955) suggested that olive rockfish may ecologically replace kelp bass north of Santa Barbara, where kelp bass dwindle in numbers (Quast 1968a; Miller and Geibel 1973).

Geographic variation in a fish's feeding habits may reflect its environmental tolerances, range limits, and numbers of competitors, as well as its food supplies. Blue rockfish are more abundant off central California, kelp bass are more abundant off southern California, and olive rockfish occur abundantly in both regions but, unlike the others, are mostly restricted to Californian coastal waters (Limbaugh 1955; Quast 1968a, d; Miller and Geibel 1973). Because the Santa Barbara Channel is near the northern limit of the San Diegan fauna (Hubbs 1960; Quast 1968a), it harbors more central Californian cool-water species (Ebeling et al. 1971; Ebeling, R. Larson, and W. Alevizon in prep.). Hence all three species abound in Santa Barbara kelp forests, and here, for example, the olive rockfish may be better at capturing nekton, thus reducing supplies for the other two. Off San Diego, on the other hand, both rockfishes may occur more sporadically (Quast 1968d) and compete less intensely with the more numerous kelp bass. Generally reduced planktivory off San Diego may either reflect lower average plankton densities there (Smith 1971, 1974), or greater abundances of larger, more preferred prey.

Within the Santa Barbara area, habitat differences may affect prey availability and the species' feeding habits. Like most areas of reef and kelp (Feder et al. 1974; Miller and Geibel 1973), Naples Reef may provide more refuges for larger prey. So here, as suggested generally both from experiments (e.g., Ivlev 1961) and theoretical models (e.g., Schoener 1971; Estabrook and Dunham 1976), predators may concentrate on fewer categories of larger, preferred prey in a greater overall abundance of food. One-Mile Reef, on the other hand, appears less intrinsically productive because it is deeper than Naples Reef and supports no giant kelp. So here larger prey may occur less predictably and olive rockfish must switch to plankton, including the tiniest of items, more frequently. Santa Cruz Island reefs are even more complex and productive than Naples Reef (Alevizon 1975; D. Laur pers. commun.). Thus Santa Cruz supports larger aggregations of olive rockfish, which tend more to segregate from equally large aggregations of blue rockfish.

Finally, food and space need not be the primary factors that limit the sizes of the switch-feeder populations. Severe storms, disease, and predators may eliminate certain numbers of individuals. Menge and Sutherland (1976) reviewed evidence

that for complex communities in stable environments, predators may crop prey populations below their environmental carrying capacity. Hence, only top predators must partition resources to avoid competitive exclusion. Thus if adult switch feeders are heavily exploited by sharks, marine mammals, man, etc., or young are decimated by smaller predators, the three species may have little, if any, competitive effect on one another.

Evolutionary Viewpoint

Ultimately, the tendency to choose different prey may be an evolutionary response to coexistence with a close relative. The two rockfishes, which cooccur throughout much of their ranges (Phillips 1957; Quast 1968a), may have coevolved their divergent food habits. Most species of rockfish are spiny types that sit on the bottom and/or live in deep water (Phillips 1957). However, the blue and olive rockfishes are members of a derived group of related species that have smoother, more streamlined bodies and inhabit the entire water column. Extending its distribution from bottom to surface, the common ancestor of this species group could eat plankton and surface nekton as well as benthic prey. Such an ancestor would have the ability to hunt in open water and exploit all three prey types by evolving a more streamlined morphotype. Then, during the process of speciation within the group, the blue and olive rockfishes may have themselves diverged in food habits as might be expected of two cooccuring congeners (e.g., Mayr 1963; MacArthur 1972).

Thus even if their numbers are not limited by predators or other disturbances, the three superficially similar species may coexist by partitioning resources. As a more distantly related serranid, the kelp bass broadly shares the food spectrum with both scorpaeniform rockfishes: the plankton-eating and browsing blue rockfish and the fish-eating olive rockfish. Yet the kelp bass and olive rockfish have the greater dietary overlap and so tend to stay out of each others' way where both are common off Santa Barbara. And if conditions warrant it, kelp bass and olive rockfish can switch to plankton and other tiny prey although they are apparently less well adapted than blue rockfish to do so.

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SCOMBEROMORUS BRASILIENSIS, A NEW SPECIES OF SPANISH MACKEREL FROM THE WESTERN ATLANTIC

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ABSTRACT

Scomberomorus brasiliensis is most closely related to *S. sierra* of the eastern tropical Pacific and more distantly related to *S. maculatus* and *S. regalis* of the western Atlantic and to *S. tritor* of the eastern Atlantic. It differs from all four of these species in having a shorter pelvic fin (3.6-5.9% fork length, $\bar{x}$ 4.53 compared with 4.4-7.1% in the other four species, means 5.07-5.71). *Scomberomorus brasiliensis* differs sharply from *S. maculatus* with which it has previously been confused in having fewer vertebrae (47-49 compared with 50-53). *Scomberomorus brasiliensis* is a more southern species than *S. maculatus*, occurring along the Atlantic coasts of Central and South America from Belize to Rio Grande do Sul, Brazil, while *S. maculatus* is confined to the Gulf of Mexico and the Atlantic coast of the United States.

RESUMO

Scomberomorus brasiliensis é uma espécie estreitamente relacionada com *S. sierra*, do Pacífico Oriental Tropical, tendo também relação com *S. maculatus* e *S. regalis*, do Atlântico Ocidental e *S. tritor*, do Atlântico Oriental. Diferencia-se dessas quatro espécies por ter a nadadeira ventral de menor tamanho (3,6-5,9% do comprimento zoológico, $\bar{x}$ 4, 53, comparado a 4,4-7, 1% nas outras quatro espécies, que tem medias de 5,07 a 5,71). *Scomberomorus brasiliensis* difere claramente de *S. maculatus*, com a qual foi confundida anteriormente, por apresentar menor número de vértebras (47-49 comparado a 50-53). *Scomberomorus brasiliensis* ocorre na costa Atlântica da América Central e América do Sul, desde Belize (Honduras britânica) até o Rio Grande do Sul (Brasil), enquanto *S. maculatus* está confinada ao Golfo de México e à costa Atlântica dos Estados Unidos.

While revising the tribe Scomberomorini (Collette and Russo in prep.), two apparently undescribed species of *Scomberomorus* were discovered, one from Australia and New Guinea and the other from the Atlantic coasts of Central and South America. Because completion of the revision will be delayed and because Atlantic Spanish mackerels are of recreational and commerical fishing concern, we describe the Atlantic species herein. Naming of this species adds one to the currently recognized (Rivas 1951; Mago Leccia 1958) three species of western Atlantic *Scomberomorus*—the king mackerel, *S. cavalla* (Cuvier), Spanish mackerel, *S. maculatus* (Mitchill); and cero, *S. regalis (Bloch)*.

METHODS AND MATERIALS

The methods of counting, measuring, and dissecting are those used by Gibbs and Collette (1967) in revising *Thunnus* and by Collette and Chao (1975) in revising the Sardini. Extensive anatomical data on the undescribed species will be presented in a future revision of the Scomberomorini by Collette and Russo. Only relevant diagnostic characters plus standard descriptive meristic and morphometric data are presented here. Statistical tests were performed on the IBM 370-148 computer[4] at the George Washington University using computer programs written for the revision of the genus *Scomberomorus* following the statistical methods presented by Zar (1974).

Material examined is in the following collections: ANSP (Academy of Natural Sciences, Philadelphia); BMNH (British Museum, Natural History, London); CAS (California Academy of

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

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Sciences, San Francisco); FMNH (Field Museum of Natural History, Chicago); LACM (Los Angeles County Museum of Natural History); MCZ (Museum of Comparative Zoology, Harvard University); MNHN (Museum National d'Histoire Naturelle, Paris); MPIP (Museu de Pesca do Instituto de Pesca, Santos); MZUSP (Museu de Zoologia da Universidade de São Paulo); NHMV (Naturhistorisches Museum, Vienna); NMC (National Museum of Canada, Ottawa); RMNH (Rijksmuseum van Natuurlijke Historie, Leiden); ROM (Royal Ontario Museum, Toronto); SIO (Scripps Institution of Oceanography, La Jolla); SU (Stanford University, specimens now at CAS); UDONECI (Universidad de Oriente, Nueva Esparta, Centro de Investigaciones, Venezuela); UF (Florida State Museum, University of Florida, Gainesville); UMML (Rosenstiel School of Atmospheric and Marine Science, University of Miami); USNM (National Museum of Natural History, Washington, D.C.); ZMA (Zoological Museum, Amsterdam); ZMH (Zoologisches Institut und Zoologisches Museum, Hamburg); ZMK (Zoological Museum, Copenhagen).

SERRA SPANISH MACKEREL

Scomberomorus ***brasiliensis*** n.sp.

Diagnosis.—A spotted species of Spanish mackerel without a dip in the lateral line, without scales covering the pectoral fins, with a moderate number of vertebrae (47-49, usually 48) and gill rakers (12-16, usually 13-15), and with a short pelvic fin (3.6-5.9% FL).

Scomberomorus brasiliensis is most closely related to *S. sierra* Jordan and Starks of the eastern tropical Pacific and more distantly to *S. maculatus* (Mitchill) of the western Atlantic and to *S. tritor* (Cuvier) of the eastern Atlantic. It differs from *S. maculatus* in having fewer vertebrae (47-49 compared with 50-53, Table 1).

Morphometrically, *S. brasiliensis* differs from its four closest relatives in having a much shorter pelvic fin (Figure 1): 3.56-5.86, $\bar{x}$ = 4.53% FL compared with *S. sierra* (4.71-6.37, $\bar{x}$ = 5.51), *S. maculatus* (4.59-5.76, $\bar{x}$ = 5.71), *S. tritor* (4.97-7.14, $\bar{x}$ = 5.07), and *S. regalis* (4.41-6.33, $\bar{x}$ = 5.54). The linear regression of pelvic fin length on fork length was tested by analysis of covariance. The slopes of the regression lines of all five species were not significantly different at the 0.01 level of significance (Table 2). The elevations of the five regression lines were significantly different at the 0.001 level ($P<1.0 \times 10^{-7}$). The Student Newman-Keules multiple range test indicates that the elevations of the regression lines for *S. sierra, S. maculatus, S. tritor,* and *S. regalis* were not significantly different ($P>0.2$); however, *S. brasiliensis* was found to be different from the other four species ($P<0.001$). Data from *S. maculatus, S. sierra, S. tritor,* and *S. regalis* were resubmitted to analysis of covariance after removal of *S. brasiliensis*. This reduced the calculated F from 54.72 to 6.79 showing that most of the variance was caused by inclusion of *S. brasiliensis* with four other more or less homogeneous species.

TABLE 2.—Regression equations of pelvic fin length on fork length for five species of *Scomberomorus*.

Species	*N*	*Y* intercept	Slope	Coefficient of determination (r^2)
S. tritor	30	2.137	0.053	0.965
S. brasiliensis	49	−0.013	0.045	0.963
S. sierra	50	1.510	0.051	0.957
S. maculatus	32	1.029	0.054	0.960
S. regalis	37	1.179	0.051	0.933

Description.—Lateral line without a prominent dip in the region of the second dorsal fin (present only in *S. cavalla* among American and Atlantic

TABLE 1.—Numbers of precaudal, caudal, and total vertebrae in five species of *Scomberomorus*.

	Precaudal							Caudal								Total										
Species	18	19	20	21	22	*N*	$\bar{x}$	26	27	28	29	30	31	32	*N*	$\bar{x}$	45	46	47	48	49	50	51	52	53	*N*	$\bar{x}$
S. tritor (E. Atlantic)	6	30				36	18.8	2	30	4					36	27.1	6	29	1							36	45.9
S. brasiliensis (W. Atlantic):																											
Central and northern South America			24	2		26	20.1		4	21					25	27.8			3	21	2					26	48.0
Brazil		2	59	1		62	20.0		6	53	3				62	28.0			8	50	4					62	47.9
S. sierra (E. Pacific):																											
Mexico		2	14	2		18	20.0		3	12	3				18	28.0			2	14	2					18	48.0
Central and South America			16	1		17	20.1		3	13	1				17	27.9			2	14	1					17	47.9
S. maculatus (W. Atlantic):																											
Eastern United States				23	4	27	21.1					9	18	1	28	30.7							5	20	3	28	51.9
Gulf of Mexico				16	2	18	21.1				1	10	7		18	30.3						1	9	7	1	18	51.4
S. regalis (Caribbean)		5	47	2		54	19 9		5	36	13				54	28.1			4	42	9					55	48.1

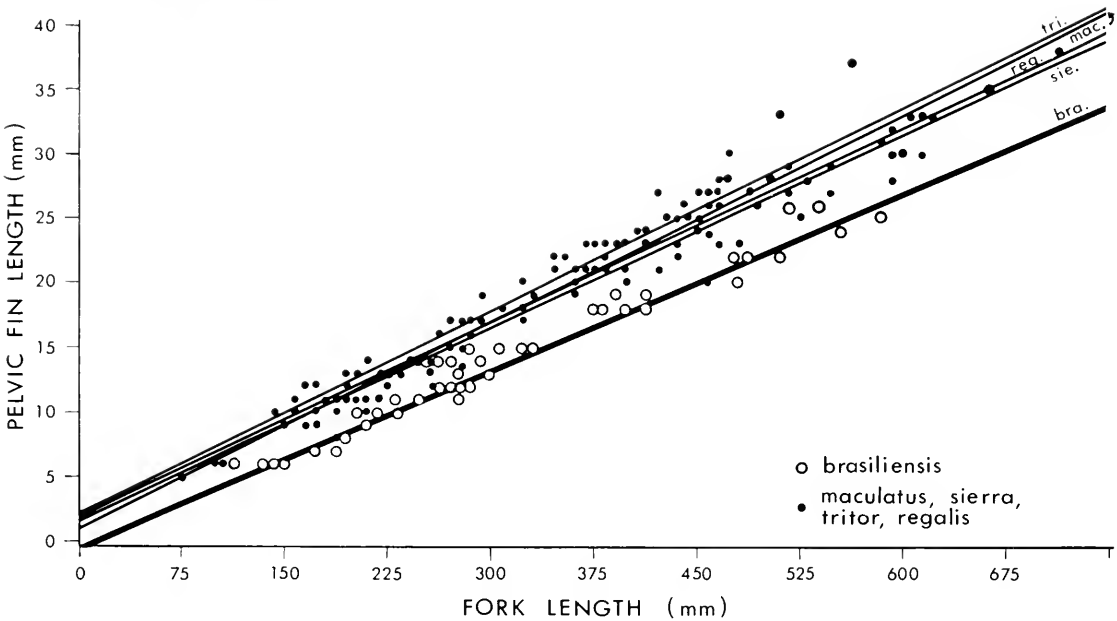

FIGURE 1.—Regression of pelvic fin length on fork length in five species of *Scomberomorus*. The regression line for *S. brasiliensis* is significantly different from those for *S. maculatus*, *S. sierra*, *S. tritor*, and *S. regalis*. The regression lines for these four species do not differ significantly from each other so the same symbol is used for plotting specimens of the four species.

species). Pectoral fin without scales (covered with scales in *S. regalis*). Vertebrae (19-21) + (27-29) = 47-49 usually 20 + 28 = 48. Gill rakers (1-3) + 1 + (9-12) = 11-16, usually 13-15 (Table 3) more than in *S. cavalla* (7-12) and many fewer than in *S. concolor* (21-27). Pectoral fin rays 21-24, usually 22 or 23, usually 21 in *S. tritor*, *S. sierra*, and *S. maculatus*, 21 or 22 in *S. regalis* (Table 4). Dorsal spines 17-19, usually 17 or 18; second dorsal fin rays 17-19; dorsal finlets 8-10; anal fin rays 18-20; anal finlets 8-10, usually 8 or 9. Morphometric data are summarized in Table 5. Intestine with three limbs and two folds (Figure 2).

Sides with several rows of round yellowish-bronze (in life) spots similar to *S. maculatus* and *S. sierra* but without any lines or streaks such as are present in *S. regalis*. The number of yellowish-

TABLE 4.—Number of pectoral fin rays in five species of *Scomberomorus*.

Species	Pectoral fin rays						
	20	21	22	23	24	*N*	$\bar{x}$
S. tritor (E. Atlantic)	1	19	9			29	21.3
S. brasiliensis (W Atlantic):							
Central and northern South America		6	13	11	1	31	22.2
Brazil		2	24	14		40	22.3
S. sierra (E. Pacific):							
Mexico	7	16	7			30	21.0
Central and South America	4	18	7	1	1	31	21.3
S. maculatus (W Atlantic):							
Eastern United States	2	13	5			20	21.2
Gulf of Mexico		13	1			14	21.1
S. regalis (Caribbean)		15	17	4		36	21.7

TABLE 3.—Numbers of upper, lower, and total gill rakers on the first gill arch in five species of *Scomberomorus*.

Species	Upper						Lower								Total									
	1	2	3	4	*N*	$\bar{x}$	9	10	11	12	13	14	*N*	$\bar{x}$	11	12	13	14	15	16	17	18	*N*	$\bar{x}$
S. tritor (E. Atlantic)		25	6		31	2.2		7	18	3	3		31	11.1		6	14	8	3				31	13.3
S. brasiliensis (W Atlantic):																								
Central and northern South America		14	7		21	2.3	1	2	10	8			21	11.2	1	2	6	9	3				21	13.5
Brazil	1	68	35		104	2.3		11	47	37	8		103	11.4		7	42	29	21	4			103	13.7
S. sierra (E. Pacific):																								
Mexico		9	20	4	33	2.8			11	15	6	1	33	11.9			4	10	10	8	1		33	14.8
Central and South America		2	31	1	34	3.0		1	5	13	13	2	34	12.7			1	5	14	12	2		34	15.3
S. maculatus (W. Atlantic):																								
Eastern United States		13	6	1	20	2.4	2	8	7	2	1		20	10.6	2	5	7	4	1	1			20	13.0
Gulf of Mexico	1	13			14	1.9		2	8	3	1		14	11.2		2	9	2	1				14	13.1
S. regalis (Caribbean)		8	26	4	38	2.9		1	4	12	17	4	38	12.5		1	2	2	16	11	5	1	38	15.4

TABLE 5.—Summary of morphometric data of *Scomberomorus brasiliensis* expressed as percent fork length.

Character	N	$\bar{x}$	Min	Max	SD
Snout-anal distance	51	53.80	51.21	69.19	2.67
Snout-second dorsal distance	51	51.13	48.31	67.21	2.64
Snout-first dorsal distance	51	24.09	19.65	33.69	2.10
Snout-pelvic distance	51	25.15	21.75	35.86	2.21
Snout-pectoral distance	51	21.93	19.08	31.71	2.12
Pectoral-pelvic distance	50	10.83	8.75	15.95	1.12
Head length	51	21.20	12.12	30.90	2.34
Maximum depth	51	19.86	16.40	26.31	1.57
Maximum width	49	7.99	5.42	11.38	1.09
Pectoral length	51	12.29	9.66	14.32	1.00
Pelvic length	49	4.53	3.56	5.86	0.41
Pelvic insert-vent	49	27.51	23.87	34.86	1.65
Pelvic tip-vent	46	22.83	19.72	29.82	2.90
Base first dorsal	50	26.51	23.16	36.04	1.82
Height second dorsal	48	11.58	9.19	13.94	1.11
Base second dorsal	51	11.86	10.05	15.32	0.97
Height anal	48	11.30	8.27	14.86	1.18
Base anal	50	11.20	9.74	14.23	0.94
Snout (fleshy)	51	8.18	6.88	11.98	0.87
Snout (bony)	51	7.31	6.16	10.18	0.70
Maxillary length	50	12.23	8.16	18.83	1.50
Post orbital distance	51	9.48	8.43	12.70	0.69
Orbital (fleshy)	51	3.73	2.70	5.74	0.62
Orbital (bony)	51	5.27	4.15	7.66	0.71
Interorbital distance	51	5.66	4.78	10.65	0.83
Second dorsal-base caudal peduncle	50	49.34	42.75	59.37	3.29

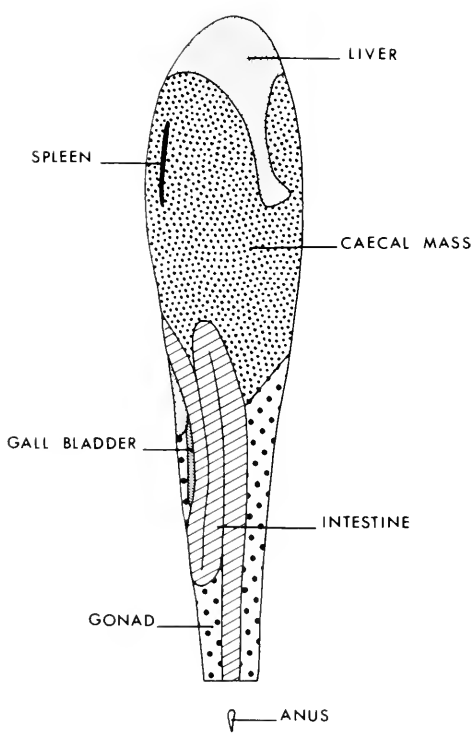

FIGURE 2.—Ventral view of viscera in *Scomberomorus brasiliensis*, 556 mm FL, Belém, Brazil, dissected 17 June 1975.

bronze spots on the sides of the body increases with the size of the fish, young specimens (200 mm) have about 30 spots; adults more, 45 spots (422 mm), 47 (455), 46 (470), 45 (516), and 58 (530). The spots are arranged in 3 or 4 rows (sometimes in 2 rows). The rows are not very well defined but it is possible to recognize them. The spots in *S. maculatus* are not arranged in rows.

The first dorsal fin is black in the anterior half (first 7 membranes) and the posterior half is white with the upper edge black. Pectoral fin dusky; pelvic and anal fins white. In young specimens (192-240 mm) (collected from estuarine waters) the caudal and pectoral fins are yellow (in the pectoral fin, yellow over the dusky color) and the whole body and the anal fin are slightly yellow.

Range.—Atlantic coasts of Central and South America from Belize at least as far south as Lagoa Tramandaí, Rio Grande do Sul, Brazil (Figure 3). Not known to overlap with *S. maculatus* which occurs in the Gulf of Mexico and along the Atlantic coast of the United States. Replaced in the West Indies by *S. regalis*.

Material examined.—Inasmuch as there is abundant material from Brazil, and because further study might show some differentiation within the range of *S. brasiliensis*, the type-material is restricted to the specimens examined from Brazil.

Holotype.—USNM 217550 (502 mm FL); Belém market; 22 May 1975; B. B. Collette 1642.

Paratypes.—103 specimens (110-630 mm FL) from 54 Brazilian collections. USNM 217551-57 (7, 509-588); Belém market; May 1975; B. B. Collette 1639, 1642, and 1645. MCZ 17131 (1, 220); Pará (= Belém). NHMV uncat. (2, 410-538); Pará; Brasil Exped.; Steindachner. NHMV uncat. (1, 325); Maranhão; Brasil Exped.; 1903. USNM 188424 (3, 153-281); *Oregon II* stn. 4250, 2°23'S, 40°31'W; 12 Mar. 1973. CAS-SU 52981 (1, 483); Ceará, Fortaleza, Mucuripe. CAS-SU 52989 (1, 359); Ceará, Fortaleza. CAS-SU 52988 (1, 300); Ceará, Fortaleza. CAS-SU 52987 (1, 220); Ceará, Fortaleza. MZUSP 13263-4 (2, 375-405); Ceará; May 1976. MPIP 0001-2 (2, 354-380); Ceará; May 1976. MZUSP 13262 (1, 385); axial skeleton; Rio Grande do Norte; Feb. 1976. CAS-SU 52971 (1, 340); Pernambuco, Recife. CAS-SU 52973 (1, 236); Pernambuco, Recife. MCZ 48894 (2, 392-412); Recife market; Equalant Exped.; *Chain*; R. H. Bakus;

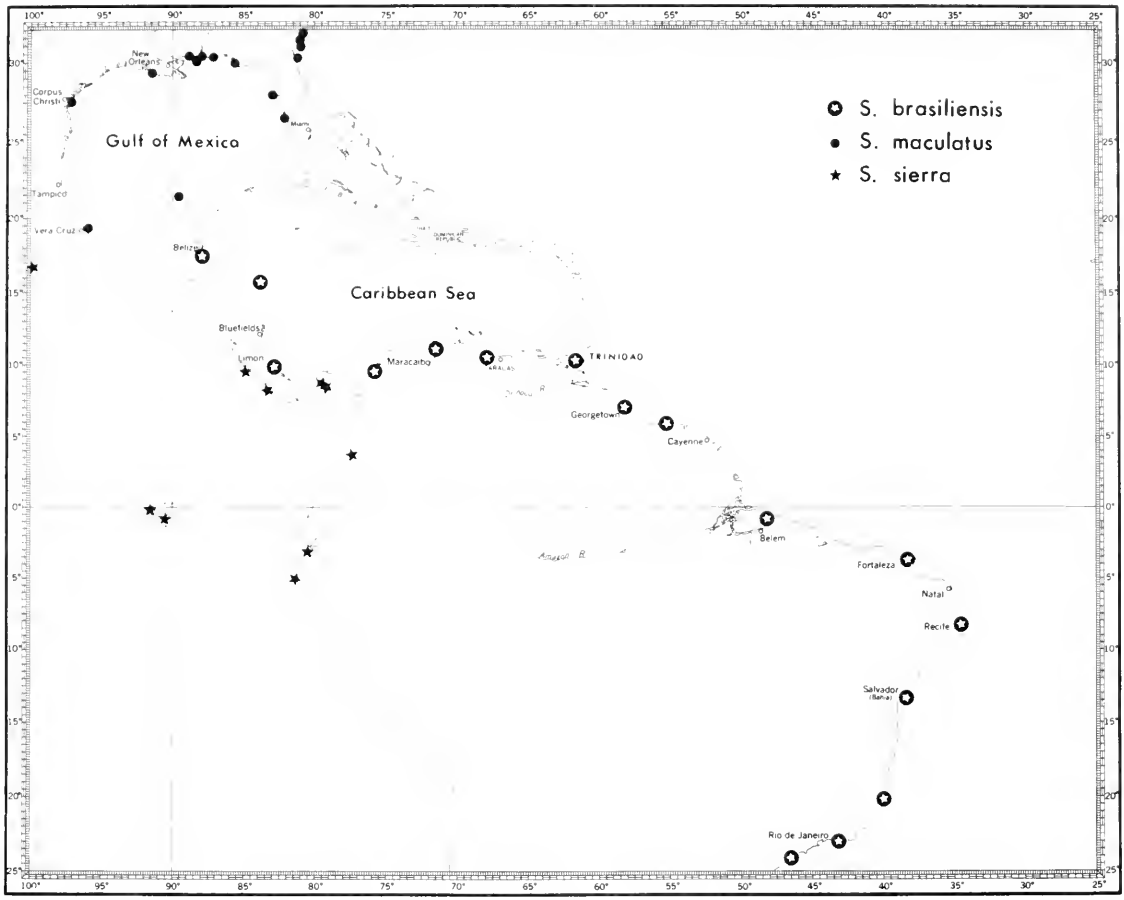

FIGURE 3.—Distribution of *Scomberomorus brasiliensis* (stars in circles) and adjacent populations of *S. maculatus* (dots) and *S. sierra* (stars). The ranges of *S. maculatus* and *S. sierra* extend farther north and that of *S. brasiliensis* farther south.

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Santa Catarina; Aug. 1976. MPIP 0013 (1, 425); Santa Catarina; Aug. 1976. MZUSP 1329-30 (2, 405-600); Santa Catarina; Dec. 1976. MPIP 0014 (1, 405); Santa Catarina; Dec. 1976. MZUSP 13294 (1, 372); axial skelton; Santa Catarina; Jan. 1977. CAS-SU 52986 (1, 416); Rio Grande do Sul. MZUSP 13295-6 (2, 240-245); Rio Grande do Sul. Lagôa Tramandaí; May 1977; MCZ 17158 (4, 136-216); Brazil.

Other material.—28 specimens (111-520 mm FL) from 15 collections arranged here by country from north to south. BELIZE: BMNH 1864.1.26.304-5 (2, 217-230); Salvin. HONDURAS: UF-TABL 67-106 (1, 243); 15°21'N, 83°34'W; 10 Apr. 1967. COSTA RICA: 3(172-194) from 2 collections. LACM 30727-13 (2, 191-194); Canuita Bay; W. Bussing and party. LACM 30726-3 (1, 172); Canuita Bay; W. Bussing and party. PANAMA: 4(114-225) from 2 collections. ANSP 86721 (1, 225); Balboa; 5th G. Vanderbilt Exped.; 11-14 Apr. 1941. ANSP 45270 (3, 114-182); Colon market; D. E. Hanover; June 1945. COLOMBIA: USNM 217433 (1, 326); *Choco* cruise 6908, stn. 127, 9°22.1'N, 75°36.4'W; 6 Sept. 1969. VENEZUELA: 9(89-520) from 3 collections. ZMA 114.581 (1, 520); Puerto Cabello; 10 Aug. 1905. USNM 121802 (2, 296-330); Maracaibo market; L. P. Schultz; 15 May 1942. UDONECI 1071 (6, 89-198); Pedernales; 3 July 1974. TRINIDAD: 8(260-311) from 5 collections. BMNH 1931.12.5.173 (1, 260); Gulf of Paria; Totten, *Rodney*. ANSP 94311 (2, 278-311); Brighton Pier; L. Wehekind; 10 May 1930. ANSP 94325 (2, 280-287); Brighton Pier No. 2; L. Wehekind; 7 May 1930. ANSP 94329 (2, 268-289); Brighton Pier No. 2; L. Wehekind; 17 May 1930. UF-TABL uncat. (1, 233); M/V *Calamar* cruise 67-B, stn. 260; 13 Nov. 1967. SURINAM: RMNH 24764 (1, 111).

DISCUSSION

Although it is a common fish, *Scomberomorus brasiliensis* has not been formally described because adults closely resemble *S. maculatus* in their spotted pattern. The juveniles are similar to *S. regalis* in having low vertebral counts (47-49) and have probably been confounded with that species (which is actually uncommon in the range of *S. brasiliensis* off the coasts of Central and South America).

A fairly extensive literature pertains to *S. brasiliensis* (as *S. maculatus*) dating back to Ribeiro (1915). Particularly important are a series of 30 papers on various biological and fisheries aspects of *S. brasiliensis* from Laboratório de Ciências do Mar da Universidade Federal do Ceará at Fortaleza, Brazil. Bastos (1966) summarized morphometric and meristic data for 90 specimens (163-553 mm FL). His gill raker counts (usually 2 + 1 + 11 = 14 or 3 + 1 + 11 =15) agree closely with ours (Table 3). His vertebral counts (26 specimens with 46 and 55 specimens with 47) are 1 less than ours (Table 1) because he presumably did not include the hypural plate in his counts as we did. Menezes (1972) also counted gill rakers and found no differences between counts for 225 males and 275 females; the most typical count was 3 + 1 + 11 = 15.

The digestive tract was studied both grossly and histologically by Mota Alves (1969). The histology of the pyloric caeca of *S. brasiliensis* was found similar to that found in *S. cavalla* by Mota Alves and Tomé (1970). The pyloric caeca were found to contain the same enzymes as the intestine in both species—lipase, maltase, and trypsin but the pyloric caeca in *S. brasiliensis* also contained pepsin which was restricted to the stomach in *S. cavalla*.

The food of *S. brasiliensis* in the State of Ceará was studied around the year by Menezes (1970). Fish composed the major part of the diet; penaeid shrimps and loliginid cephalopods also were important. The most important fishes were, in order: *Opisthonema oglinum*, Engraulidae, *Chloroscombrus chrysurus*, *Hemiramphus* sp., and *Haemulon* spp. The diet of *S. maculatus* in southeastern Florida is similar to this according to Klima (1959), consisting mostly of clupeids (especially *Harengula pensacolae*) plus *Penaeus*, engraulids, and other fishes.

Mota Alves and Tomé (1968a) reported on the sexual development of *S. brasiliensis* and recognized five developmental stages in the ovary. They also (1968b) described the sperm. Gesteira (1972) found that females first become sexually mature at about 460 mm FL at an age of III or IV. She presented equations for calculating fecundity based on length, age, and weight. Klima (1959) found that the smallest mature female *S. maculatus* from southeastern Florida was 250 mm FL and that both sexes matured at age I or II.

Length-frequency data for *S. brasiliensis* (and *S. cavalla*) were collected and published annually, starting with the data for 1962 and continuing through 1969 by Costa and Paiva and then for

1971-73 by Costa and Almeida (1974). For 32,514 specimens of *S. brasiliensis* measured from 1962 through 1973, the size range was 267-1,250 mm FL. Of 16,170 specimens measured between 1962 and 1968, 9 were longer than 950 mm FL: 6 (951-1,000); 1 (1,001-1,050); 1 (1,051-1,100); and 1 (1,201-1,250). More than 60% each year from 1962 to 1968 were in the size range 401-650 mm FL. *Scomberomorus maculatus* is a much smaller species; the largest of 1,279 specimens examined by Klima (1959) from southeastern Florida was 700 mm FL and most were between 300 and 500 mm. The length-weight relationship was determined by Nomura and Costa (1968) for Brazilian *S. brasiliensis*: for males $\log W = -2.2051 + 2.973 \log L$, and for females $\log W = -2.154 + 3.035 \log L$. For 1971-73, the age composition of the catch was II to X, concentrated at III to VI, and mostly III or IV (Costa and Almeida 1974).

Color pattern, possession of nasal denticles, lateral line curvature, and other characters suggest that *S. brasiliensis*, *S. sierra*, *S. maculatus*, and *S. tritor* are closely related. *Scomberomorus regalis* may also belong to this group of species and *S. concolor* Lockington of the eastern tropical Pacific is even more distantly related. *Scomberomorus cavalla* belongs to another species group, containing *S. commerson* (Lacepède). The center of origin of *Scomberomorus* appears to be in the Indo-West Pacific as is the case with many other groups of fishes. It appears likely that an ancestor of *S. tritor* crossed the Atlantic and populated the tropical western Atlantic and eastern Pacific. When the Panamanian isthmus emerged, this population was divided into two, which subsequently differentiated into *S. sierra* (eastern Pacific) and *S. brasiliensis*. *Scomberomorus maculatus* is presumably derived from the *S. sierra-brasiliensis* stock and developed a higher number of vertebrae along with its movements into more temperate waters along the U.S. east coast.

COMPARATIVE MATERIAL EXAMINED

Scomberomorus maculatus. East coast of United States: 24 specimens (163-712 mm FL) from 13 collections from Cape Cod, Mass.; New York; Cape Hatteras, N.C.; Charleston, S.C.; and Brunswick, Ga., at MCZ, NHMV, USNM, ZMH, and ZMK. Gulf of Mexico: 29 specimens (176-439 mm FL) from 16 collections from Captiva Key and St. Andrew Bay, Fla; Mobile, Ala.; Biloxi, Miss.; Atchafalaya Bay, La.; Aransas Bay, Tex.; Vera Cruz, Mexico; and Progreso, Yucatan, Mexico at BMNH, MCZ, NHMV, USNM, and ZMK.

Scomberomorus sierra. SIO 62-338 (1, 594), La Jolla, Calif. Mexico: 42 specimens (183-685 mm FL) from 22 collections from Baja California, Guaymas, Mazatlan, and Sonora at BMNH, CAS, LACM, MCZ, NHMV, SIO, and USNM including the lectotype SU 1720 (332 mm) from Mazatlan. Costa Rica: 6 specimens (237-515 mm FL) from 4 collections from Golfo Dulce and Golfo Nicoya at LACM. Panama: 15 specimens (226-605 mm FL) from 8 collections at FMNH, MCZ, NHMV, SU, USNM, and ZMH. Colombia: 8 specimens (202-260 mm FL) from Buenaventura at USNM. Peru: 4 specimens (135-460 mm FL) from 3 collections at LACM and NHMV. Galapagos: 4 specimens (422-621 mm FL) from 3 collections at ANSP, CAS, and NMC.

Scomberomorus tritor. Mediterranean: 2 specimens (365-475 mm FL) from Nice at NHMV and Florence. Gulf of Guinea: 36 specimens (69-600 mm FL) from 25 collections from the Canary Islands, Senegal, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria, and Angola at BMNH, CAS, MCZ, MNHN, NHMV, USNM, and ZMA including the holotype MNHN A.6871 from Gorée, Dakar.

Scomberomorus regalis. Caribbean: 40 specimens (77-525 mm FL) from 27 collections from Florida, Bahamas, Cuba, Haiti, Jamaica, Puerto Rico, Virgin Islands, Lesser Antilles, and Barbados at BMNH, MCZ, NHMV, ROM, USNM, ZMA, ZMH, and ZMK.

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pleted from our sketches by Keiko Hiratsuku Moore. Drafts of the manuscripts were read by Mark E. Chittenden, Daniel M. Cohen, Eugene L. Nakamura, William J. Richards, and Naércio A. Menezes.

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AGGREGATION OF THE SIPHONOPHORE *NANOMIA CARA* IN THE GULF OF MAINE: OBSERVATIONS FROM A SUBMERSIBLE

Large concentrations of a physonect siphonophore, *Nanomia cara* Agassiz 1865, were present in the Gulf of Maine during fall and winter of 1975. These gelatinous, colonial coelenterates were sufficiently abundant that they clogged trawl nets and occasioned considerable losses of time and money to commercial fishermen at several New England ports (Rogers in press). During October and November 1975, scuba divers on the *Helgoland* habitat in 30-m shoals off Rockport, Mass. (Figure 1), noted concentrations of *N. cara* reaching 1 colony/m^3 throughout the water column (R. A. Cooper and H. W. Pratt unpubl. data). Off Rockport again in late March 1976, divers estimated densities of 1 to 2 colonies of *N. cara*/m^3 in water only 9 m deep (H. W. Pratt pers. commun.). In April and again in early May 1976, a series of 100-m to surface oblique plankton tows was taken in the Gulf of Maine along a transect from the Wilkinson Basin to Cape Ann, Mass., by *Albatross IV*, a fisheries research ship of the Northeast Fisheries Center. In these deeper water areas, as well, high densities of *N. cara* apparently persisted through the winter months and were present at each station occupied, although the aggregations were somewhat less numerous and colonies appeared smaller than those encountered during fall 1975 (Rogers in press).

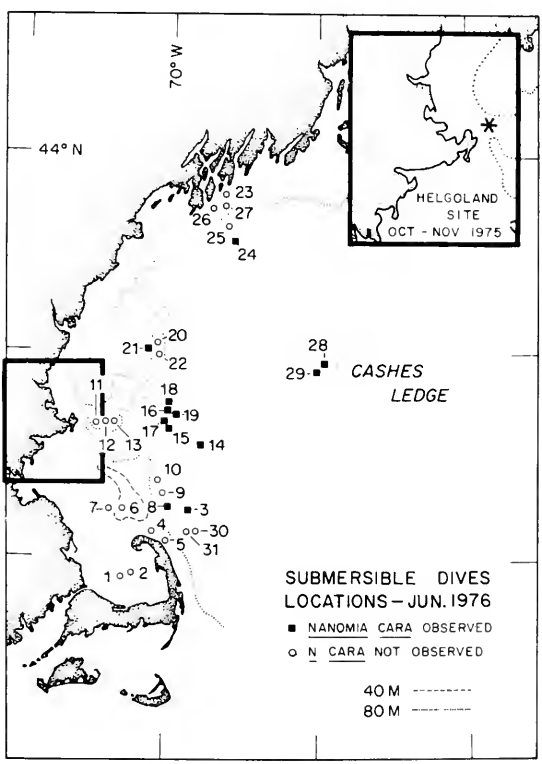

FIGURE 1.—Distribution of siphonophores at dive sites of the submersible *Nekton Gamma* and the position of the *Helgoland* habitat (insert).

The difficulties and limitations inherent in using plankton nets to sample quantitatively populations of siphonophores and other fragile gelatinous zooplankton have been reviewed by Hamner et al. (1975), who suggested in situ scuba observations as an alternative method for studying gelatinous taxa. In the present study we used the two-man research submersible *Nekton Gamma* to estimate the size and density of the *N. cara* aggregations and to evaluate some of the biotic and abiotic factors which might influence their distribution below depths easily accessible to scuba divers. In June 1976 we made six dives along a transect from Provincetown, Mass., to Cape Ann (Table 1, Figure 1). Dives were of 90 to 160 min duration during which we surveyed the water column from surface to bottom. Other observers made 25 additional shorter dives to look for siphonophores at adjacent stations. Observations were narrated and recorded on tape throughout each dive. The submersible pilot relayed information on temperature and depth and this was combined with comments on siphonophore colonies such as size, density, swimming speed, associated species, and other factors of interest. Photographs were taken with a 35-mm camera and a video tape camera with a sound track was also used to record and verify visual observations and estimates. After each dive information was transcribed from the tapes and videotapes were reviewed and discussed by the observers.

Observations

Gulf of Maine surface temperatures in mid-June 1976 ranged from 12.5°C in the Wilkinson Basin

TABLE 1.—Station locations of *Nekton gama* dives to observe depth distribution and density of the siphonophore *Nanomia cara*, 15-28 June 1976.

Dive station	Position		Station depth (m)	Bottom temp. (°C)	Depth (m) where siphonophores were observed	Estimated density (no./m³) of siphonophores
	Lat. N	Long. W				
1	41°56.4′	70°19.7′	38	7.0		
2	41°56.4′	70°18.6′	33	6.6		
3[1]	42°12.8′	69°54.2′	207	7.5	67,101-205	1-2
4	42°05.6′	70°12.0′	37	11.1		
5	42°04.7′	70°06.1′	24	8.0		
6[1]	42°11.4′	70°20.1′	34	5.5		
7	42°11.4′	70°21.9′	46	5.5		
8[1]	42°12.6′	70°03.5′	128	6.0	88-126	0.1
9	42°15.1′	70°07.0′	122	6.9		
10	42°18.8′	70°11.1′	55	6.0		
11	42°38.0′	70°27.6′	107	5.5		
12	42°38.0′	70°28.5′	85	5.0		
13	42°38.0′	70°27.6′	85	6.0		
14[1]	42°28.0′	69°52.6′	201		122-128	1
15[1]	42°36.6′	69°58.4′	180	6.8	146-177	2-4
16	42°38.5′	69°58.0′	136		91-120	1-2
17	42°38.2′	70°00.5′	183	7.0	120-181	7-8
18	42°39.1′	70°00.0′	168	5.5	140-166	
19	42°39.1′	69°58.9′	192	7.0	82-183	0.1
20	43°01.9′	70°05.4′	107	5.5		
21	43°00.5′	70°06.5′	146	5.5	107-122	0.1
22	43°01.0′	70°04.5′	53	6.5		
23	43°45.2′	69°00.0′	58			
24	43°32.0′	69°35.5′	152	6.8	149-150	1
25	43°38.6′	69°38.4′	84	6.8		
26	43°43.1′	69°41.2′	51			
27	43°44.1′	69°40.5′	76	9-10		
28[1]	42°55.0′	69°00.0′	72	7.3	45-70	0.05
29	42°54.4′	69°00.0′	98	7.0	76-85	<0.1
					91-98	1.1
30	42°07.1′	69°50.9′	124	6.0		
31	42°07.3′	69°51.1′	122	7.1		

[1]Dives conducted by authors.

(Figure 1, Station 3) to 17°C off Cape Ann (Station 15). Bottom temperatures at stations deeper than 100 m ranged from 5.5° to 7.5°C (Table 1). In general, the thermocline shoaled from about 75 m off Cape Ann to about 30 m in the Wilkinson Basin (Stations 3, 8, 14-16); the estimated zone of twilight visibility extended to about 135 m. Lateral visibility on most dives exceeded 5 m both above the twilight zone and below it where the lights on the submersible were used.

Large numbers of *N. cara* were observed at all dive stations deeper than 125 m; they were also present, though less dense, at two shallower stations, 28 (72 m) and 29 (98 m) (Table 1). During daylight, siphonophores were observed only below the thermocline. No dives were made at night so it was not possible to predict if transthermocline movement occurs during expected diurnal migrations. They appeared to be distributed in patches both horizontally and vertically. We estimated that patch diameters ranged from 5 to 30 m. At depths where *N. cara* was locally abundant, colonies could be seen out of every viewport (Figure 2). The densest concentrations often occurred between 3 and 45 m above the bottom where we estimated that their densities ranged between 1 and 7 colonies/m³. At Station 29 siphonophores occurred in two distinct layers: sparsely distributed from 76 to 85 m where concentrations were usually <0.1 colony/m³, and more densely aggregated above the bottom where concentrations were about 1 colony/m³. We found no correlation between colony density and substrate type.

Colonies ranged in size from 0.2 to 3.7 m when suspended in fishing posture with the stem and tentacles relaxed. In this configuration the distance between adjacent stem groups ranged from 10 to 15 mm. The largest colonies had over 200 salmon-colored feeding polyps (gastrozooids) and 30 to 40 swimming bells (nectophores). Unless swimming, most colonies oriented with the apical gas-filled float (pneumatophore) and nectophores upward. The rest of the flexible stem, which appeared neutrally buoyant, hung in three-dimensional series of loops and arcs.

In high density localizations of *N. cara*, colonies of several different sizes were often present. In areas of the aggregation peripheral to the highest densities of siphonophores, however, colonies were generally small, i.e., 20 to 40 cm long. Smaller colonies were also found higher in the water column than the larger ones, or occurred singly. All

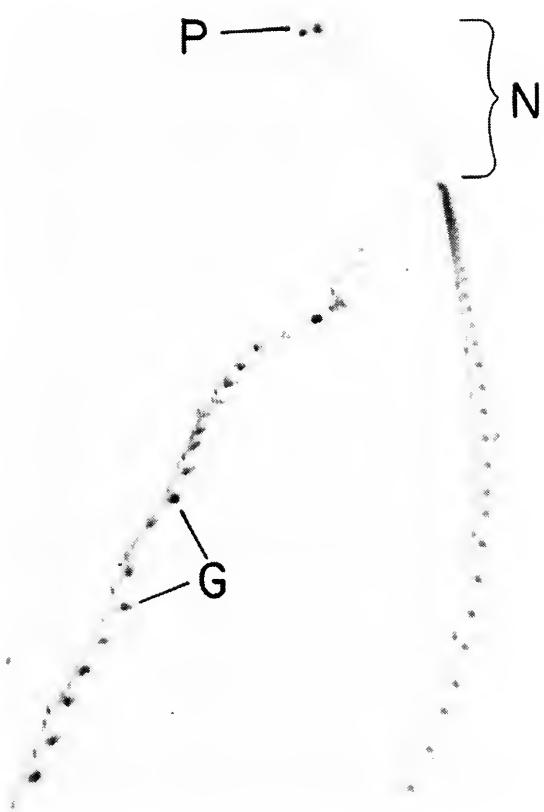

FIGURE 2.—The siphonophore *Nanomia cara* photographed from a viewport of the submersible: p, pneumatophore; n, nectophore; g, gastrozooid. An excellent schematic drawing of this species can be found in Mackie (1964).

colonies of *N. cara* were extremely fragile and isolated pieces of stem were not uncommon. When siphonophores came into contact with the submersible, their tentacles frequently adhered while stem and nectophores fragmented and floated away.

Most colonies were negatively phototactic and contracted their stem and tentacles as they drifted into the radius of the submersible's lights. Contraction usually initiated an escape swimming response. The siphonophores could move rapidly away at any orientation, and some were observed swimming with pneumatophore and nectosome pointed directly downward. We estimated that escape speeds exceeded 20 to 30 cm/s.

The most numerous invertebrates among or adjacent to the densest localizations of *N. cara* were the euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa inermis*; mysids, principally *Neomysis americanus*; and hyperiid amphipods, principally *Parathemisto gaudichaudii* and *Hyperia galba*. We observed one siphonophore which had recently ingested an euphausiid; the others had no prey of this size in their feeding polyps.

Calanoid copepods, among them the large species *Calanus finmarchicus* and *Euchaeta norvegica*, were also locally abundant among the aggregations of *Nanomia cara*. Plankton samples taken in June 1976 showed that these calanoids were rich in lipids, as a heavy slick of oil droplets formed after they were preserved in 4% Formalin.[1] The copepods were apparently being eaten by *N. cara* as fragments of siphonophores removed from the same plankton samples were distended by lipids droplets inside feeding polyps and palpons, where lipids would concentrate during digestion of prey.

Discussion

The density of siphonophore colonies in the Gulf of Maine was considerably greater than Barham's (1963) estimate of the abundance (300 colonies/1,000 m^3) of a congeneric species (*N. bijuga*) in the San Diego Trough. Barham concluded that the gas-filled floats of *N. bijuga* were of adequate dimensions to act as strong sound scatterers and that at these densities this siphonophore could contribute significantly to scattering layer formation. The pneumatophores of *N. bijuga* and *N. cara* are similar in dimension, and aggregations of *N. cara* should be equally effective sound scatterers. In fact, in fall and winter 1975-76, fishermen in the Gulf of Maine reported near-bottom, dense layers of sound-reflecting organisms in areas where trawl nets were being clogged with *N. cara* (F. E. Lux pers. commun.).

The cause of the aggregation of *N. cara* in the Gulf of Maine has not been determined. It is conceivable that widespread reproduction of *N. cara* occurred in fall and winter 1975-76 and that local patterns of circulation aided in concentrating and maintaining the aggregation and prey items. It is clear, however, that localization of siphonophores like *N. cara* at densities exceeding 1 colony/m^3 will interfere with commercial fishing efforts by clogging the meshes of nets trawled for shrimp, silver hake, and redfish. Aggregations of siphonophores

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

may produce serious indirect effects as well. Biggs (1976) has shown that siphonophores like *N. cara* can eat prey ranging in size from zooplankton nauplii to small fish. As Fraser (1962) and Zelikman (1969) have proposed for aggregations of other gelatinous carnivores capable of eating zooplankton and larval fish, areas or seasons in which siphonophores are locally abundant could conceivably suffer dramatic reductions of ichthyoplankton. Lough[2] cited indirect evidence of possible heavy predation by siphonophores upon Atlantic herring larvae based on changes in population densities and distributions of the two species during winter 1975-76 in the Nantucket Shoals-Georges Bank area. Since the Gulf of Maine historically has been an important commercial fishing ground, future research on interaction between siphonophores and ichthyoplankton could lead to a better understanding of the regional food chain and the factors which influence year class success of ichthyoplankton.

Summary

Aggregations of the physonect siphonophore *Nanomia cara* were observed at several dive sites in the Gulf of Maine from *Nekton Gama*. This siphonophore occurs throughout the Gulf of Maine although the vertical and horizontal distribution is patchy. Densities as high as 1 to 7 colonies/m^3 were observed. Colony length ranged in size from 0.2 to 3.7 m and most aggregations included several different sizes. *Nanomia cara* was negatively photoactic and initiated escape swimming response at speeds which exceeded 20 to 30 cm/s. All siphonophores were observed below the thermocline and generally occurred only where water depth was >128 m.

Euphausiids, mysids, and hyperiid amphipods were observed among populations of siphonophores, but we observed only one colony which had eaten prey of this size. In seasons and areas of maximum abundance, siphonophores could conceivably influence the success of a year class of ichthyoplankton by heavy predation as well as cause losses of time and money to commercial fishermen by clogging trawl gear.

[2]Lough, R. G. 1976. The distribution and abundance, growth and mortality of Georges Bank-Nantucket Shoals herring larvae during the 1975-76 winter period. Int. Comm. Northwest Atl. Fish. Res. Doc. 76/VI/123, 30 p.

Acknowledgments

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COMPUTER PROGRAM FOR ANALYSIS OF THE HOMOGENEITY AND GOODNESS OF FIT OF FREQUENCY DISTRIBUTIONS, FORTRAN IV

Routinely, in the study of the dynamics of a fish population, one of the initial steps is the examination of length measurements, viz, the frequency distribution of lengths, average length at age, and differential length distribution by gender. Often, length measurements are the only information available from which to estimate the age structure of the population. Standard statistical techniques such as chi-square tests are often used to analyze length-frequency distributions before pooling data, e.g., to estimate the age structure of the population (Yong and Skillman 1975).

I have developed a computer program which forms frequency distributions from length measurements and then calculates a chi-square statistic which is used to test the homogeneity of the frequencies for the purpose of pooling. Theoretical frequencies from a normal distribution based upon the sample mean and variance of each length-frequency distribution are used in calculating chi-square tests of goodness of fit (Li 1959). The program does not partition the chi-square test of homogeneity but does pool adjacent class frequencies when expected frequencies are small in the case of the test of goodness of fit. Observed adjacent class frequencies are pooled if their expected frequencies are too small and then the test of goodness of fit is calculated. The usual caution against using small samples and expected frequencies less than five in chi-square tests of goodness of fit should be followed (Sokal and Rohlf 1969).

Data required are either individual length measurements in millimeters (from 1 to 1,000 mm) or pairs of length class midpoint and frequency for each of up to five length-frequency distributions per data set; maximum frequency must be less than 1 million. Program storage could be increased to accommodate more than five length-frequency distributions, depending on the capacity of the computer being used. Class interval width must be specified; lengths are then tallied by up to 100 classes which are identified by midpoint on the output. Multiple data sets are processed sequentially without limit.

Output includes listings of arithmetic mean, variance, standard deviation, standard error of the mean, total sample size, and chi-square statistic of goodness of fit for individual groups and for the pooled frequency distribution. The chi-square value for the test of homogeneity is printed with its degrees of freedom; appropriate tables should be consulted for critical values used in testing hypotheses. The goodness of fit test for the pooled data would not apply to the situation where the distribution is clearly multinomial. Histograms of all frequency distributions are produced as full-page printer charts, scaled if necessary to 50 units by up to 100 class intervals. The pooled frequencies and class midpoints are punched on cards to facilitate additional analyses.

The program was developed on an IBM 360/65 OS System[1] and required 56,811 bytes of storage. A copy of the FORTRAN IV source program listing, example input and output, and an instruction manual are available from the author.

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PORTABLE TRIPOD DROP NET FOR ESTUARINE FISH STUDIES[1]

Since the introduction of a portable drop net system by Jones et al. (1963) several designs have been utilized for freshwater and estuarine fish studies (Moseley and Copeland 1969; Kjelson and Johnson 1973; Kushlan 1974; Adams 1976). The value of these sampling systems in estimating the density and biomass of certain fish species has been well documented by these authors (Table 1).

[1]Contribution No. 83 from the Harbor Branch Foundation, Inc.

TABLE 1.—Basic drop net design characteristics of previous studies and the current net system.

Author	Fixed or portable	Mesh size (mm)	Sample area (m^2)	Method of sample collection	Dominant species in the sample
Hellier 1958, 1962	fixed	9.5	252.9 1,011.7	seine	*Anchoa, Mugil* *Lagodon*
Hoese and Jones 1963	fixed	19.0	118	seine	*Lagodon, Gobiosoma, Mugil*
Jones et al. 1963, Jones 1965	portable, helicopter	19.0	100.4	pursed net	*Brevoortia, Mugil, Cynoscion*
Moseley and Copeland 1969	portable, float	10.0	16	pursed net	*Brevoortia, Mugil, Cynoscion*
Kjelson and Johnson 1973	portable, float	6.0	16	pursed net	*Anchoa, Lagodon, Eucinostomus*
Kjelson et al. 1975	fixed	3.0	4	pursed net	*Lagodon, Leiostomus, Anchoa*
Adams 1976	portable, float	3.2	9	pursed net	*Anchoa, Lagodon, Orthopristis*
Current design	portable	3.2	10	seine	*Gobiosioma, Lagodon, Eucinostomus, Anchoa*

A drop net design was needed which would not significantly disturb the water surface and yet take an adequate sample. Some previous portable drop net designs sampled a larger area, but with greater water surface contact (Moseley and Copeland 1969; Kjelson and Johnson 1973). This new gear design allows less water surface disturbance (i.e., noise and shading) than previous drop nets and yet is capable of sampling 10 m^2 without compromising portability. The sample area is rigidly controlled and all fishes are collected from the sample area. The design criteria and success of this drop net system is comparable with, and in some cases surpasses, previous drop net designs in the literature with regard to sample area control and the capture of certain small demersal fish species. This study was conducted to compare this new drop net system with a larger haul seine system sampling 1,160 m^2 used concurrently for shallow water estuarine fish studies. The duration of this study was from April to December 1976.

Drop Net Description and Operation

The drop net apparatus consists of two primary sections: the collapsible aluminum tripod with the trigger mechanism and the drop net (Figure 1). The 5.2-m tripod legs are held together by aluminum hinges at the upper end and three 4.0-mm flexible steel support cables attached to the legs below the upper hinges. Two sheaves are mounted to the upper ends of two of the tripod legs, one to carry the winch line (i.e., upper frame harness line) to hoist the net and the other to carry the drop frame harness line that is released as the net is triggered.

After the sample site is straddled by the tripod, the drop net (3.16 × 3.16 m) is deployed using a pontoon boat. The boat is floated under the open tripod legs to prevent disturbing the bottom within the sample area. To lift the net, the drop frame harness plate and the upper frame harness plate are coupled together with a steel set pin (Figure 1a). The net is then lifted from the boat deck using the winch. After the net is in the set position, the drop frame harness line is set on the trip lever via a set ring (Figure 1b), and the pontoon boat is pushed out from under the net. The trip lever is held down with a notched trigger pin attached to the remote trigger line. The remote trigger line has a fluorescent floating jar attached to the distal end 20 to 30 m from the net apparatus. Once the net is set at the correct height, the steel set pin is pulled, and the drop frame plate and harness are free to fall when the trigger mechanism is tripped. Within 15 min three people can deploy a single net set to drop.

The trigger mechanism and drop frame are released with one pull of the remote trigger line. Once the net has fallen, the drop frame harness is unclipped from its harness plate and a drop net seine, made of tubular aluminum and 3.2-mm mesh netting, is used to seine the enclosure (Figure 1c). The seine fits closely against the inside walls of the drop net, and it is pulled by three people, two on either handle and one pulling a line attached to the bottom, center of the seine. The seine frame is kept firmly on the bottom and a standard five hauls are made to collect the sample. For night operations, an amber flashing light is attached to one tripod leg. Once the net has dropped, a lantern can be hung from the flexible steel support cable. Although night operations may take longer, ½ h is generally taken from the drop to complete sample removal.

To store and disassemble the drop net the pontoon boat is brought under the raised net. The net and frame are lowered onto the deck. The harness

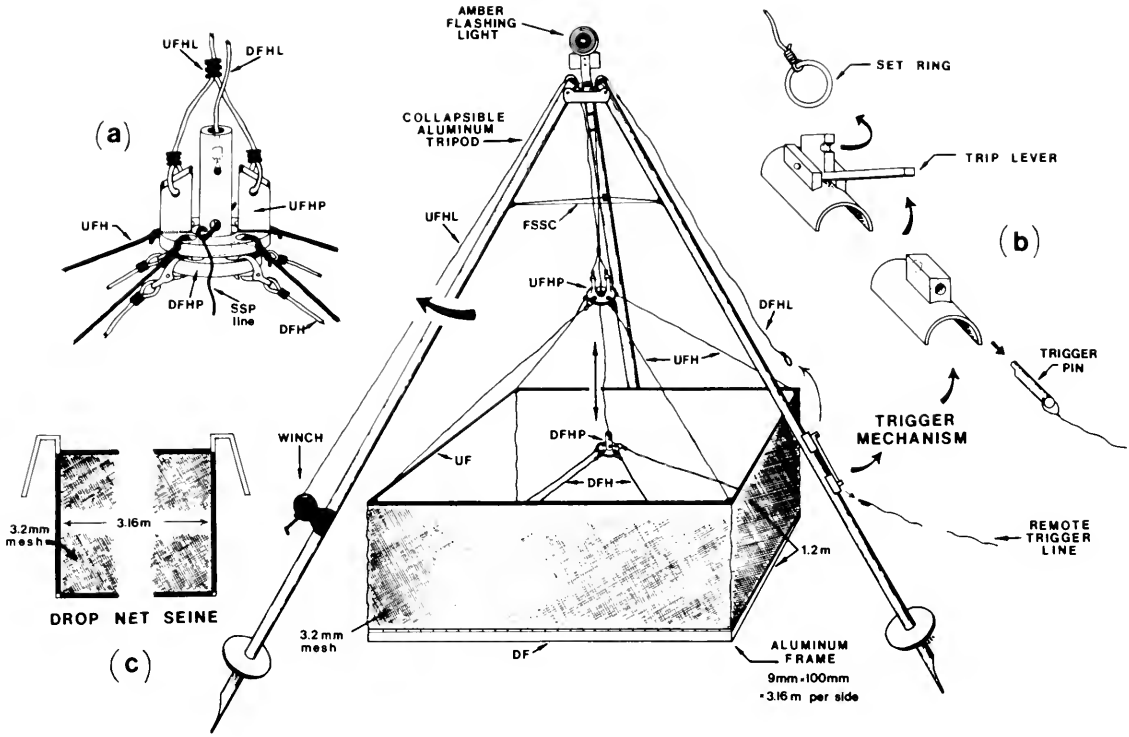

FIGURE 1.—Drop-net apparatus with insets of (a) harness plates, (b) trip lever mechanism, and (c) seine. UFHP = upper frame harness plate; UFH = upper frame harness; DFHP = drop frame harness plate; DFH = drop frame harness; DFHL = drop frame harness line; UFHL = upper frame harness line; UF = upper frame; DF = drop frame; SSP = steel set pin; FSSC = flexible steel support cable.

clips to the upper frame harness and drop frame harnesses are released from their respective plates. The tripod (weight 56.3 kg) can now be collapsed and stowed with the drop net (weight 52.7 kg) on the pontoon boat. Disassembly of the drop net apparatus generally takes 10 min. Not counting the arbitrary waiting period between set and drop, the described procedure takes approximately 1 h.

The drop net was released 1 h after it was set once a month beginning in April 1976. These samples were taken in a shallow seagreass bed (i.e., *Thalassia, Halodule,* and *Syringodium*). This drop net design is limited to depths <1.2 m. A seine haul was made within an hour of each drop net sample in a seagrass bed approximately 75 m from the drop net site. A 62 × 1.8 m bag seine (3.2-mm mesh) was pulled with one end anchored on shore and the seaward end stretched perpendicular to shore. A 15.2 × 1.8 m barrier net (3.2-mm mesh) was set 30.5 m down the beach and parallel to the 62-m seine. The seaward end of the large seine was pulled by hand to the seaward end of the barrier net and then to shore covering approximately 1,160 m^2/haul. The entire seine haul is made within 10 min.

All specimens taken using both drop net and seine were identified, counted, measured, and weighed (wet weight). The percent occurrence was calculated based on the number of samples in which a species occurred out of the total number of samples taken. A comparison was then made between fish samples taken by both gear types (Table 2).

Results and Discussion

The drop net captured fewer individuals and species than the seine and mostly small demersal and semidemersal forms (Table 2). However, the total fish density and biomass values from drop net samples surpassed seine sample values. April to December drop net samples gave fish density values from 1.8 to 19.3 fish/m^2 ($\bar{x}$ = 9.0) and biomass values from 1.3 to 29.4 g/m^2 ($\bar{x}$ = 15.0). In seine samples fish density ranged from 0.09 to 2.14

TABLE 2.—Partial species comparison, numerical catch, fish densities (no./m²), and percent occurrence in samples for simultaneous seine and drop net collections (nine samples each). This is a partial species list, 17 of 61 species taken with the seine and 12 of 29 species taken with the drop net.

Type and species	Seine (10,440 m²)			Drop net (90 m²)		
	No.	No./m²	Occurrence	No.	No./m²	Occurrence
Schooling planktivores:						
Anchoa mitchilli	97,981	9.38	1.00	452	5.58	0.33
A. hepsetus	539	.05	.78	0	—	—
A. nasuta	656	.06	.67	1	.01	.11
A. cubana	248	.02	.44	1	.01	.11
Harengula jaguana	2,725	.26	.67	0	—	—
Opisthonema oglinum	521	.05	.33	0	—	—
Sardinella anchovia	3	.00	.11	0	—	—
Semidemersal predators:						
Bairdiella chrysura	1,102	.11	1.00	14	.16	.22
Cynoscion nebulosus	22	.00	.44	2	.02	.22
Diapterus auratus	944	.09	1.00	0	—	—
Eucinostomus sp.	1,404	.13	1.00	43	.48	.67
Lagodon rhomboides	1,225	.12	1.00	191	2.12	1.00
Lutjanus griseus	23	.00	.89	1	.01	.11
Orthopristis chrysoptera	326	.03	.56	25	.28	.33
Demersal species:						
Achirus lineatus	0	—	—	3	.03	.22
Bathygobius soporator	6	.00	.22	0	—	—
Gobiosoma robustum	632	.06	.44	336	4.15	.89
Gobionellus boleosoma	0	—	—	6	.07	.44
Microgobius gulosus	8	.00	.33	18	.22	.67

fish/m² ($\bar{x}$ = 0.53) and biomass from 1.3 to 4.0 g/m² ($\bar{x}$ = 2.0). The high fish density and biomass values of drop net methods versus lower values using seine methods has been demonstrated in previous studies (Kjelson and Johnson 1973; Kjelson et al. 1975). Schooling, nektonic species (e.g., anchovies and herring) and adults of larger species (>150 mm SL) were seldom taken in the drop net yet proved common in seine samples (Table 2). The drop net bias toward nonschooling fishes or those that do not have a clumped distribution has been documented by Kjelson and Johnson (1973) and Kjelson et al. (1975). However, the drop net designs of Hellier (1958, 1962), Hoese and Jones (1963), Jones et al. (1963), Jones (1965), and Moseley and Copeland (1969) captured large numbers of schooling fishes (e.g., *Brevoortia* and *Anchoa;* Table 1). These schooling fishes, because of their irregular occurrence (Table 2), occasionally presented a problem with subsequent sample analysis (Jones 1965). Small gobies (e.g., *Gobiosoma robustum* and *Microgobius gulosus*) were common in our drop net samples and were only occasionally seen in our seine samples. Most of those fishes captured by the drop net were grass flat residents and resident juveniles of adult populations living elsewhere. The seine not only captured grass flat residents and juvenile fish but adults and juveniles of migratory schooling forms and large top predators (≥250 mm SL).

When catch records of our drop net system are compared with those of others many sample similarities and differences are seen. Hellier's data demonstrates that drop nets with a smaller mesh size will capture a greater fish biomass when the sample area is kept constant (Hellier 1958). The current drop net design incorporates a 3.2-mm mesh (Table 1). This enables the capture of nearly all small fishes (<150 mm SL) present. Very small species (e.g., *Gobiosoma robustum*, 13-30 mm TL) were not commonly captured using other drop net methods, except in the samples taken by Hoese and Jones (1963) (Table 1). *Gobiosoma robustum* is a common seagreass bed resident from Corpus Christi, Tex., to the Indian River lagoon in eastern Florida (Hoese 1966; Springer and McErlean 1961); therefore, it would not be expected in the samples of Kjelson and Johnson (1973), Kjelson et al. (1975), and Adams (1976). Demersal flatfishes (e.g., *Paralichthys, Etropus, Citharichthys, Symphurus,* and *Achirus*) were captured in drop nets used by Jones et al. (1963), Mosely and Copeland (1969), Kjelson and Johnson (1973), Adams (1976), and our design. Juvenile commercial and sport fishes (15-50 mm SL) caught by the current drop net design were *Cynoscion nebulosus, Lutjanus griseus, L. analis, L. synargris, Albula vulpes, Archosargus probatocephalus,* and *Haemulon parrai. Lagodon rhomboides* was also taken in large numbers (15-145 mm SL), showing densities

well over seine estimates. Other authors also found *L. romboides* to be common in their drop net samples (Table 1).

The current drop net system is the only design to use a rigid frame seine and a solid aluminum drop frame in conjunction with 3.2-mm mesh netting. This probably accounts for the goby and flatfish captures and also accurately delineates the sample area. It is possible that the sample area may change due to wind or current effects on falling pursing nets (Table 1; Jones et al. 1963; Kjelson et al. 1975). Disadvantages with the aluminum drop frame are its bulk, limited maneuverability, and operations limited to a level bottom. A collapsible frame or one which can be disassembled may eliminate the maneuverability problem. Moseley and Copeland (1969) indicated that noise and shadows may have affected their samples. We tried to eliminate the shadow effect and noise with as little water surface contact as possible using a tripod which suspended the net over the water with an open center. It may be possible to have vibrations in the tripod apparatus transmitted through the submerged portion of the tripod legs; however, this possibility and its effect is not known. Portable float and portable helicopter drop nets (Table 1) could drop in deeper water (depths of 2.5-4.6 m) than our system (1.2 m). Most other drop net designs require two people to operate. The helicopter drop net requires six while our design requires three. A smaller version of this tripod design would require fewer operators. It takes 60 min to set up, drop, retrieve the sample, and dismantle our drop net without the arbitrary 1 h waiting period. Kjelson and Johnson (1973) and Kjelson et al. (1975) were the only authors to publish operational times and these were 25 min and 15 to 20 min respectively.

The 10-m^2 sample area in the current design is a compromise between maneuverability and sample size. The small sample precludes adequate capture of mobile fishes >150 mm SL. Fishes with a clumped distribution or that form schools will also occur in these drop net samples less frequently than if other gear were used (e.g., seines and trawls). However, to obtain an accurate fish density and biomass estimate in nursery areas or of fish populations in which the adult size is small (e.g., gobioids) the current design has produced adequate samples.

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SURFACE FEEDING BY A JUVENILE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*

Recently Ray and Schevill (1974) summarized information on the feeding habits and feeding behavior of *Eschrichtius robustus*. The gray whale is primarily a bottom feeder whose diet consists mainly of six species of benthic gammaridean amphipods taken in the Bering and Chukchi Seas during the summer months (Zimushko and Lenskaya 1970; Rice and Wolman 1971). It is generally assumed that gray whales fast during migration and while at the breeding grounds along the Mexican coast. Several reports, however, suggest the possibility that feeding may occur occasionally outside of the Arctic region and may include a wide array of different food items, e.g., smelt, anchovylike fish; planktonic crustaceans—*Euphausia* and *Pleuroncodes* (Howell and Huey 1930; Matthews 1932; Gilmore 1961; Balcomb in Ray and Schevill 1974). In addition to these, reports of bits of woods, stones, tube worms, shell, etc., including kelp fragments have been reported in stomach contents of gray whales (Tomilin 1957). However, most of these items are probably attributable to incidental swallowing.

Herein we report observations made on a juvenile gray whale,[1] ca. 6-m long, exhibiting unusual surface feeding behavior in a kelp, *Macrocystis angustifolia,* bed near Refugio Beach State Park, 38 km west of Santa Barbara, Calif. Between 1 and 9 April 1976, four visits were made to the area and a total of 8 h were spent detailing the observed behavior. Throughout the study period the whale's activities were confined to the extensive kelp bed situated between Refugio Beach State Park and Arroyo Hondo—a distance of 3.2 km. This feeding activity was restricted to the kelp canopy and occurred in shallow water (<5-10 m depth) and 50 to 200 m offshore. We last saw the whale on 9 April 1976. Apparently it left the area shortly thereafter as subsequent searches were made on 16 and 18 April 1976.

Description of Feeding Behavior

When first sighted, the whale's head was protruding a meter or more above the surface of the water in the center of a dense kelp bed (Figure 1A). Shortly after surfacing snout first, its mouth opened and a large volume of water and kelp flowed into the oral cavity (Figure 1B). Next the jaws closed (Figure 1C) and in the process a small squirt of "excess" water issued from the most anterolateral margins of the mouth. Within moments entrapped water was forced out of the mouth across the baleen plates through the lips in a strong flush directed posterolaterally (Figure 1D). This sequence was repeated several times before the whale submerged. Prior to submerging, the head was raised at an angle approximately 60° normal to the surface of the water. The body then slid backwards through the kelp canopy with its jaws slightly agape releasing the kelp present in its mouth. Resurfacing generally occurred a short distance away. There was little deviation from this pattern during the entire observation period. Visits were made at all hours of daylight during which the intensity of the feeding behavior appeared consistent.

During a typical 27-min period when the whale was exhibiting feeding behavior, we noted that it emerged in the kelp, fed, submerged, and then reemerged a total of 18 times. A single feeding-submergence interval averaged 90 s, of which 56 s were spent feeding and 34 s submerged. Frequency of breaths during this period were recorded for 11.5 min. The average time from inhalation to exhalation was 48 s; the maximum was 70 s and the minimum 20 s. The act of breathing (i.e., exhaling, then inhaling) at the surface averaged 2 s. These data clearly demonstrate that the whale was quite active in its behavior.

At first impression the whale appeared to be "biting and eating" the kelp, but on closer inspection the fronds and stipes of the kelp incurred little if any damage. While there is no direct evidence available from stomach analyses, we suggest the whale's activities among the kelp were directed to procuring quantities of the small kelp mysid crustacean, *Acanthomysis sculpta.* Sampling of the mysid fauna was accomplished using a 50-gal plastic trash can which was lowered into the water at a horizontal angle from the boat in such a fashion that the surface water down to 30 cm flowed freely into the container. The mysids were subsequently filtered out, counted and volume determinations made. A total of four replicates provided a conservative estimate of 5 to 10 mysids/l at the canopy surface. The size range for individual mysids in our sample was 6 to 12 mm,

[1] On a number of occasions the whale laid nearly horizontal on the surface of the water only a meter from our boat (7-m Boston Whaler), thus we were able to make a reasonably accurate estimate of it's overall length. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

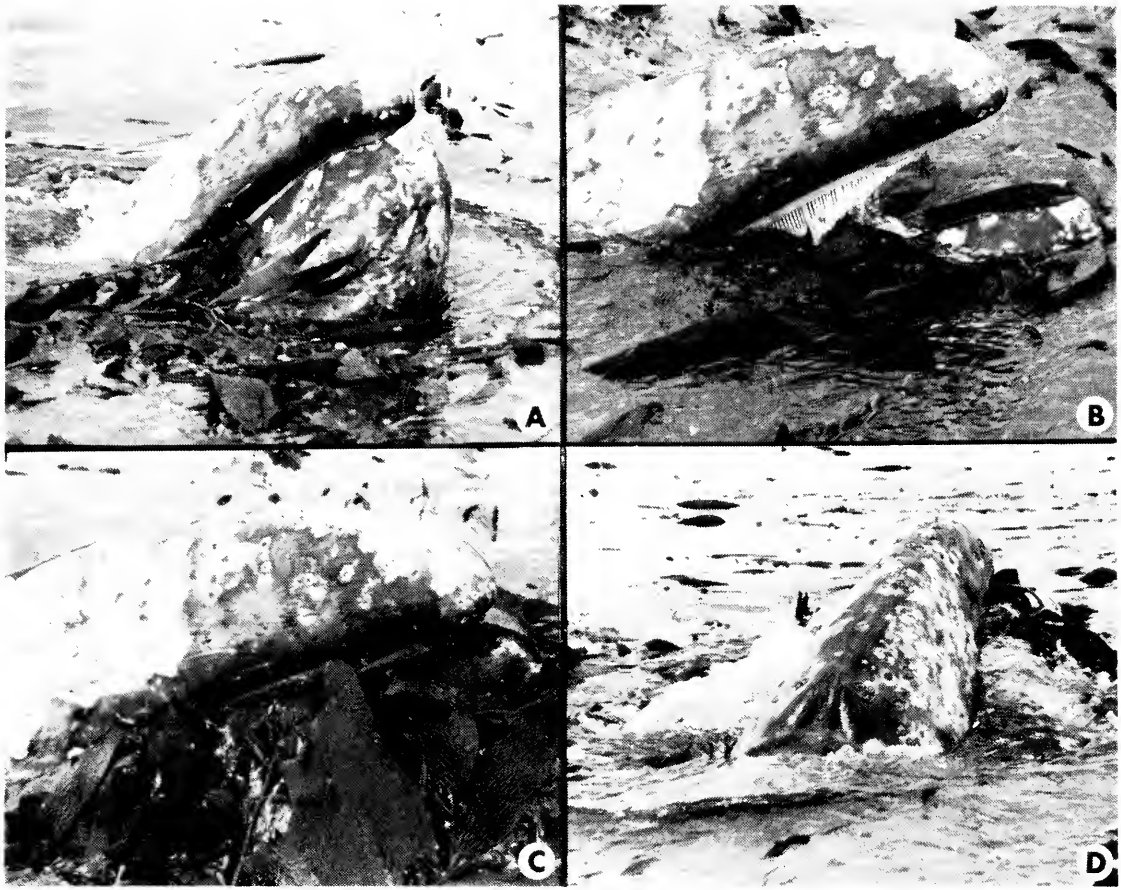

FIGURE 1.—Time sequence photographs showing the observed feeding behavior: A, the gray whale first emerging in the kelp canopy; B, jaws extended open allowing surface water to enter mouth; C, mouth closed entrapping water and kelp fronds; D, water expelled through baleen in posterolateral direction.

which falls well within the size range of the gammaridean amphipods reportedly composing 95% of the whale's diet in Arctic seas (Rice and Wolman 1971).

In addition to these observations, we noted that during feeding, water was expelled predominately through the right side of the mouth. Kasuya and Rice (1970) found that of 34 whales examined, 31 showed disproportionate wear of the baleen on the right side. Analysis from movie footage (8 mm) taken by us shows that of 31 consecutive expulsions, water passed exclusively from the right side 20 times—in the remaining cases it was passed equally or nearly equally from both sides. At no time, however, was the water expelled on the left side exclusively. It is not clear what causes the wear on the baleen plates; perhaps it is unequal mechanical rubbing action of the tongue pushing water through the plates. Possibly related to this are observations made by Ray and Schevill (1974) on the captive juvenile gray whale, Gigi. At first this whale was hand fed by her trainers on the left side exclusively. Later, after hand feeding was discontinued and feeding became voluntary, food continued to be ingested solely on the left side.

Interpretations and Conclusions of Observations

Several aspects concerning the physical characteristics of our whale are worthy of comment. The mean length at birth (January) for a normal gray whale is reported to be ca. 4.9 m and by the time of weaning (August), the animal can be expected to reach a total length of 8.5 m (Rice and Wolman

1971). The size of our whale (ca. 6 m) would indicate a juvenile at the nursing stage. However, during our observations no large whale was noted in the vicinity which could have been interpreted as a parent. Thus we suggest that this animal may be a yearling runt. Further evidence in support of this notion is the fact that the epizoic barnacles (*Cryptolepas rhachianecti*) were of a large class (>2.5 cm), too large to be considered 4 to 5 mo of age, which would be the approximate age of the whale were it born in the most recent calving season. Also, since all barnacles were of only one distinct size class we further suggest that the whale we observed had not been south to the breeding grounds this year (1975-76). Rice and Wolman (1971) stated that northbound whales have two distinct size classes of barnacles, one adult and one juvenile (2-3 and 0.3-0.5 cm in diameter, respectively).

We can only speculate on the events which may have occurred prior to our observations (e.g., abandonment or loss of the mother during the northbound journey in the previous year and consequent exploitation of an alternative food source, i.e., kelp mysids by a preweaned juvenile whale). However, we have been able to ascertain by comparative photographic analysis of barnacle scar patterns (Figure 2) that this whale was present in the San Diego area (approximately 320 km south of Santa Barbara) from early January to early February 1976 (P. Zovanyi and H. Hall pers. commun.)—just over 4 mo prior to our encounter in April.

In conclusion, this report would seem to indicate that gray whales can display plasticity in their feeding behavior. While conclusive evidence of feeding is lacking (i.e., gut content analysis), this appears to be the most logical explanation accounting for this unusual behavior.

Acknowledgments

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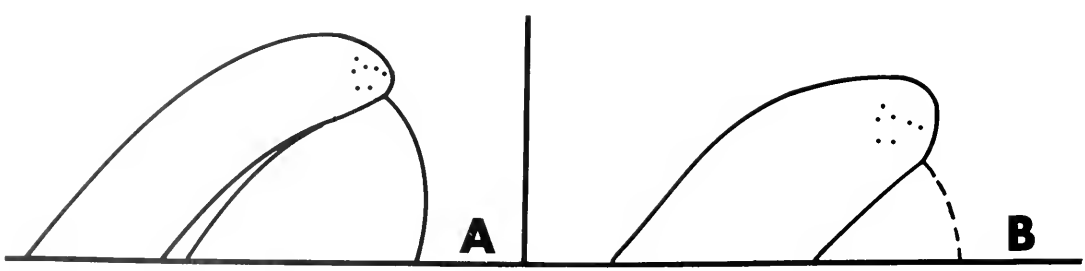

FIGURE 2.—Line drawings of barnacle scar patterns on a gray whale: A, after Figure 1A, seven barnacle scars on the gray whale seen in Santa Barbara in April 1976; B, drawn from photograph taken by H. Hall (Graves 1976) of a gray whale seen in San Diego in January 1976. The same seven barnacle scars are evident.

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HOMING OF MORPHOLINE-IMPRINTED BROWN TROUT, *SALMO TRUTTA*

Homing for the purpose of spawning is well documented for lake-run brown trout, *Salmo trutta* (Stuart 1957; Niemuth 1967), but the mechanism by which they find their natal tributary is not understood. Our own recent studies on related species—coho salmon, *Oncorhynchus kisutch*, and rainbow trout, *Salmo gairdneri*—suggest that they become imprinted to the odor of their natal tributary when they begin their downstream migration and later use this information for homing (Hasler and Wisby 1951; Scholz et al. 1973, 1975, 1976; Cooper and Scholz 1976; Cooper et al. 1976). In these experiments 18-mo-old hatchery-raised fish were exposed to a synthetic chemical, morpholine, for 40 days and then stocked in Lake Michigan. During the spawning migration the fish homed to a simulated home stream which was scented with morpholine. Since the life cycle of migratory brown trout is similar to that of coho salmon and rainbow trout, we conducted the present study to determine if odor imprinting could be extended to brown trout. The methods used in this study were similar to procedures reported by Cooper and Scholz (1976) since both experiments were conducted concurrently.

Methods

In 1972, hatchery-raised, 18-mo-old brown trout fingerlings were transported to South Milwaukee, Wis. (Figure 1). The fish were marked with fin clips, divided into three groups of 300 each, and held in separate tanks at the South Milwaukee Water Filtration Plant. Lake Michigan water was supplied to all three tanks from an intake crib

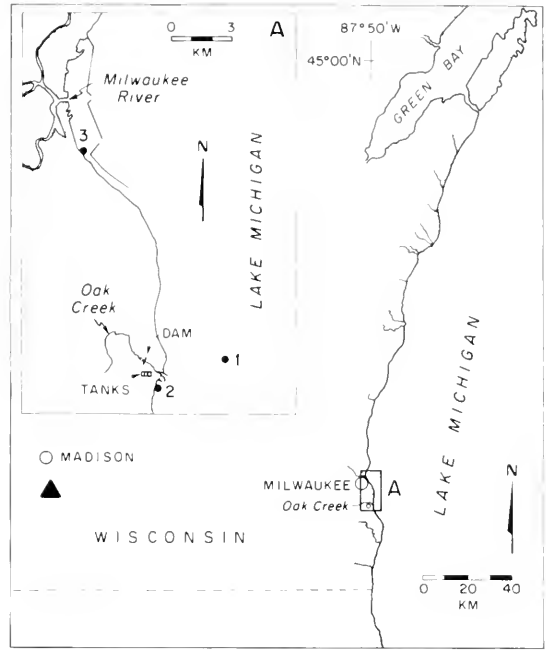

FIGURE 1.—Research area, South Milwaukee, Wis. (after Cooper et al. 1976). The solid triangle indicates the location of the hatchery where the fish were reared. Inset (A) shows detail of: 1) the water intake for the tanks at the South Milwaukee Water Filtration Plant, 2) the Oak Creek stocking site, and 3) the Milwaukee Harbor stocking site.

located 1.5 km offshore. Morpholine (C_4H_9NO) was metered into one tank for 34 days in May and June. This period was selected because it is the time when brown trout would normally begin their downstream migration (Stuart 1957; Niemuth 1967). A concentration of 5×10^{-5} mg/l morpholine was maintained in the tank throughout the exposure period.

The morpholine-exposed group and one unexposed control group were then stocked in Lake Michigan at Milwaukee Harbor, 13 km north of Oak Creek (Figure 1). The second control group was released at the mouth of Oak Creek. During the spawning migration in fall 1972 and 1973, morpholine was metered into Oak Creek at the same concentration used for imprinting. The stream was surveyed for marked fish by gillnetting, electrofishing, and creel-census methods (summarized in Table 1). Fish were unable to move past a dam situated 1.5 km from the mouth. Surveys began before the spawning migration started and continued until no fish were left in the river. The results are recorded in Table 2.

TABLE 1.—Summary of effort spent in monitoring Oak Creek during the spawning migrations of brown trout in fall 1972 and 1973. Creel-census surveys were conducted three to five times each day and electrofishing surveys were made once or twice each week. A total of 51 marked brown trout were caught by anglers; 17, by electrofishing; and 2, in gill nets.

Fall	Creel census	Electrofishing	Gill net
		Number of trips	
1972	274	11	62
1973	451	24	54

TABLE 2.—Recoveries of brown trout at Oak Creek in fall 1972 and 1973 from those released in spring 1972. Morpholine-exposed and control fish were released 13 km north of Oak Creek and a second control group was released at the mouth of Oak Creek. Fin clip: RP, right pectoral; LP, left pectoral; LM, left maxillary.

Experimental group	Fin clip	Number released	Number recovered			Percent of fish stocked
			1972	1973	Total	
Morpholine	RP	300	23	30	53	17.7
Control	LM	300	1	2	3	1.0
Oak Creek	LP	300	3	11	14	4.7

Results

A total of 53 morpholine fish (17.7% of the total number originally stocked) were captured as compared with 3 control trout (1.0%) released at Milwaukee Harbor and 14 control trout (4.7%) released at Oak Creek. Thus, the data show that morpholine-exposed brown trout returned to the scented stream in larger numbers than either control group. Both control and morpholine fish experienced uniform stocking procedures after the initial treatment. If the selection of the morpholine-scented stream were attributed to a cue learned after the treatment, we would have expected to capture as many control fish as morpholine-treated fish in the scented stream. The fact that this was not the case implies that the cue was morpholine. Therefore we conclude that morpholine-exposed brown trout used morpholine as a cue for homing. To locate the scented stream morpholine fish were able to search a distance of at least 13 km. This experiment should be repeated because of the low numbers of fish stocked but the results are of interest because of the high percentage of morpholine-exposed fish captured in the scented stream.

Discussion

In view of our findings it is of interest to consider two unpublished observations made by Stuart[1] on homing of brown trout at Dunalastair Reservoir in Scotland. In one case brown trout were marked in one branch of a forked stream which flowed into the reservoir. After the fish had migrated to the reservoir, all of the water from the home fork was diverted into a new channel. The original channel was also maintained with water from the second fork. During the spawning migration, adult trout homed to the new channel in preference to the channel by which they had entered the reservoir.

In the second instance Stuart reported that, when a different stream broke its banks, the stream bed below the break dried up and the entire flow of water was diverted into a marsh through which it percolated into the reservoir. During the spawning migration, brown trout congregated off the marsh where the percolating water entered the reservoir and not off the dry stream mouth.

Both of Stuart's observations clearly indicate that the fish homed to water originating from the home tributary, rather than to a specific home location and are, thus, consistent with our conclusion that it is a characteristic of the home water, specifically odor, which provides brown trout with homing cues.

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DIURNAL VARIATIONS IN CATCHES OF SELECTED SPECIES OF ICHTHYONEUSTON BY THE BOOTHBAY NEUSTON NET OFF CHARLESTON, SOUTH CAROLINA[1, 2]

The Boothbay neuston net is becoming a standard gear for collection of ichthyoneuston. Sherman and Lewis (1967) reported using this gear for collection of lobster larvae. Personnel participating in Cooperative Investigations of the Caribbean and Adjacent Regions (CICAR) activities have prepared a "Plan for Sampling the Early Development Stages of Pelagic Fish during CICAR Operations" which describes the use of the neuston net (FAO[3]). The Boothbay neuston net, initially adopted as the standard for the Marine Resources Monitoring, Assessment and Prediction Program (MARMAP), consists of a pipe frame 2 m wide by 1 m deep with an 8.5-m long net.[4] Because little was known concerning the sampling performance of this gear, an experiment was designed to test the operating characteristics of two types of frame (galvanized pipe and aluminum pipe) and two lengths of net (4.9 m and 8.5 m with ratios of mouth to open mesh aperture areas of 1:6 and 1:11, respectively). The nets were of 0.947-mm Nitex[5] mesh.

The results of the experiment defining the operating characteristics of the two types of frame and two lengths of net were described by Eldridge et al. (1977). The present report will describe mainly diurnal variations in catches of ichthyoneuston during the latter experiment, which was conducted during 9-15 July 1973 utilizing the RV *Dolphin*.

Materials and Methods

The neuston net was towed from a boom extending 3 m from the starboard side of the RV *Dolphin*, and the ship was ordered in an arc of radius 1 n.mi. or less to starboard to keep the net mouth out of the ship's wake. The net was towed so that one-half the height (0.5 m) was in the water.

Towing speeds of 1, 2, and 3 m/s were employed with a total of 48 tows being conducted. Twenty-four daylight tows were made between 1107 and 1627 EST and 24 night tows between 2206 and 0432 EST. After setting (which took an average of 29 s), nets were towed 10 min and then retrieved

[1]Contribution No. 74 from the South Carolina Marine Resources Center. This work is the result of research sponsored by the MARMAP Program, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service under Contract No. 4-35137. MARMAP Contribution No. 117.

[2]Contribution No. 451 from the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, Fla.

[3]FAO-UNDP Fisheries Program, Mexico City. 1970. A plan for sampling the eggs and larvae of the fishes of Mexican waters. Unpubl. manuscr.

[4]MARMAP is now using a 0.5 × 1 m neuston net.

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

(average time of retrieval was 32 s). After each tow, the catch was drained on a 0.85-mm mesh sieve and preserved in 5% buffered Formalin. Sorting and identification of ichthyoplankton occurred at the Marine Resources Research Institute (MRRI). Fork lengths were measured in forked tail species; total lengths in all others. Relative volume of water strained was determined by the formula: Relative volume strained = (Speed)(Total tow time)(Average fraction of net in water). The reader should consult Eldridge et al. (1977) for further details concerning material and methods as well as the experimental design.

Results

The 4.9-m net was superior to the 8.5-m net in both ease of handling and minimizing damage to specimens after capture. There was no significant difference in catching ability of the two nets although the 4.9-m net actually caught more specimens during the experiment (Eldridge et al. 1977). The galvanized pipe frame was superior to the aluminum.

A total of 10,621 specimens of ichthyoneuston were collected. The 20 most abundant taxa made up 85.6% (9,088) of the total number of specimens. The remaining 92 taxa composed 14.4% (1,533) of the total (see Table 1 for most numerous taxa collected).

Analyses of variance and covariance tests revealed that total tow duration, speed, and relative volume strained did not vary significantly between day and night tows (Eldridge et al. 1977). Thus, catches between diurnal periods did not appear biased by the conduct of the experiment.

TABLE 1.—Numbers of individuals of selected ichthyoneuston collected in neuston experiment (+ = significantly more abundant for day or night, or no significant difference in catch between day and night at 5% level of significance).

Taxon	Total number caught	Number in night catches	Number in day catches	Day	Night	Both	Range total length (mm)	Number of tows present
Auxis sp.	3,576	3,573	3		+		2-16	26
Exocoetidae	1,245	700	545		+		4-83	45
Scombridae	907	906	1		+		4-15	8
Gerreidae	513	229	284			+	5-14	43
Tetraodontidae	409	15	394	+			4-14	29
Mullidae	348	7	341	+			5-21	29
Mugil curema	230	77	153	+			6-18	40
Priacanthidae	223	222	1		+		3-30	25
Coryphaena hippurus	217	188	29		+		9-62	34
Caranx crysos	191	67	124	+			7-37	42
Gobiidae	180	179	1		+		5-14	22
Anguilliformes	143	142	1		+		6-84	24
Carangidae	128	125	3		+		3-5	21
Psenes maculatus	125	125	0		+		6-49	20
Hemiramphidae	124	97	27		+		6-57	31
Decapterus punctatus	118	46	72	+			24-47	32
Monacanthus setifer	103	11	92	+			9-35	30
Scorpaenidae	102	92	10		+		3-11	29
Holocentridae	93	93	0		+		3-17	21
Caranx sp	91	87	4		+		4-32	24
Synodontidae	88	88	0		+		5-32	18
Euthynnus alletteratus	67	67	0		+		3-10	18
Monacanthus hispidus	64	3	61	+			14-58	22
Opisthonema oglinum	62	55	7		+		5-15	20
Istiophorus platypterus	59	26	33			+	3-18	26
Decapterus sp.	54	53	1		+		7-11	18
Coryphaena equisetis	54	50	4		+		8-18	21
Aluterus sp.	49	6	43	+			1-105	17
Trachinotus falcatus	48	31	17		+		7-18	19
Balistidae	46	21	25			+	3-12	23
Pomacentridae	46	29	17			+	5-20	28
Labridae	44	43	1		+		5-18	18
Scomberomorus cavalla	41	39	2		+		5-10	18
Serranidae	40	40	0		+		3-16	15
Cynoglossidae	39	39	0		+		5-16	16
Kyphosus sp.	39	15	24			+	7-21	18
Selar crumenophthalmus	38	18	20			+	6-69	15
Bothus sp.	34	33	1		+		3-22	16
Canthigaster sp.	33	31	2		+		3-17	14
Monacanthus sp.	33	3	30	+			8-30	11
Dactylopterus volitans	30	3	27	+			8-30	11
Seriola sp.	26	4	22	+			5-18	14
Seriola rivoliana	25	0	25	+			14-43	9
Caranx hippos	23	21	2		+		6-32	14
Syngnathidae	22	19	3		+		7-69	15
Apogonidae	22	22	0		+		4-10	12
Rachycentron canadum	19	19	0		+		6-13	11

Partial correlation analyses indicated that catches of flyingfishes, Exocoetidae, and silver driftfish, *Psenes maculatus,* were positively correlated with speed. Catches of the planehead filefish, *Monacanthus hispidus,* pygmy filefish, *M. setifer,* and dolphin, *Coryphaena hippurus,* increased with concentrations of sargassum weed which corresponds to earlier observations by Dooley (1972). Catches of Exocoetidae were negatively correlated with manatee grass (Eldridge et al. 1977).

Chi-square analyses indicated that catches of 41 taxa were significantly affected by changes in diurnal period (Table 1). Catches of 29 were greater at night, whereas collections of 12 were greater during daylight hours. There was no evidence to suggest that catches varied significantly between diurnal periods for six species groups.

Data in Table 1 indicate that specimens of *Auxis* sp., Scombridae, Priacanthidae, Gobiidae, Anguilliformes, Carangidae, *Psenes maculatus,* Holocentridae, *Caranx* sp., Synodontidae, *Euthynnus alletteratus, Decapterus* sp., *Coryphaena equisetis,* Labridae, *Scomberomorus cavalla,* Serranidae, Cynoglossidae, *Bothus* sp., *Canthigaster* sp., Apogonidae, and *Rachycentron canadum* could be considered "faculative neuston" (Hempel and Weikert 1972). Specimens of Gerreidae, *Istiophorus platypterus,* Balistidae, Pomacentridae, *Kyphosus* sp., and *Selar crumenophthalmus* appear to be "euneuston" as defined by Hempel and Weikert (1972). Similarly, *Mugil curema, Caranx crysos,* and *Decapterus punctatus* appear to be "pseudoneuston."

Mugil cephalus was identified as an euneustonic species by Hempel and Weikert (1972); whereas *M. curema* in our samples appeared to be pseudoneustonic. The difference may be real because different species are involved or simply a sampling artifact. Similarly, although young stages of Exocoetidae were reported as rarely encountered and as concentrating at the surface during daytime by Hempel and Weikert (1972), Exocoetidae were the second most abundant taxa in our samples and were taken mostly at night. The reason for this is unknown, but may be due to differences in location, species sampled, or random error associated with sampling of ichthyoneuston.

Tetraodontidae, puffers, were taken most often during the day and were positively correlated with density of manatee grass.

Results of the neuston gear experiment indicated that 1) the 4.9-m net is the superior net for routine surveys, and 2) choice of sampling hours should take into account variation in catches associated with changes in light conditions.

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We thank members of the crew and scientific party of RV *Dolphin,* who performed the field work, especially Bruce Stender, Bill Leland, and Oleg Pashuk. Thanks are also due to Howard Powles, Paul Sandifer, and Edwin B. Joseph, who reviewed the manuscript and to Patricia Dupree and Lexa Ford who typed the manuscript.

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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.

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Vol. 76, No. 2 April 1978

Continued on back cover

Seattle, Washington

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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.

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CONTENTS

Vol. 76, No. 2 April 1978

(Continued on next page)

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ASPECTS OF ESTUARINE INTERTIDAL ECOLOGY OF JUVENILE STRIPED MULLET, *MUGIL CEPHALUS*, IN HAWAII[1]

PETER F. MAJOR[2]

ABSTRACT

Behavior and distribution of schools of young striped mullet, *Mugil cephalus*, were examined in the field and laboratory. Prejuvenile fish approximately 20 mm standard length leave the open ocean to enter intertidal estuarine regions, where they select the shallowest water, areas with extensive diel temperature and salinity fluctuations. At about 50 mm standard length, the mullet move into deeper intertidal waters. It is at this size that mullet are thought to have completed their metamorphosis to juveniles. In a vertical thermal gradient, fish generally <50 mm standard length selected final mean temperatures of 30.0°-32.4°C at the salinities tested (0, 15, 34‰). In the field, they were found in water with high (34.0°-37.2°C), often near lethal (39.0°-42.5°C), temperatures in shallow pools with salinities of 2-30‰. Juveniles generally >50 mm experimentally selected final mean temperatures of 29.0°C at 34‰ salinity to 19.5°C at 0‰ salinity. In the field, fish ≥50 mm remained seaward of the tide line in water of lower and more uniform temperature and higher and more uniform salinity than those recorded for mullet <50 mm. Mullet <50 mm occur seasonally when there are a maximum number of low tides ≤0.0 mm and a minimum number of high tides ≥0.6 m. This allows the mullet increased time to feed undisturbed in areas where there are no predators and intraspecific and possible interspecific competitors for food and space. By the time fish reach 50 mm standard length, the tidal situation changes, allowing predators and competitors access to the shallow areas during low tide. When in the presence of predators, the schooling habit increases chances of survival for individual mullet.

The marine environment includes the highly complex estuarine and intertidal habitats, which undergo continuous fluctuation. Organisms dwelling within these areas must be able to tolerate or escape from the consequences of extreme temperature and salinity oscillations brought about by tidal and meteorological changes. Coral and rocky intertidal tidepools and the estuarine environment serve as nursery and feeding grounds for the young of many species of fishes (Randall 1961; Norris 1963; Lauff 1967; Carr and Giesel 1975).

The purpose of this study was twofold: to determine whether young striped mullet, *Mugil cephalus* Linnaeus, select specific environmental conditions, particularly with respect to temperature and salinity, as found in intertidal estuarine environments in Hawaii, and to explore the possible causal mechanisms that might lead to the selection of such conditions. An experimental vertical thermal gradient (use of such gradients was reviewed by Mantelman 1958; Ivlev and Leizerovich 1960; Fry 1964) in a tank was used to study the relationship between salinity and temperature and the distribution of schools of young striped mullet, and field observations were made of the distribution, feeding, and predator-prey behavior of schooled mullet.

METHODS AND MATERIALS

Field Sites and Capture of Fish

Young striped mullet were observed and collected in estuarine intertidal habitats at a number of locations on the island of Oahu (Figure 1) in the Hawaiian Archipelago during 1972 and 1973. All experimental fish were captured with hand or beach seines near stream mouths or springs and on tidal mud flats in Maunalua Bay on the southeast side of the island. Schools were usually caught in the morning at low tide and transported <16 km to the Oceanic Institute, Makapuu, Oahu.

Observations were made along Wailupe Beach, Wailupe Stream, and Kuapa Pond Streams (Hawaii Kai Development drainage culverts) in Maunalua Bay, and along Kahana River and a silted Hawaiian fishpond in Kahana Bay on the east side

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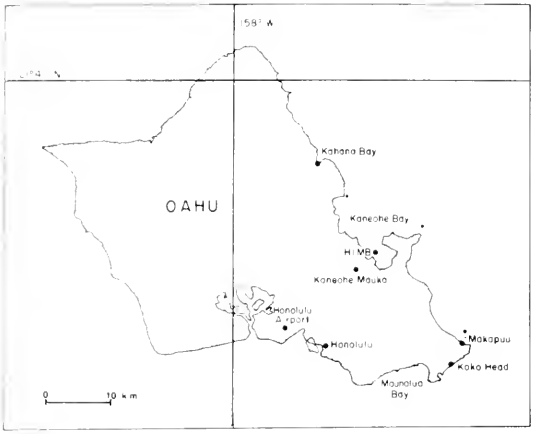


FIGURE 1.—The island of Oahu, Hawaii, showing the major study areas and the locations at which environmental data were collected.

of Oahu. Observations were made primarily during daylight hours, but a few night observations were made as well at Kahana River and Wailupe Beach. Field observations were recorded as I followed at a distance schools of mullet as they swam about estuarine intertidal regions and estuarine streams. Information about the distribution of mullet was also collected by using seines. Behavioral and distributional records were kept and the temperature and salinity of the water through which the fish passed were measured with a telethermometer and compensated salinity refractometer, respectively.

Young *Mugil cephalus* were distinguished and differentiated from the young of a second sympatric species of mullet, *Chelon engeli*, an introduced species (Randall and Kanayama 1972), by differences in body pigmentation pattern and opercle coloration. In addition, young *C. engeli* ≤50 mm standard length (SL) occurred in the intertidal estuarine regions predominantly during the summer and fall, whereas, striped mullet predominated in the winter and spring months. Only observations of mullet that were unquestionably identified as striped mullet were used in this report.

Experimental Methods

Experiments were carried out at the Oceanic Institute during 1972 and 1973 (Table 1). An experimental thermal vertical gradient was established in a 566-l cylindrical Plexiglas[3] tank, 91 cm high and 89 cm in diameter, inside a lighttight enclosure (Figure 2). Epoxy-coated copper coils spiraled around the inside of the tank, having entered through the surface above and through the side at the bottom. These separate sets of coils exited at midtank through the side. Pumps con-

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

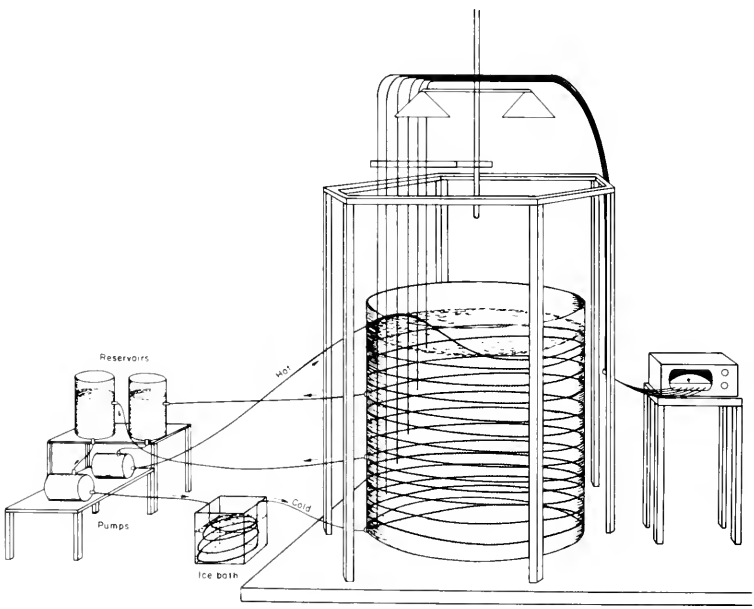


FIGURE 2.—Experimental apparatus (diagramatic). Light excluding sides and covering have been removed from frame.

TABLE 1.—Summary of experimental conditions and fish statistics.

Experimental salinity (‰) (actual test salinity)	Month and year of experiments	Min-max tank temp (°C)	Number fish in size range (mm SL)								Length to nearest mm		Total number fish	Experimental group code (see Figure 3)
			17-19	20-29	30-39	40-49	50-59	60-69	70-79	80-130	Mean	(range)		
34(32)	Feb. 1972	16.8-36.0	2	36							24	(19-28)	38	A1, 2, 3
32	Mar. 1972	15.1-38.6		39	11						27	(21-38)	50	
34	Mar. 1972	17.0-40.1		3	29	2					34	(29-43)	34	
			2	78	40	2					28	(19-43)	122	
34(33)	May 1972	17.8-40.8			7	29	2				42	(37-52)	38	B1, 2, 3
33	May 1972	17.5-41.0				14	17				51	(46-59)	31	
					7	43	19				46	(37-59)	69	
34(36)	July 1972	15.8-39.2					5	4	7	2	68	(55-83)	18	C1, 2, 3
34	July 1972	15.0-39.2					7	3	10	11	75	(56-98)	31	
32	Mar. 1973	15.0-37.8				1		5	9	22	80	(48-103)	37	
32	Mar. 1973	17.0-40.0								20	109	(82-129)	20	
						1	12	12	26	55	82	(48-129)	106	
15(16)	Jan. 1972	16.9-40.0		13	3						27	(24-31)	16	D1, 2, 3
(14)	Mar. 1973	13.0-39.0	1	39							26	(19-29)	40	
(15)	Mar. 1973	13.2-39.9		27	23						28	(20-39)	50	
			1	79	26						26	(19-39)	106	
15(14)	Aug. 1972	15.5-39.8						1	3	18	88	(69-114)	22	E1, 2, 3
15	Mar. 1973	14.1-39.8							1	10	98	(75-125)	11	
								1	4	28	92	(69-125)	33	
0	Feb. 1972	15.9-36.9		26	4						26	(22-34)	30	F1, 2, 3
·	Mar. 1972	16.4-38.9	2	36							22	(19-26)	38	
·	Mar. 1972	16.0-40.1	1	47	10						27	(17-34)	58	
·	Mar. 1973	14.8-39.0		35	2						26	(21-31)	37	
			3	144	16						24	(17-34)	163	
0	May 1972	17.0-38.5			10	19	4				43	(35-51)	33	G1, 2, 3
0	Jan. 1973	18.8-38.2							1	35	98	(76-118)	36	H1, 2, 3
·	Mar. 1973	16.2-38.6								16	102	(87-130)	16	
									1	51	99	(76-130)	52	

nected to reservoirs circulated water, chilled as it passed through a set of coils in an ice bath, before entering the bottom of the tank, and water heated by a braided glass heating tape wrapped around a section of the coil, before it passed into the tank at the surface. The reservoirs allowed air bubbles to escape and the addition of water to the coils.

Vinyl-coated thermistor probes (and leads), extending through plastic tubes to various levels in the tank, ran above the top of the tank and out to a telethermometer recorder.

Fine mesh plastic window screen was attached to the inside circumference of the coils to keep fish in the central area of the tank. The volume of water in the tank available to the fish was approximately 486 l, 88 cm in diameter and 80 cm deep. Observations were made through narrow eye-width slits cut at various levels in each side of the enclosure. A light-excluding cover surrounded the observer during observations. The viewing slits were closed when not in use.

Water samples were taken from the surface, middepth, and bottom before and after each experiment for oxygen, pH, and salinity analysis. Oxygen measurements could not be made continuously during the experiments, but oxygen measurements before and after each experiment did not change noticeably. In addition, respiratory movements of mouth and opercles, which might have been indicative of oxygen deficiencies, in the mullet did not change with increased heating. The above measurements were made primarily to ensure that mullet were not orienting to factors other than temperature.

Illumination was provided by two 15-W incandescent light bulbs fixed in reflectors 84 cm above the surface of the water. Due to the position and low wattage of the light sources, a light gradient was established in the tank. The behavioral and distributional responses of the fish in a continuously changing thermal environment indicated that orientation to temperature and not light gradients occurred. The same observations were used to control for any orientation to pressure gradients, which inevitably existed in the 80-cm deep tank.

One of three experimental salinity conditions, freshwater (range 0-2‰), 15‰ (range 14-16‰), and 34‰ (range 30-36‰), was established prior to placing the fish in the tank. Freshwater was

thoroughly mixed with seawater of 36‰ salinity until a desired salinity was obtained in the tank. Frequently, schools of fish in the field were not caught in water of identical salinity to that used experimentally. Before placing these fish in the experimental tank, freshwater slowly ran into the container of water in which the fish were transported to the laboratory. When the desired lower salinity was reached by dilution and overflow of the water in the container (this required about 60 min to accomplish), the fish were transferred by dip net to the experimental tank. The experimental tank had a water temperature within 1° or 2°C of the water in which the fish were caught and transported or in which dilution occurred.

Within 30-60 min after being placed in the tank, schools and individual mullet swam throughout the tank at relatively uniform speeds. Single and grouped individuals "grazed" along the sides and bottom of the screen in the tank. The behavior of the mullet at this time appeared to be similar to the behavior of undisturbed fish observed in the field.

The water in the tank was cooled and heated simultaneously after the fish demonstrated what appeared to be "normal" schooling and grazing behavior. At half-hour intervals the temperature at various levels was recorded and the behavior and depth and temperature distribution of the mullet were noted. The observations required about 1 or 2 min to complete. Observations continued until the vertical distribution of the mullet did not change with respect to specific water temperatures during two or three consecutive observations. This occurred between 4 and 8 h after commencing the experiments, when the maximum water temperature in the tank was between 36.0° and 40.8°C, and the minimum temperature was between 13.0° and 19.0°C. Upon termination of the observations, the heating and chilling equipment was turned off, water samples were collected, and one of the sides of the enclosure around the tank was slowly removed. The lights were dimmed slowly and turned off by a rheostat. The fish were left in the tank overnight, exposed to natural twilight conditions in the evening and morning, the room having a number of large windows. During the evening and overnight periods the tank temperature gradually became more uniform.

Well before a second series of observations was to be made during the next day, the side of the tank's enclosure was replaced, the lights having been turned on during the twilight period by a rheostat. The tank was also oxygenated for approximately 30 min, followed by at least an additional 30-min period during which the tank was not disturbed. The second day of observations served to check on the experimental procedures and results obtained the first day, and to achieve higher tank temperatures than reached during the first day. Statistical comparisons between first and second day activity were not significant ($P \geq 0.05$), indicating that the fish did not change their depth or temperature distributions.

RESULTS

Experimental

Prior to the onset of heating and chilling, fish generally <50 mm SL (Table 1), with one exception, initially concentrated near the surface or in the upper half (40-80 cm) of the tank. Fish in the 30- to 50-mm SL size ranges in 0‰ salinity were initially concentrated in the lower half (0-40 cm) of the tank. Fish generally ≥50 mm SL initially concentrated near or on the bottom, or in the lower half of the tank. However, fish of all sizes continuously moved throughout the 80-cm deep tank, indicating that the light and pressure gradients and the depth of water were not limiting. When left for hours in the tank at constant temperature conditions at each test salinity, the mullet exhibited the same behavior, distribution patterns, and movements as those observed in mullet before heating and chilling were initiated during the experiments. These observations served as a control for the distributional patterns of mullet observed under test conditions.

Experimental results were grouped and analyzed according to test salinities (0, 15, and 34‰) and mullet size ranges (20-30, 30-50, and ≥50 mm SL) (Table 1). There was overlap and occasional fish outside of specific size ranges in some experiments due to the size composition of the individual mullet caught in schools in the field and subsequently put into the experimental tank. The experimental time period was divided for analysis into five observation intervals, each consisting of three observations (i.e., 1 complete hour of observation with observation being made each half hour). Only data for observation intervals 1, 3, and 5 are presented in Figure 3. Each graph consists of open histograms for the temperature and depth distributions for fish of specified size ranges, test salinity, and observation interval. Observations of

depth distribution were made to within 5-cm intervals; the means given in the graphs being the mean of a given interval (e.g., 47.5 cm for 45-50 cm).

Statistical comparisons for depth or temperature distributions were significant (analysis of variance, $P \leq 0.001$) in all but a few cases. The following comparisons were made, the exceptions to $P \leq 0.001$ values being noted in parentheses: 1) between observation intervals for given fish size ranges and test salinity (no exceptions), 2) between salinities for given fish size ranges and observation interval (depth distribution for fish ≥50 mm SL in observation interval 5 and salinities 15 and 34‰ ($P = 0.27$); depth distribution for fish 20-30 mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.003$); temperature distribution for fish ≥50 mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.002$)), and 3) between size ranges for a given test salinity and observation interval (depth distribution for a salinity of 34‰ in observation interval 5 and fish size ranges 30-50 and ≥50 mm SL ($P < 0.004$); temperature distribution for salinity 34‰ in observation interval 5 and fish size ranges 20-30 and 30-50 mm SL ($P = 0.46$)).

Changes in depth distribution of fish are readily discernable in the histograms in Figure 3. At each test salinity, with the exception of 30-50 mm SL fish at 0‰ salinity, mullet ≤50 mm SL moved downwards in the tank to a mean depth of 47.5 or 52.5 cm by the last observation interval. Fish ≥50 mm SL moved up to mean depths of 32.5 to 42.5 cm. Fish 30-50 mm SL at 0‰ moved from an initial distribution in the bottom half of the tank to a mean of 52.5 cm during the remainder of the experiments (observation intervals). As test salinities decreased so did the final depth distribution for given fish size ranges, except for 30- to 50-mm SL fish.

Changes in fish depth distribution were directly related to tank temperature, since water temperature decreased with depth. However, temperature values changed rapidly between depths 60 and 20-30 cm and were relatively isothermal and cold between 20-30 cm and the bottom of the tank, and isothermal and hot above 60 cm. As a result only small differences in final depth distribution corresponded with relatively large differences in final temperature distribution.

The mean selected temperature tended to increase between observation intervals 1 and 5 at each test salinity for given fish size ranges. The exception to this tendency was fish ≥50 mm SL at 0‰ salinity (20.9°-19.5°C). Fish ≤50 mm SL (20-30 and 30-50 mm) tended to select higher final observation interval 5) mean temperatures (30.0°-32.3°C) than did fish ≥50 mm SL (20.0°-19.5°C) at each test salinity. For all fish size ranges the final mean selected temperature tended to decrease as the test salinity decreased. This decrease was greatest for fish ≥50 mm SL (29.0°-19.5°C).

The depth and temperature distribution results taken together indicate that temperature selection was the more important, depth distribution being secondarily related. Other gradients such as light, pressure, and oxygen, if present, did not appear to influence the distribution of the mullet at least to the extent that temperature did. Fish ≤50 mm SL appeared to have a predilection towards the surface whereas fish ≥50 mm SL appeared to be predisposed towards the bottom. This was evident before the initiation of heating and chilling in each experiment and during constant temperature control experiments. As the experiments progressed it also appeared as if mullet ≤50 mm SL, in most instances, were "forced" downwards by rising temperatures. Similarly, mullet ≥50 mm SL were "forced" upwards by decreasing water temperature, and then downwards by rising temperature, such that their final temperature and depth distributions were somewhat lower than those for fish ≤50 mm SL in similar conditions.

Just how important the actual temperature and depth distribution values selected by mullet are is unknown. What does appear to be important is the relative difference between distributions for fish generally <50 mm SL as compared with those for fish generally >50 mm SL at each salinity, and the relative changes which occurred between salinities for each fish length interval. The predisposition of fish <50 mm SL towards the surface (and higher temperatures) may be adaptive in the field. Warm water rises and the warmest (hottest) water is usually on the surface. By moving in the surface layer fish <50 mm SL may be able to orient towards the shallowest water inshore, which at low tide should also be the warmest. The predisposition of fish >50 mm SL towards the bottom of the tank (and cooler temperatures) may similarly be adaptive in the field. In this case movement away from areas subjected to tide pool formation may be important for survival.

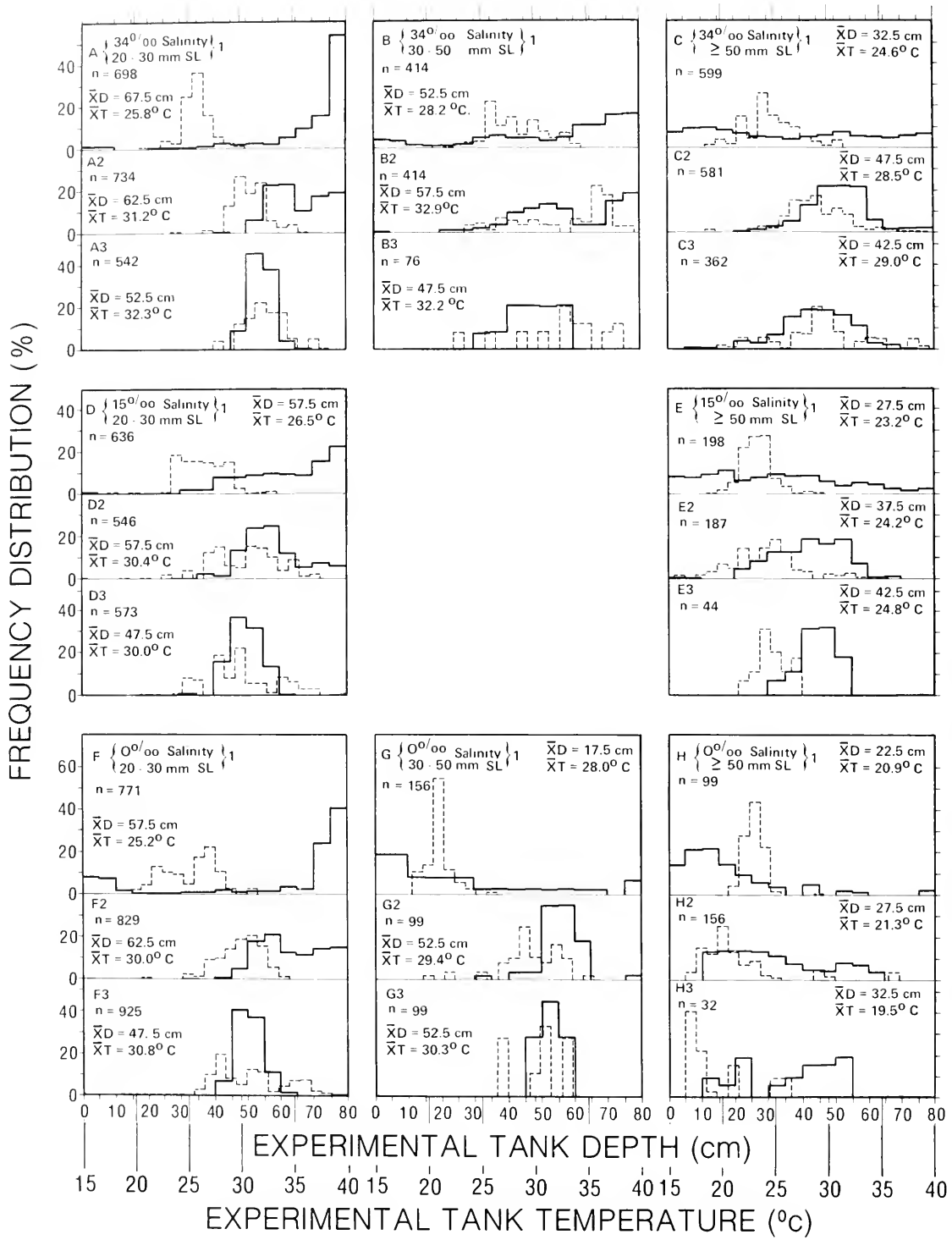

FREQUENCY DISTRIBUTION (%)
A 34°/oo Salinity 20 - 30 mm SL
n = 698
X̄D = 67.5 cm
X̄T = 25.8° C
A2
n = 734
X̄D = 62.5 cm
X̄T = 31.2° C
A3
n = 542
X̄D = 52.5 cm
X̄T = 32.3° C
B 34°/oo Salinity 30 - 50 mm SL
n = 414
X̄D = 52.5 cm
X̄T = 28.2 °C.
B2
n = 414
X̄D = 57.5 cm
X̄T = 32.9°C
B3
n = 76
X̄D = 47.5 cm
X̄T = 32.2 °C
C 34°/oo Salinity ≥ 50 mm SL
X̄D = 32.5 cm
X̄T = 24.6° C
n = 599
C2
n = 581
X̄D = 47.5 cm
X̄T = 28.5° C
C3
n = 362
X̄D = 42.5 cm
X̄T = 29.0° C
D 15°/oo Salinity 20 - 30 mm SL
X̄D = 57.5 cm
X̄T = 26.5° C
n = 636
D2
n = 546
X̄D = 57.5 cm
X̄T = 30.4° C
D3
n = 573
X̄D = 47.5 cm
X̄T = 30.0° C
E 15°/oo Salinity ≥ 50 mm SL
X̄D = 27.5 cm
X̄T = 23.2° C
n = 198
E2
n = 187
X̄D = 37.5 cm
X̄T = 24.2° C
E3
n = 44
X̄D = 42.5 cm
X̄T = 24.8° C
F 0°/oo Salinity 20 - 30 mm SL
n = 771
X̄D = 57.5 cm
X̄T = 25.2° C
F2
n = 829
X̄D = 62.5 cm
X̄T = 30.0° C
F3
n = 925
X̄D = 47. 5 cm
X̄T = 30.8° C
G 0°/oo Salinity 30 - 50 mm SL
X̄D = 17.5 cm
X̄T = 28.0° C
n = 156
G2
n = 99
X̄D = 52.5 cm
X̄T = 29.4° C
G3
n = 99
X̄D = 52.5 cm
X̄T = 30.3° C
H 0°/oo Salinity ≥ 50 mm SL
X̄D = 22.5 cm
X̄T = 20.9° C
n = 99
H2
n = 156
X̄D = 27.5 cm
X̄T = 21.3° C
H3
n = 32
X̄D = 32.5 cm
X̄T = 19.5° C
0 10 20 30 40 50 60 70 80
EXPERIMENTAL TANK DEPTH (cm)
15 20 25 30 35 40
EXPERIMENTAL TANK TEMPERATURE (°C)

FIGURE 3.—Experimental temperature (dashed line) and depth (solid line) distributions for indicated mullet size ranges in the 80-cm deep tank at the indicated salinity (34, 15, or 0‰). No experiments were conducted with fish 30-50 mm SL at 15‰ salinity. Each of the eight salinity-fish size range "conditions" are subdivided into three observation intervals: 1) observation interval 1, corresponding to the first three experimental observations (1-3); 2) observation interval 3 (7th-9th observations); and 3) interval 5 (13th-15th observations). Also presented are mean depth ($\bar{X}D$) and temperature ($\bar{X}T$) data. Sample size (n) is based on the pooled data for the number of times each fish was observed within the observation interval for all experiments at a given salinity and for a given fish size range. Experiments varied in duration and number of observations made. Thus, the sample size fluctuates. See Table 1 for the actual (maximum) number of fish and experiments for each salinity-fish size range condition.

Field

Mullet Distribution

The initial appearance of the 17- to 35-mm SL mullet prejuveniles, a distinct silvery, countershaded pelagic stage (Hubbs 1958), in the estuarine intertidal regions varied between 1972 and 1973. In 1972 they were observed and collected along the tide line (the most shoreward edge of falling or rising water, which is contiguous with deeper offshore water) in sand and mud flat tide pools and around freshwater streams and springs at the end of January. In 1973 they did not appear in these areas until the end of February. Prejuveniles were particularly abundant in areas with the finest silt, mud, and/or sand particles near the outlets of freshwater rivers, streams, or springs.

Fish ≥50 mm SL could be seen year around in the intertidal areas. The main body of this study concentrated on those fish that entered the intertidal in 1972. Also observed were juveniles of the 1971 year class, fish ≥80 mm SL, in the intertidal in early 1972, and prejuveniles and juveniles of the 1973 year class, ≤50 mm SL, in early 1973. The disappearance of prejuveniles-juveniles from the low tide intertidal swash zone (Hedgpeth 1957) and tide line regions appeared to be completed by the end of June each year, although occasional schools were seen as late as August. However, these schools were composed of fish usually about 40 mm SL or larger, that moved with the tide line.

Prejuvenile mullet undergo metamorphosis to juveniles after entering the estuarine intertidal region. The most evident change is the loss of the pelagic silvery coloration with a general darkening of all surfaces, especially the dorsal side. However, a general countershaded pattern remains. Other less obvious changes include: the elongation and convolution of the intestine, development of adipose eyelids, transformation of the third anal element from a soft ray to a spine, and changes in the morphology of lips and teeth. Metamorphosis is thought to be completed at about 50 mm SL (Jacot 1920).

During metamorphosis, diet and feeding habits change. I found copepods in the stomach contents of some prejuveniles in Hawaii in the estuarine intertidal regions. Other prejuveniles and juveniles had plant and animal material as well as mud or silt in their stomachs. I found that sediments constituted the bulk of the diet of juvenile mullet in some localities in Hawaii. In the estuarine intertidal region around the island of Oahu, the sizes of these injested particles ranged from 0.02 to 0.60 mm in diameter. Odum (1968) showed that fine particulate materials are a source of adsorbed organic matter and microorganisms, and are important in the diet of *Mugil cephalus* along parts of the east coast of the United States. The change in diet from copepods to plant material and mud or silt presumably occurs concurrently with changes in intestinal length, lips, and teeth. After metamorphosis is completed, the juvenile fish move into somewhat deeper intertidal water.

Prejuveniles and juveniles of all sizes formed schools ranging in size from tens to hundreds of individuals. Prejuveniles and juveniles <50 mm SL were always observed in the shallowest, warmest water near shore wherever they occurred (Table 2). At low tide they were located along the tide line, the shallowest water along estuarine streams, and trapped in shallow mud flat and occasionally sand tide pools (the swash zone). Intense continuous feeding activity was usually observed. The substrate in the areas in which the small mullet occurred was covered usually by the finest inorganic sediment (sand and silt 0.02-0.60 mm in diameter).

Salinity and temperature values changed daily depending on tide level (water depth), wind, bottom type (particle size, color, etc.), insolation, and the location of springs and streams. Often a spatial as well as temporal kaleidoscope of temperature and salinity values was recorded, especially along Wailupe Beach.

On 15 March 1972 the last hour (1200-1300 h local time) of a natural fish kill was observed in

TABLE 2.—Summary of field data collected during observations of prejuvenile and juveniles *Mugil cephalus* in Hawaii during 1972-73.

Locality	Habitat	Size (mm SL)	Month	Tide	Temperature range (°C)	Salinity range (‰)	Water depth (cm)	School size	Remarks
Wailupe Beach, Maunalua Bay[1]	Inshore of tide line in swash zone, tide pools, freshwater springs	<50	Feb. to May	Low	19.8-37.2 (22.0-26.9 in center of springs)	2-29.5	0.6-15	10's-100's	Mullet trapped in tide pools. No predators observed. No mullet ≥50 mm SL observed or collected.
	Coral rock/rubble tide pools with open connections/channels to deeper water	≥50	Feb. to May; Dec.	Low	23.0-35.1 (22.0-26.9 in springs)	2-35 (2-10 in springs)	2.5-30	10's-100's	Seaward of tide line. Occasionally attacked by predatory fish.
	Mud/sand flats, sandy beach, coral rock/rubble	<50	Feb. to June	High	26.1-30.1	10-35	5-30	10's-100's	In wave wash (tide line); attacked by predators.
		≥50	Feb. to June; Dec.	High	26.1-30.1	10-35	2.5-90	10's-100's	Feeding. Attacked by predators.
Wailupe Stream, Maunalua Bay[1]	Tidal stream	20-200	May	Low/high	27.8	—	1.8-200	10's-100's	In shallowest water. Feeding during low tide. Attacked by predators at high tide.
Kaupa Pond, Maunalua Bay[1]	Cement drainage culverts	<50	Feb. to July	Low	21.9-36.2	0-32	0.6-13	10's	Tideline. Feeding in shallowest water.
	Mud bottomed channel	≥50	Feb. to July	Low	21.6-30.1	15-32	13-30+	10's	Feeding on surface. Unable to see below surface.
		<50	Feb. to July	High	28.1-34.0	15-32	0.6-13	10's	Along tide line—shallowest water.
		≥50	Feb. to July	High	28.1-34.0	15-32	30+	10's	Feeding.
Kahana Bay[1]	Silted areas, fishpond	<50	May	Low	—	—	0.6-5	10's	Feeding. No predators observed.
	Fishpond channels	30-200	May	Low	24.0-26.5	2-15	0.6-15+	10's	Feeding. No predators observed.
	River; mud/sand spits (bars)	<50	May	Low	24.1-29.6	2-30	0.6-5	10's	Feeding in tide line/shallowest water.
		≥50	May	Low	24.1-29.6	2-31	2.5-7.5	3-5	Feeding.
		<50	May	High	20.0-25.0	—	2.5-15	10's	Feeding in tide line/shallowest water amongst mangrove roots.
Kahana Bay[2]	River, mangrove vegetation	<50	May	Low/high	—	—	2.5-15	—	In shallowest water. Individuals spread out motionless on bottom.
Wailupe Beach, Maunalua Bay[2]	Mudflats; coral rocks/rubble	<50	Feb. to July	Low/high	—	—	2.5-15	—	In shallowest water. Spread out or in compact groups motionless on bottom.
		≥50	Feb. to Aug.	Low/high	—	—	7.5+	—	In shallowest water. Individuals spread out motionless on bottom.

[1]Daylight observations of mullet.
[2]Night observations of mullet.

one of the cement culverts in Kuapa Pond (Hawaii Kai), Maunalua Bay. The tide was low and just starting to turn and flood. Prior to this day heavy rains washed down large amounts of silt, rocks, and debris to a depth of about 0.2-0.5 m. A narrow channel was cut through the mud by the trickling stream, and isolated "tide pools" or pockets of water were common. An estimated several thousand prejuvenile and juvenile mullet 18-80 mm SL were found dead along the bottom of the culvert. Although it appeared that the fish had a free exit at higher tide levels, via the shallow (1 cm deep at low tide) channel to the cooler tidal region (26°-30°C), the fish were presumably trapped physically by the debris and/or by a very rapid increase in water temperature. Dead mullet were found in the pockets with water temperatures of 39.5°-42.5°C. The only survivors observed were mullet 20-35 mm SL slowly swimming in small pockets at temperatures as high as 39.0°-41.1°C. Salinity measurements were not made, but would be expected to be low.

Juvenile mullet ≥50 mm SL were not observed or collected in tide pools at low tide. At low tide these larger fish occurred beyond the tide line in tide pools with open connections to deeper water or along sills and sand/mud flats which sloped into deeper water. These areas were characterized by

higher but more uniform salinities and lower but more uniform temperatures than areas in which fish <50 mm SL were generally found.

At high tide, water temperature and salinity values were nearly uniform throughout a given location. Mullet <50 mm SL were concentrated along the tide line on the beach or along the sides of rivers in the shallowest water available. Schools were dense and often composed of more individuals than found in schools at low tide in the same area. Little feeding occurred; evasion of predators was seen more commonly. At high tide, schools of mullet with individuals ≥50 mm SL moved into the former tide line and tide pool areas, and were observed feeding in the areas from which the smaller mullet retreated.

The results of the experiments and field observations demonstrate that dynamic differences occur in the behavior and distribution of schools of mullet composed of individuals generally <50 mm SL as compared with schools with juveniles of greater length. In the field young mullet <50 mm SL prefer and select areas characterized by minimal water depth, tide pool formation, relatively high fluctuating temperatures, and relatively low fluctuating salinities. Juveniles ≥50 mm SL, on the other hand, seek somewhat deeper water and tide pools with lower more uniform temperatures and higher more uniform salinities.

Experimentally, a wide range of temperature values (13°-40.8°C) was available to the fish. However, mullet <50 mm SL tended to concentrate in water of higher temperature near the surface of the tank and fish >50 mm SL tended to occur deeper in the tank at lower temperatures for each test salinity. Although the experimental tank allowed fish a means of behaviorally escaping lethal or near lethal conditions (as presumably did deeper tide pools for mullet ≥50 mm SL in the field), entrapment in shallow intertidal tide pools in the field did not. Fish <50 mm SL appeared to actively seek such near lethal conditions in the field (and experimentally), and as observed in a Kuapa Pond stream culvert, occasionally perished as a result.

Predators

Most predators observed interacting with mullet during this study were solitary stalking or stationary "sit-and-wait" species (Table 3). Attacks by predators upon schools of mullet with individuals <50 mm SL were almost nonexistant at low tide.

Where deeper water was immediately contiguous with a shallow water shelf (e.g., along Kahana River), predators (e.g., barracuda) in the deeper water were observed orienting towards and paralleling the movements of schools of the small mullet feeding in the shallower water. When mullet strayed off the shelf into deeper water, they were attacked. Predation upon mullet ≥50 mm SL during low tide was occasionally observed as schools moved and fed in the deeper intertidal region.

At high tide, schools of these larger mullet continued to be attacked by predators, as they were at low tide. Similarly, during high tides and ebb and flood periods, predators attacked mullet schools with individuals <50 mm SL.

At night, along Wailupe Beach and the Kahana River (Table 2), mullet schools broke up and individuals spread out and remained relatively motionless near the bottom. The fish slowly moved

TABLE 3.—Predatory fish observed interacting with schools of mullet.

Location	Species	Standard length (mm)	Water depth (cm)	Tide	Remarks
Wailupe Beach	Lizardfish *Saurida gracilis*	60-175	5-23	Low/high	In tide pools with open connections and channels to deeper water. Attacked and chased juveniles of all sizes.
	Needlefish *Tylosurus crocodilus*	100-300	30-75	High	A possible predator, moved in with flood tide. Observed following schools of mullet near surface.
	Great barracuda, *Sphyraena barracuda*	50-225	30-75	Low/high	Moved inshore with flood tide; attacked and chased individuals of all sizes in schools. Followed feeding individuals in schools. Swam slowly along the shoreline at high tide.
Wailupe Stream	Great barracuda	40-600	30-90	Low/high	Mullet <50 mm SL usually in shallowest water 1.8-75 cm deep. Barracuda in deeper water followed or paralleled movements of mullet in shallow water and attacked when the mullet strayed into deeper water.
Hawaii Kai (Kuapa Pond) culverts	Great barracuda	30-250	15-75	High	Moved in with flood tide. Water turbid; caught in seines with juvenile mullet. No mullet found in stomach contents
Kahana Bay River	Great barracuda	125-500	15-60	Low/high	At low tide mullet < 50 mm SL in shallowest water 15 cm deep, barracuda followed (paralleled) schools of mullet in shallower water (see above).
	Eleotris sandwichensis	78	7.5-30	Low	Single unsuccessful attack on school of mullet of individuals about 40 mm SL. Caught after attack.

(drifted) with the tides. The break up of schools may have been a result of reduced predation and/or lowered visual sensitivity thresholds (Munz and MacFarland 1973).

When a school was attacked, it usually split into two or more segments and passed around behind the predator to reform a single school again. When a predator was successful in separating an individual from a school, a chase occurred, the results of which were seldom observed. Of the approximately 50 lizardfish stomach contents analyzed, one contained a juvenile mullet. None of the 10 barracuda stomach contents analyzed contained juvenile mullet.

Potential invertebrate predators were abundant in the various habitats where mullet occurred. However, only individuals of a single crab species, *Thalamita crenata*, were observed stalking and extending their chelipeds toward passing mullet. In one instance an individual crab did capture a juvenile mullet, but only after it had been wounded by and escaped from a barracuda.

DISCUSSION

Mugil cephalus is a worldwide (lat. 42°N-42°S, Thomson 1966) inhabitant of the estuarine intertidal as well as freshwater and coastal marine environments (Broadhead 1953, 1955; Hendricks 1961; Thomson 1963, 1966; Johnson and McClendon 1970). In Hawaii, selective pressures appear to have favored prejuvenile and juvenile mullet that are able to survive in the shallowest, warmest estuarine intertidal waters, waters that are characterized by temporal and spatial heterogeneity with respect to temperature, salinity, and depth. Before discussing the adaptations evolved by striped mullet making possible survival in estuarine intertidal regions, a discussion of the environmental variables important to young mullet in Hawaii might be in order.

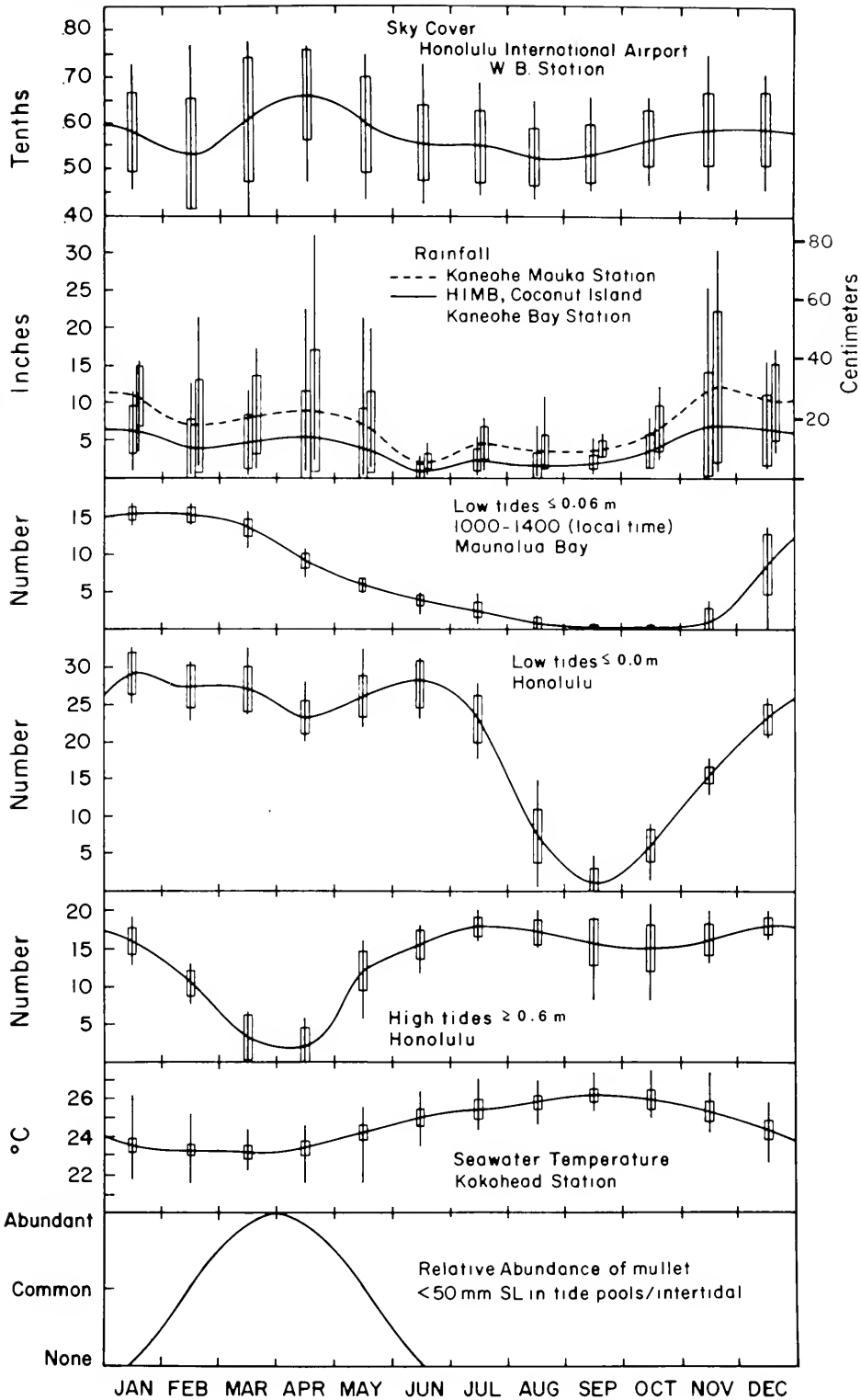
The monthly occurrence of mullet <50 mm SL observed in 1972 and 1973 in Hawaii is presented with data for 12 consecutive years (1962-73) of recorded (skycover, rainfall, seawater temperature) and predicted (tidal) data in Figure 4. These appear to be the most important environmental factors that bear directly upon the lives of mullet in the estuarine intertidal region. Indirectly, the length of daylight (time from sunrise to sunset) may also be important; it is shortest (about 10.9 h) about 22 December each year, and longest (13.3 h) about 21 June each year.

Visual observations and collections of mullet <50 mm SL indicate that these mullet occur in the Hawaiian intertidal estuarine regions during the months when there are a maximum number of low tides ≤0.0 m (mean tide level at Honolulu is 0.2 m (0.8 ft)). Perhaps of greater importance is the occurrence of mullet when there is a minimum number of high tides ≥0.6 m (2.0 ft). In Maunalua Bay, tide pools begin to form when the tide level is approximately 0.06 m (0.2 ft). The number of tides that would result in tide pool formation at noon (1000-1400 h local time) begins to decrease during the time of the year mullet are undergoing metamorphosis in the intertidal estuarine region, but is still maximal when prejuveniles first enter the inshore areas. Thermal and salinity stresses should be maximal during the noon time period. It is not known whether this tidal-estuarine intertidal situation is unique to Hawaii or of more wide spread occurrence. Also unknown is whether the peak occurrence of young mullet during such tidal relationships is fortuitous, or whether selection pressures have resulted in a shift of the peak occurrence from either earlier or later in the winter-spring season to its present "position" in April.

The extent to which stress occurs in the intertidal estuarine region may be ameliorated by low ambient (oceanic) seawater temperatures and maximum cloud cover. During the time mullet <50 mm SL are found in the intertidal estuarine region in Hawaii, seawater temperatures are minimal and increasing, and average cloud cover is seasonally maximal. During the late winter-spring, the lowest seasonal seawater temperatures occur in the tropical-temperate Northern Hemisphere, and increase until maximum levels are reached about September.

The average maximum amount of cloud cover, which occurs in Hawaii during April (when young

FIGURE 4.—The relative abundance of mullet <50 mm SL in the Hawaiian estuarine intertidal tide pools compared with environmental data collected (seawater temperature, rainfall, and sky cover) and predicted (tides). The monthly means (connected by horizontal lines), ranges (vertical lines), and standard deviations (vertical boxes) were derived from data for the 12-yr period, 1962-73. Mullet abundance data were from field observations and collections in 1972-73. Sky cover data were derived from monthly average values. Sky cover and rainfall data were taken from *Climatological Data, Hawaii*, U.S. Weather Bureau, NOAA; tidal information from *Tide Tables*, West Coast of North and South America including the Hawaiian Islands, National Ocean Survey, NOAA; seawater temperature data were collected by the National Marine Fisheries Service, Honolulu.


Sky Cover
Honolulu International Airport
W B Station
Tenths
80
70
60
50
40
Rainfall
Kaneohe Mauka Station
HIMB, Coconut Island
Kaneohe Bay Station
Inches
30
25
20
15
10
5
Centimeters
80
60
40
20
Low tides ≤ 0.06 m
1000-1400 (local time)
Maunalua Bay
Number
15
10
5
Low tides ≤ 0.0 m
Honolulu
Number
30
25
20
15
10
5
High tides ≥ 0.6 m
Honolulu
Number
20
15
10
5
Seawater Temperature
Kokohead Station
°C
26
24
22
Relative Abundance of mullet
<50 mm SL in tide pools/intertidal
Abundant
Common
None
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

mullet are most abundant), reduces insolation and thus reduces the potential for the attainment of lethal conditions in tide pools. These relationships are particularly important since young mullet congregate in areas of springs and freshwater run-off. However, cloud cover during February through May varies more than during any other period of the year and points to the fact that the environment in which mullet <50 mm SL occur fluctuates tremendously within a season and from year to year.

Seasonal rainfall is maximal during winter-spring in Hawaii. Rainfall in the mountains (Kaneohe Mauka Station) exceeds that in nearby shore regions (Hawaii Institute of Marine Biology Station). Fluctuations in rainfall from month to month and year to year are great and appear to be unpredictable, particularly during the season when mullet <50 mm SL are abundant in the intertidal estuarine region. Run-off is maximal during this season due to the heavier mountain rainfall. This run-off could contribute to potentially lethal or near lethal conditions in the intertidal region by reducing its salinity, particularly during periods when low tides occur during noon. Intertidal spring water temperatures, on the other hand, were recorded to be as much as 10° cooler than surrounding water of higher salinity (Table 2). This cooler water may serve to reduce overall intertidal estuarine temperatures, at least during nontide-pool forming tide levels, but at the same time it increases the thermal and salinity heterogeneity of the environment.

Returning to a discussion of adaptations of mullet, experimental studies indicate that temperature acclimation is important in the ability of striped mullet (at least larger juveniles) to survive higher temperatures (Heath 1967; Sylvester 1974, 1975; Sylvester et al. 1974). Heath, although not providing fish length or salinity data at which tests were made, reported critical thermal maxima (CTM) of 42.4°-43.1°C for mullet in the northern Gulf of California. Sylvester (1974, 1975) and Sylvester et al. (1974) demonstrated increased CTM (29.0°-41.6°C) with increasing acclimation temperatures at a salinity of 32‰ for juvenile striped mullet, 70-125 mm SL, in Hawaii. At a lower acclimation temperature, and a salinity of 0‰, the CTM's were reduced. In general, CTM's were lower at lower salinities. Sylvester (1974) also found that juveniles adjusted or acclimated faster at higher temperatures, and that their thermal resistance to lethal temperatures decreased slightly when they were exposed to fluctuating low, rather than constant, temperatures.

Sylvester (1975) also demonstrated the existence of increased CTM at noon and lower CTM in the morning and afternoon for fish 78-122 mm SL.

There is good evidence that underlying biochemical changes are responsible for acclimation to changing thermal regimes (reviews in Hochachka and Somero 1971, 1973; Haschemeyer 1973; Somero 1975). Hochachka and Clayton-Hochachka (1973) provided some evidence that this may also be the case for striped mullet about 120 mm long in Hawaii.

Whether the ability of mullet to tolerate increasingly higher temperatures, seasonally and daily, is a result of interacting endogenous factors (biological rhythms) as is indicated in other animals (Sweeney and Hastings 1960; Wilkins 1965), and/or exogenous factors (direct exposure to increasing temperatures) is not known.

Sylvester's (1974, 1975) studies were conducted between August and January and those of Heath (1967) in March and September. As the discussion above and Figure 4 indicate, ambient seawater temperatures are highest during August to October and lowest during February to April in the tropical-temperate Northern Hemisphere. Although the seasons varied during which the experiments of Sylvester and Heath were conducted, the CTM data obtained were similar for the experimentally acclimated fish. Doudoroff (1957) and Allen and Strawn (1971) reported that relatively brief exposure to high nonlethal temperatures usually increased heat resistance in a number of species of fish. This increased resistance was not readily lost when fishes were subsequently exposed to low temperatures. This also appears to be true for striped mullet as Sylvester's (1974) study indicates. Thus, striped mullet appear to have an ability to modify their thermal tolerance in direct response to prevailing environmental conditions (exogenous factors). The ability to increase their heat resistance even after a brief exposure to high nonlethal temperature would be especially advantageous to mullet in the estuarine intertidal, at least in Hawaii.

If exogenous factors are solely responsible for the ability of striped mullet to survive high temperatures, it is difficult to explain the differences in the distribution of striped mullet presented in this report.

Prejuveniles enter the intertidal estuarine regions from the far more environmentally uniform

oceanic waters, and appear to be "preadapted" to the near lethal conditions inshore. This may indicate the existence of an ontogenetic biological rhythm (cued by slight monthly changes in photoperiod or water temperature?) in these mullet, which biochemically and physiologically preadapts these fish for life in the intertidal estuarine regions, while they are still in oceanic waters. Seasonal and daily acclimation to existing thermal and salinity regimes may then occur after the prejuveniles arrive inshore.

Factors affecting the distribution of striped mullet ≥50 mm SL are more complex. In Hawaii, field acclimated fish behaviorally select or prefer water temperatures well below their experimental CTM. The natural fish kill observed in March also indicates that the larger juveniles (and most prejuveniles) were not able to survive exposure to high temperatures (at least for relatively long periods of time). Behavioral selection of temperature regimes well below CTM has also been observed in the estuarine goby, *Gillichthys mirabilis* (de Vlaming 1971).

Mullet ≥50 mm SL in Hawaii moved seaward to pools with open connections to deeper water with ebbing tides during the spring. During the non-tide-pool forming low tides in the late summer, the larger juveniles may be acclimated to tolerate higher ambient seawater temperatures in Hawaii as they are in the northern Gulf of California. In Hawaii, however, intertidal waters reach their maximum temperatures during the period from late winter to early summer when shallow tide pools are formed, although ambient oceanic temperatures are higher during late summer. Heath (1967) indicated that inshore water temperatures in the northern Gulf of California are highest during the late summer-early fall period. It is not known whether CTM's are similar for field acclimated striped mullet ≥50 mm SL in the spring in Hawaii and in the late summer in the northern Gulf of California, or whether mullet from both locations have CTM's parallelling seasonal changes in ambient (oceanic) seawater temperature.

Selected temperatures are lower for young mullet ≥50 mm SL compared with smaller fish at each salinity, and much lower at decreasingly lower salinities (Figure 3). Presumably, physiological changes mediated hormonally/biochemically occur during metamorphosis, resulting in a preference for reduced temperatures by the larger juveniles. This decrease in temperature "tolerance" with metamorphosis (age) is somewhat contrary to the discussion thus far. It may only be a behavioral trait not directly correlated with CTM (i.e., CTM may actually be increasing). Behavioral selection of lower temperatures appears to be adaptive in the field during the period between April and August. In addition to having widely varying salinity values, many of the tide pools formed during this period may have been too shallow for larger juveniles to feed and swim. Many of the pools were shallower than the body depth of the older juveniles. Thus, those individuals that remained seaward of the tide line as they completed metamorphosis may have reduced or escaped the possibility of entrapment and exposure to lethal conditions in tide pools and shallow water; conditions observed once during this study.

These relationships may indicate the existence of an endogenous rhythm involved in the movement of (behavioral selection by) juvenile mullet towards deeper, relatively cooler, more saline water during or after metamorphosis. This rhythm may be acting in opposition to the presumably increased acclimation to higher ambient (oceanic) seawater temperatures. The change in behavior with metamorphosis may be a result of endogenous rhythms perhaps coupled with exogenous factors, such as the slight monthly changes occurring in seawater temperature and/or photoperiod, or it may be due directly to these exogenous factors. The reproductive cycle of striped mullet appears to be coupled with both these environmental variables (Kuo et al. 1974; Kuo and Nash 1975), so presumably younger individuals could use these same cues as well. It is difficult to separate cause from effect, but the shallowness and volume limitations of tide pools may be critical. Thus, selection may have favored those metamorphosed individuals with reduced physiological tolerance to high fluctuating temperatures and low fluctuating salinities as found in the estuarine intertidal (i.e., those individuals that behaviorally moved away from such conditions).

If selection favored those metamorphosed (metamorphosing) individuals that moved into deeper intertidal waters, what selection pressures may have favored individuals able to survive the kaleidoscopic conditions of the estuarine intertidal tide pools?

Experimental and field evidence demonstrate the importance of refugia for species from their competitors and/or predators (Gause 1934; Crombie 1946; Connell 1961; Paine 1969). Connell

proposed that intertidal species are limited in their upper distributional range by physiological (and presumably biochemical) adaptive abilities to environmental stress. At the lower end of the range, organisms are limited by biotic factors such as competition and predation. Field observations indicated that there was essentially no predation, including that by birds, of mullet <50 mm SL when they occupied the intertidal estuarine tide line and swash zone areas at low tide (Tables 2, 3). At high tide, and during ebb and flood, mullet <50 mm SL were exposed to predators, but the potential for being attacked and caught was reduced by occupying the shallowest tide line waters and by the schooling habit.

The absence of predatory fishes in the shallow intertidal estuarine regions at low tide may be related to 1) a subminimal depth or area of water in which to maneuver, and 2) possibly, although data are lacking, an inability of predators to adjust to rapidly fluctuating thermal and salinity regimes. Predators escaped entrapment by remaining seaward of the tide line during ebbing tides just as juvenile mullet ≥50 mm SL did. In addition, potential invertebrate predators were absent from the shallow intertidal areas presumably escaping seaward and/or, as often observed or caught, burrowing to a level below the surface of the mud/sand substrate.

Juvenile mullet ≥50 mm SL as well as adult mullet appear to be competitors with individuals <50 mm SL for food resources in the intertidal estuarine region. At high tides the larger fish moved into and fed in the areas used by the younger fish during low tides. With the incoming tide, the younger fish moved shoreward with the tide line. In addition, other species of fishes moved in with the flood tides. It is not known whether these fishes utilized the same food resources as the young mullet.

Space also may be at a premium in the shallow intertidal estuarine regions, particularly in tide pools. As discussed previously, the volume of water in the tide pools as well as the depth of pool water may be critical. Formation of large schools is characteristic of larger juvenile mullet as it is for the species as a whole and inter- and intraspecific competition for space may occur. Other species of fishes, as well as the larger juvenile mullet, were not observed in the shallowest water during low tide. The ability of small mullet to occupy the shallowest, warmest water may also occur in the northern Gulf of California (Heath 1967), where they (no length data) are one of two species penetrating the farthest up seawater drainages along the margin of the desert.

Mullet <50 mm SL formed loose schools with individuals constantly feeding during low tides, particularly in tide pools. At high tides, or in more exposed environments, feeding often ceased and tight dense schools were formed. This was evident when predators were nearby, approaching, or attacking. When exposed to predators at high tides and changing tides, the schooling habit confers an increased advantage to the mullet in terms of survival (Major 1977, in press). Most of the attacks by predators on schools that I observed, failed. The formation of schools appears to be yet another adaptive feature in the behavioral repertory of mullet. The schooling habit increases the ability of individual mullet to survive as prejuvenile and juveniles in the intertidal estuarine region and presumably as prejuveniles in oceanic waters.

Prejuvenile and small juvenile mullet have presumably evolved the necessary biochemical and physiological adaptations to exist successfully in the fluctuating, often near lethal, intertidal estuarine environment in the spring months. In Hawaii, this has allowed them to use this intertidal refugium to escape their predators and competitors for food and space, making possible undisturbed feeding activity. Kinne's (1960) work with *Cyprinodon macularius* and Norris's (1963) study of *Girella nigricans* suggest that high temperatures increase the rate of food uptake and digestion. Food conversion (to growth) efficiencies are highest at lower temperatures, however. De Silva and Perera (1976) experimentally determined that young mullet grow more rapidly at 20‰ salinity than at salinities of 30, 10, or 1‰. This was comparable to Kinne's (1960) work with *C. macularius*.

The widely fluctuating environmental variables in the estuarine intertidal in Hawaii may provide the necessary conditions for rapid growth in mullet. This would allow metamorphosis to be completed in all mullet by the time the tidal situation becomes less favorable, as predators gain access to the small mullet and intra- and interspecific competitors gain access to their feeding areas as well. The formation of large schools during all stages of life appears to be important in reducing predation and possibly also in competing with other species for food and space in the estuarine intertidal region.

It is interesting to note that the environmental conditions and the behavior of prejuveniles and juvenile striped mullet in Hawaii appear to be very similar in many instances to those of various species of western U.S. desert pupfish, *Cyprinodon* (Barlow 1958, 1961; Kinne 1960; Lowe and Heath 1969; Brown and Feldmeth 1971; Deacon and Minckley 1974), and to the African cichlid, *Tilapia grahami* (Coe 1966). Daily and seasonal changes in water temperature and possibly salinity (ionic) regimes in the low tide, tide pools in Hawaii and desert springs and pools appear very similar. The pupfish and *T. grahami* young live in the shallowest, hottest water often at near lethal temperatures. Adults, generally, did not occur in these areas at the same time as the young. Feeding appeared to be continuous and was directed at the substrate, as it was in mullet <50 mm SL. The shape, size, and length of the pupfish and *T. grahami* also appear to be very similar to those of the small mullet.

The changes occurring in the behavior and distribution of mullet prejuveniles transforming to juveniles is also very similar to the changes occurring in prejuvenile and juveniles opaleye, *Girella, nigricans,* in the intertidal areas along southern California and Baja California, Mexico (Norris 1963).

The ability of certain life history stages of these diverse species of fishes to tolerate fluctuating conditions and/or near lethal thermal and ionic (salinity) regimes in shallow water possibly indicates convergence of adaptations to similar environments. The physiological adaptations may be mediated biochemically (hormonally) and may be a result of the interaction of both endogenous and exogenous factors or cues. The evolutionary driving or selection forces operating appear to include predation and at least intraspecific competition for food and space.

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AGING OF GULF MENHADEN, *BREVOORTIA PATRONUS*

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ABSTRACT

Length-frequency distributions, returns of tagged juveniles, and scale annuli indicate that over 97% of Gulf menhaden, *Brevoortia patronus*, caught in the purse seine fishery are ages 1 and 2. Few fish survive to age 3. About 50% of the fish examined for the years 1971-73 could be aged by scale annuli. Those with no scale annuli or with indistinct or false annuli could be assigned to age 1 or younger or age 2 or older on the basis of length.

When large numbers of fish are routinely sampled for age and size distributions, they must be aged by some technique that consumes relatively little time. One common method is to count scale annuli, another is to group the fish by length frequencies. Counting otolith rings usually is impractical because of the large amount of time and effort it takes to collect, prepare, and observe the otoliths.

As pointed out by Struhsaker and Uchiyama (1976), "Attempts to age tropical fishes by conventional methods have generally been thwarted by the absence of well-defined annuli in calcarious structures and protracted spawning periods which make length-frequency mode progression analysis difficult." In temperate regions where the winter water temperature may not fall low enough to cause a cessation of fish growth for an extended period, aging fish by counting scale annuli may also be difficult.

Gulf menhaden, *Brevoortia patronus*, range along the coasts of the United States and Mexico from Florida to Yucatan. They spawn offshore in the Gulf of Mexico from about October to April (Suttkus 1956; Turner 1969). The eggs hatch in about 48 h and the larvae are transported by onshore currents to estuaries, where they metamorphose into adult form (Fore and Baxter 1972). In late summer the juveniles, ranging from about 45 to 120 mm fork length (FL), congregate in the lower estuaries before moving to offshore waters (Kroger and Pristas 1975).

Gulf menhaden, the basic resource for a large meal and oil industry, are caught exclusively in a purse seine fishery extending from western Florida to eastern Texas. Processing plants, now operating only in Mississippi and Louisiana, formerly operated in Florida and Texas also. During routine sampling of the catch during the fishing season, usually lasting from late April to October, scales have been removed from, and weights and fork lengths recorded for, about 13,000 fish annually since 1964.

Aging these fish by conventional methods has been a problem. Although some fish had well-defined rings that appeared to be annuli, others had no rings, or rings that were unclear or oddly spaced. Length-frequency distributions indicated two major age-groups with overlapping lengths, and a third group that appeared in late summer.

Since neither length frequencies nor scale rings alone were satisfactory for aging all fish, ages subsequently were based on a combination of factors: appearance of scales, number and spacing of visible rings, and length of fish at the time it was caught. This method of aging could be criticized as being too subjective. But until returns of fish tagged at a known age, such as juveniles, were available there were no distributions of known ages to which distributions of estimated ages based on scale rings and lengths could be compared.

A study to resolve the problem was not begun until returns of juveniles tagged in late summer and early fall 1970-73 became available. In 1975 we began a study of fish collected from 1971 to 1973. We choose those years because returns of tagged juveniles of the 1970-73 year classes were available, and we limited our material to 3 yr to keep it manageable. Age-0 fish were defined as young-of-the-year that would have no scale ring, age 1 as those in their second year that should have one ring, and age 2 as those in their third year that should have two rings.

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Our primary objective was to determine if rings visible on some scales were true annuli. If they were, our second objective was to determine if fish that had scales with no visible rings or with a profusion of unclear rings could be aged on the basis of length; if the rings were not annuli, our second objective was to explore other methods of aging Gulf menhaden.

COLLECTION OF DATA

Samples of the catch are taken daily by field personnel stationed at four ports, each comprising two or three plants grouped in close proximity. After weighing and measuring a fish, samplers remove a cluster of scales from just above the lateral line below the dorsal fin and deposit them in a 0.1% phenol solution. Later, six scales from each fish are cleaned and mounted between two glass slides. Each fish and its scales are identified by port, collection, and scale number. From 1964 to 1971, two samples of 20 fish each were taken daily at each port. Since 1972, three samples of 10 fish each have been taken.

Juveniles ranging from about 80 to 120 mm FL were marked in late summer and early autumn with numbered internal ferro magnetic tags similar to, but smaller than, those used for adults (Pristas and Willis 1973). Tags were recovered on magnets in various parts of the processing plants (Parker 1973), although all tags passing through a plant were not retained.

To estimate the numbers of field tags not retained on magnets, batches of 100 fish marked with test tags were periodically planted in the catches. The percentage subsequently recovered was an estimate of the efficiency of the magents to recover field tags. The number of annual tests at each plant varied from 2 to 15 (200-1,500 tags). Annual recovery rates varied from 2 to 60%, but over one-half were between 15 and 40%.

Some test tags were not recovered until 1, 2, or even 3 yr after they had been placed in catches (Table 1). Delayed recoveries were caused by 1) tags lodging in various parts of a plant before later being dislodged, 2) tags remaining in fish scrap stored for long periods before being ground, 3) tags remaining in various scrap storage areas before being mixed with new scrap. The number varied by plant and year and amounted to about 1% or less of the number of test tags applied, although in 1972 it was 6% at plant 58 and 5% at plant 57.

TABLE 1.—Number of test tags applied and number recovered at Gulf menhaden processing plants, 1971-73.

Plant no.	Year tags applied	No. of tags	No. recovered			
			1971	1972	1973	1974
54	1971	900	28	0	(1)	(1)
	1972	1,300		703	(1)	(1)
55	1971	900	100	4	6	0
	1972	1,400		598	13	0
	1973	700			255	7
56	1971	900	448	0	1	1
	1972	1,300		617	2	0
	1973	600			199	2
57	1971	200	40	1	1	0
	1972	1,300		301	59	3
	1973	1,200			322	7
58	1971	300	43	5	0	0
	1972	1,500		425	93	0
	1973	1,200			396	3
62	1971	1,200	470	1	0	0
	1972	1,300		654	1	0
	1973	1,100			658	2
63	1971	1,000	203	12	0	0
	1972	1,000		379	8	0
	1973	1,200			217	13
64	1971	930	395	8	0	0
	1972	1,200		314	4	0
	1973	1,100			241	6
65	1971	800	399	(2)	(2)	(2)
68	1971	1,100	436	2	0	0
	1972	900		311	12	0
	1973	400			214	0
69	1971	1,000	163	1	0	0
	1972	1,100		265	3	0
	1973	1,300			273	1
71	1971	1,100	205	0	1	0
	1972	1,100		317	0	0
	1973	1,200			186	0

[1]Plant did not operate after 1972.
[2]Plant did not operate after 1971.

OBSERVATION OF SCALES

Scales were viewed on a scale projector at 48× magnification. If no rings were evident, or if no one ring could be considered as an annulus, no measurements were made. If rings were evident, the distances from the focus to each ring and to the scale edge of the projected image were measured. Each ring had to be discernable on three or more scales or it was not measured. Each fish was assigned an age corresponding to the number of rings on the scales except when the only ring visible was in the area of the scale usually occupied by the second ring. Then the fish was called age 2 rather than age 1. The decision to assign a ring the number one or two position was based on the distance of the ring from the scale focus.

VALIDITY OF RINGS AS YEAR MARKS

To determine if observed rings were true annuli, we examined three different sets of data: length-

frequency distributions of sampled fish, returns of tagged juvenile menhaden, and spacing of rings on the scales.

Length-Frequency Distributions

From the general shape and the number of modes of a length-frequency distribution curve, it is often possible to infer the number of age-groups represented. Length-frequency curves of Gulf menhaden sampled during 1964-73 fishing seasons had two distinct modes. Since distributions in all years were similar, we have shown only those for 1967-70 (Figure 1). A prominent mode, usually evident in May at around 135 to 150 mm, shifted progressively to the right during the season and by September varied from about 155 to 170 mm. A smaller mode at about 170 to 180 mm in May tended to shift farther right during the season and disappear by midsummer, so that the curve became unimodal and greatly skewed. This small mode apparent in May appeared to be a continuation of the mode that was prominant during the preceding September.

From the general shape of the length-frequency curves there appears to be only two dominant age-groups in the fishery. The younger and more numerous tends to dominate the fishery as the

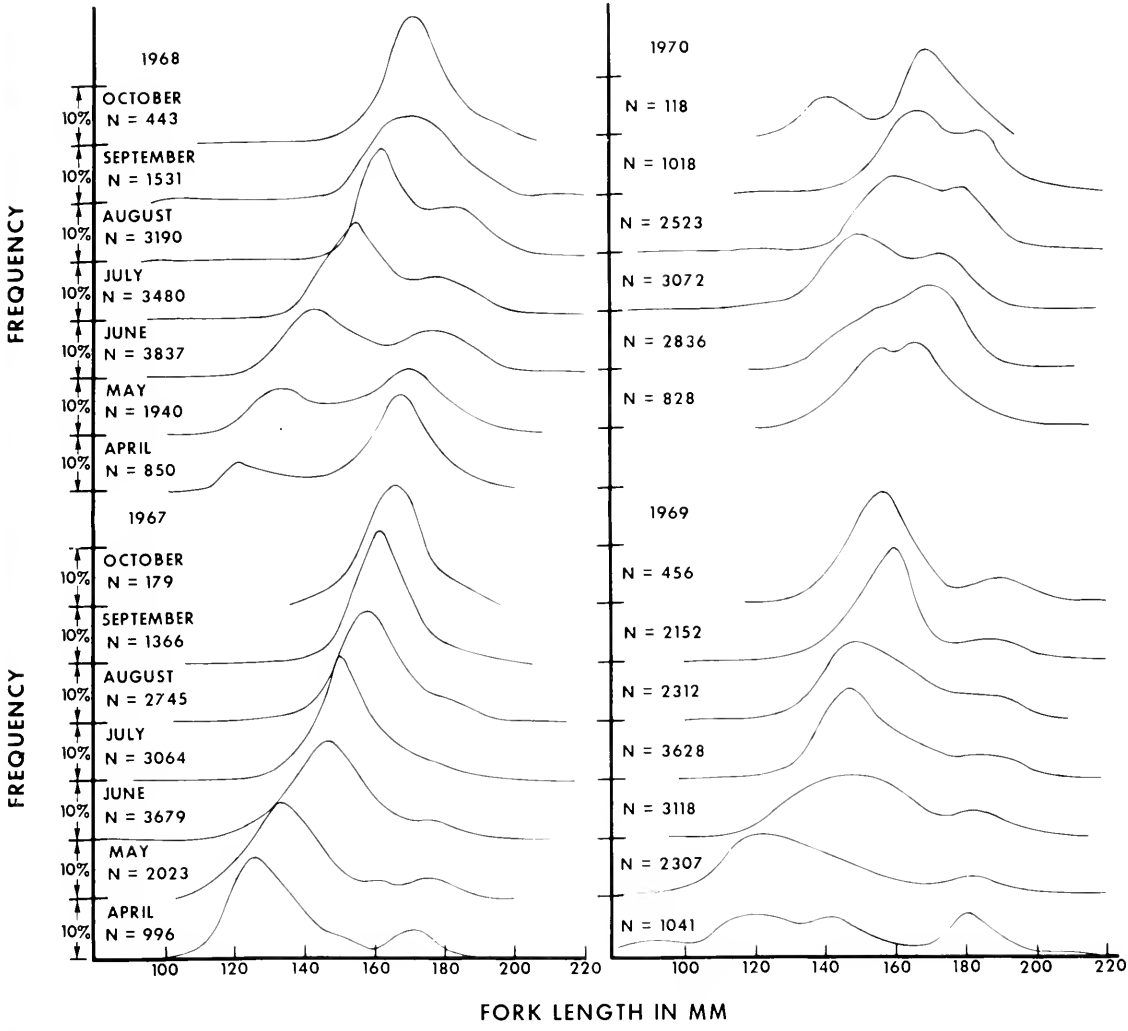

FIGURE 1.—Length-frequency distributions of Gulf menhaden in percent, by month, 1967-70.

season advances, so that by the end of the season the catch is composed almost entirely of this age-group. The considerable variation in the relative numbers of the two major age-groups from year to year is probably a reflection of the differences in the relative abundance of each year class. Small numbers of a third age-group of still younger fish may enter the fishery in some years in August or September.

Juvenile Tagging

An advantage of tagging juveniles is that the age of each fish is known when it is recaptured. Unfortunately, recovery of some tags a year or more after they had entered a plant caused some fish to appear older at the time of recapture than they actually were. Although the number was relatively small, it had an important bearing on inferences pertaining to longevity and the proportion of older fish in the catch.

By the end of the 1974 fishing season 1,137 field tags had been recovered (Table 2). Of these 1,069 (94.0%) were recovered in the 2 yr following tagging, 62 (5.5%) in the third year, and 6 (0.5%) in the fourth year. Only tags applied in 1970 had an opportunity to be recovered in the fourth year, and only tags applied in 1970 and 1971 had an opportunity to be recovered in the third year.

The tendency for test tags to remain in plants for one or more years leads us to believe that all field tags recovered in the fourth year and most of those recovered in the third year were holdovers from previous years. All of these tags were recovered at plants that had the highest percentage of test tag holdovers.

We conclude, therefore, that at least 97% of Gulf menhaden caught in the purse seine fishery are age 1 or age 2, and that very few, probably less than 1%—live to age 3. If ring marks are valid annuli, they also should indicate that the catch is composed primarily of age-1 and age-2 fish.

Incidence and Spacing of Scale Rings

The scale length-fish length relation for Gulf menhaden was linear. Correlation coefficients for 1971, 1972, and 1973, based on fish ranging from 95 to 225 mm FL, was 0.790, 0.765, and 0.768, respectively; for log transformed data the coefficients decreased to 0.729, 0.695, and 0.681. Sample sizes were 4,674, 4,457, and 4,902, respectively. The regression equation for the 3 yr combined was: Scale length = 5.392 + 0.865 Fish length.

TABLE 2.—Numbers of field tags of juvenile Gulf menhaden recovered from 10,458 fish tagged in 1970, 15,511 in 1971, 15,262 in 1972, by plant.

Plant no.	Year tagged	No. recovered 1971	1972	1973	1974
54	1970	2	30	(1)	(1)
	1971		5	(1)	(1)
55	1970	16	3	3	1
	1971		14	31	5
	1972			76	35
56	1970	29	30	3	2
	1971		10	33	7
	1972			54	30
57	1970	5	5	4	0
	1971		4	14	2
	1972			16	3
58	1970	2	19	18	1
	1971		2	24	6
	1972			6	12
62	1970	0	3	1	1
	1971		18	13	2
	1972			12	17
63	1970	3	2	0	0
	1971		49	2	1
	1972			28	4
64	1970	19	0	0	0
	1971		95	1	1
	1972			54	1
65	1970	7	(2)	(2)	(2)
68	1970	3	7	3	0
	1971		45	16	2
	1972			36	17
69	1970	1	7	2	1
	1971		5	7	1
	1972			9	6
71	1970	4	2	0	0
	1971		43	1	1
	1972			21	1

[1]Plant did not operate after 1972.
[2]Plant did not operate after 1971.

Not all fish had scales with clearly discernable rings. The percentage with no rings varied from 45.0 to 55.8. Of the fish considered as age 2, <2% had a ring in the number one position only and 25.1% in 1971, 39.1% in 1972, and 30.6% in 1973 had a ring in the second position only. A relatively small number of fish had scales with three clearly discernable rings.

The length frequencies from May to September of fish with one or two rings clearly indicated two distinct ages. In Tables 3-5 length groups below the first containing fish with both one and two rings have been lumped into one group. For one-ring fish the mode is the group, other than the lumped one, containing the most fish. The only exception is for May 1971 when the mode for fish with one ring was 155 mm. It is clear that the modes and means of one- and two-ring fish increased and that the distributions shifted toward larger sizes as the season progressed.

TABLE 3.—Length frequencies and mean lengths of Gulf Menhaden, by month and number of scale rings (0-3), 1971.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<165	50	150			560	747			587	503			663	330			260	48		
165-169	1	14			31	99	3		36	80	1		74	61			55	17		
170-174	4	14	6		45	74	16		32	95	1		49	69	1		29	22		
175-179	14	6	9		67	42	56		41	69	27		28	76	2		19	18	4	
180-184	11		22		84	18	111		53	43	100		44	61	6		27	19	10	
185-189	12		26		78	2	134		56	14	108	1	36	32	32		15	5	15	
190-194	4		29		53		83	3	42		144	5	44	15	48	2	22	6	17	
195-199	3		10	1	30		49	7	29		68	2	28	1	52	3	10	2	9	1
200-204	3		4	2	18		14	3	14		35	17	16		35	5	11		4	1
205-209				1	1		6	1	2		11	7	4		6	4	1		4	2
210-214	1				2		1	4				8	5		3	5	2		1	3
215-219								1				2	1			2	1			2
220-224	1							1												
Total number	104	184	106	4	969	982	473	20	892	804	495	42	992	645	185	21	452	137	64	9
Mean length	—	148	187	202	—	154	186	202	—	160	189	203	—	165	194	204	—	169	191	209

TABLE 4.—Length frequencies and mean lengths of Gulf menhaden, by month and number of scale rings (0-3), 1972.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<155	288	353			264	338			198	102			97	39			41	6		
155-159	64	79	3		158	134			204	107			136	51			14	7		
160-164	109	94	5		170	114	1		339	169			280	129			47	11		
165-169	109	75	12		192	88	3		236	126			347	134	1		33	19		
170-174	79	47	52		120	99	24		178	78	9		180	83	3		43	10		
175-179	53	5	71		86	48	42		136	64	39		118	54	7		57	14		
180-184	44	1	72		45	7	59		97	41	52		102	33	24		44	7	1	
185-189	20		55	1	36		72		70	6	102		78	8	74		28	1	1	
190-194	16		27	2	17		66	2	37	1	89	2	79	3	105		25	1	5	
195-199	7		13	7	15		31	3	42		79	3	65		77		17		8	
200-204	8		4	4	11		12	4	19		40	3	30		46	3	26		1	
205-209	2			2	4		3	4	16		20	4	19		10	4	10		1	
210-214				1	9		2	9	13		10	7	9		5	3	7			
215-219					3			4	5		1	3	7		1	3	1			
220-224				1	1				2		1	3	2		1	8	1			
225-229								1	1		1	1	1			1				
Total number	799	654	314	18	1,131	828	315	27	1,593	694	443	26	1,550	534	354	22	394	76	17	
Mean length	—	151	181	198	—	157	186	208	—	164	191	209	—	166	193	215	—	170	194	

TABLE 5.—Length frequencies and mean lengths of Gulf menhaden by month and scale rings (0-3), 1973.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<155	162	55			265	109			181	41			171	10			49	2		
155-159	80	28	1		217	105			187	103			26	22			1			
160-164	94	17	13		151	117			229	190			77	71			2	1		
165-169	69	16	27		93	80	2		210	169			127	164			11	12		
170-174	44	16	45		96	79	14		204	207	2		138	295			16	26		
175-179	40	4	44		90	39	70		150	138	24		237	100	3		34	26	3	
180-184	21		42		68	11	169		95	89	73		143	71	32		31	28	7	
185-189	6		30		28	5	196		82	43	114		75	35	80		19	16	12	
190-194	7		26	1	16	1	119		34	19	117		50	12	88		15	3	28	
195-199	4		12		15		71	3	15	1	81		14	1	64		17	2	16	
200-204	1		12	1	10		46	6	10		49	4	14		42	6	8	1	16	2
205-209	1		4	2	2		28	2	7		26	3	8		28		5		5	1
210-214	3		4	4	8		13	8	5		12	5	5		8	6	9			
215-219				3	2		1	5	1		6	3	2		2	8	2			2
220-224					1			5	1		2	3	4		1	4	3			2
225-229								2	1			2	1			2	1			
Total number	532	136	260	11	1,062	546	729	31	1,412	1,000	506	20	1,092	781	348	26	223	117	87	7
Mean length	—	158	182	210	—	162	188	211	—	169	192	213	—	172	194	214	—	178	193	211

TABLE 6.—Mean distance from last ring to scale edge expressed as the percent of the distance from focus to scale edge for Gulf menhaden.

Period	1971			1972			1973		
	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3
1-15 May	36.7	9.9	5.0	24.6	11.6	—	29.6	13.3	6.7
16-31 May	37.0	10.6	—	35.8	12.5	5.2	32.6	15.2	7.3
1-15 June	40.1	12.4	7.7	39.1	13.8	5.7	34.8	17.4	8.8
16-30 June	42.1	12.6	7.3	39.9	15.6	5.8	38.0	18.9	8.7
1-15 July	43.2	13.0	7.4	42.1	15.7	6.7	40.4	20.7	8.6
16-31 July	43.5	12.7	7.4	41.6	15.0	6.7	41.1	19.6	8.8
1-15 Aug.	45.6	14.2	8.6	42.9	15.8	6.9	42.1	20.6	10.4
16-31 Aug.	47.5	13.4	8.9	44.9	14.1	7.5	43.7	19.6	11.0
1-15 Sept.	44.6	10.4	—	42.3	14.4	—	36.8	25.6	—
16-30 Sept.	45.2	13.8	8.7	47.3	15.0	—	40.3	21.8	8.7
1-15 Oct.	—	16.0	—	—	—	—	42.3	20.0	8.4

Fish with three rings were not clearly differentiated as a distinct age-group. Because of small numbers neither modes nor general shapes of the distributions could be clearly determined. Means tended to increase slightly as the season progressed. There was considerable overlap of the lower end of the length range with the upper end of the length range of two-ring fish.

If the rings we observed were true annuli, the distance from the last ring to the scale edge should have decreased as the number of rings increased, and should have increased throughout the season for fish having the same number of rings. Both of these trends were apparent (Table 6).

Mean lengths back-calculated to the age of annulus formation from fish with one, two, or three rings were similar, and the mean lengths at the time of first ring formation calculated from two-ring fish were slightly smaller than those calculated from one-ring fish, as would be expected (Table 7). This tendency for mean lengths back-calculated from successively older ages of the same year class to become progressively smaller is commonly known as Lee's phenomenon and may be caused by a variety of factors. Mean lengths calculated from three-ring fish, however, were slightly larger, rather than smaller, than mean lengths calculated from either one- or two-ring fish.

Frequency distributions of lengths back-calculated to the time of the first, second, and third ring formation were well separated from each other, with only a small overlap between one- and two-ring and two- and three-ring fish (Figure 2). Those at the time of the first ring formation were similar in shape, whether calculated from one-ring, two-ring, or three-ring fish. Those calculated from two-ring fish were shifted slightly farther to the left than those calculated from one-ring fish, as

TABLE 7.—Mean lengths (millimeters) of Gulf menhaden at the time of each ring formation calculated from one-, two-, and three-ring fish, 1968-72 year classes.

Year class	First ring			Second ring		Third ring
	1-ring fish	2-ring fish	3-ring fish	2-ring fish	3-ring fish	3-ring fish
1968	—	—	88.4	—	157.4	186.4
1969	—	95.2	96.6	164.5	166.1	195.1
1970	90.3	85.1	92.9	165.0	166.3	195.3
1971	95.0	86.3	—	158.9	—	—
1972	100.3	—	—	—	—	—

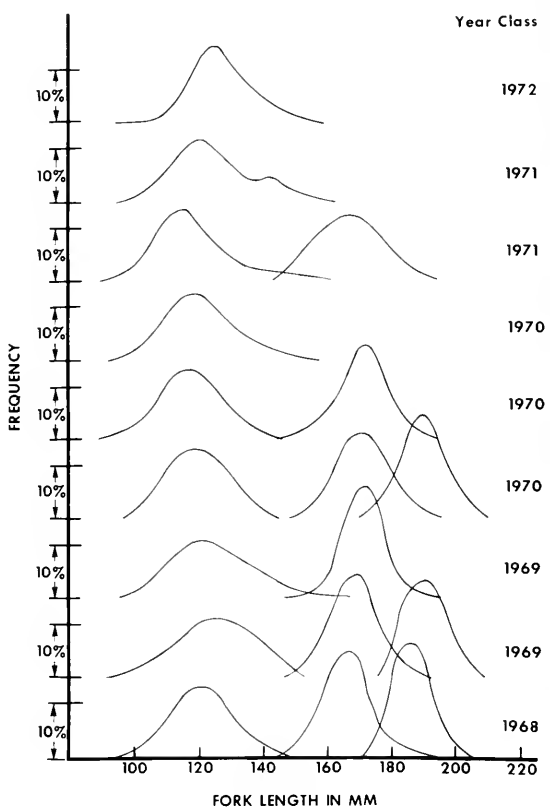

FIGURE 2.—Length-frequency distributions at time of first, second, and third ring formation, back-calculated from one-ring, two-ring, and three-ring Gulf menhaden, 1968-72 year classes.

would be expected. Those at the time of the second ring formation, whether calculated from fish with only a ring in the second position or from fish with both rings, were nearly identical and were shifted slightly to the right of distributions calculated from fish with three rings.

CONCLUSIONS

On scales of most Gulf menhaden with one or two rings, the rings appear to be true annuli. A relatively large number of fish that do not form a ring at the end of the first year form a ring at the end of the second year. A very small number that form a ring at the end of the first year do not form a ring at the end of the second year. It is possible, therefore, to separate age-2 from age-1 fish by the number of rings, or the location of the ring if only one is visible.

For fish having scales with more than two rings, or with two rings that are oddly spaced, it is difficult to differentiate between true and false annuli, or to determine to what year a particular ring should be assigned. On scales of some fish that could be age 3 on the basis of length, only two rings are visible, in what appears to be either the first and second or second and third positions. On some scales that have three well-defined rings, the spacing appears too unusual to be true annuli. For those fish that are called age 3, the lengths overlap those of age-2 fish, the mean lengths and ranges progress very little during the season, and the mean increments from the last annulus to the scale edge show little increase. We concluded that it is impossible to separate age-3 from age-2 fish with a high degree of certainty on the basis of the number or the location of scale rings.

From late August until October a small number of fish ranging from about 115 to 135 mm appear. We believe most of these fish, which have no scale rings, are age 0, but we cannot be certain because many of the fish in this size range of age-1 fish also have no scale rings.

The small number of tags recovered after 2 yr from fish tagged as juveniles, or age 0, the scarcity in the catch of fish larger than those with two rings, and the small numbers of fish with more than two rings, indicate that few Gulf menhaden live to be older than age 2. Since both age-0 and age-3 fish compose <2% of the catch, and since each age-group is either impossible or difficult to identify, we believe it is practical to recognize only two age-groups of Gulf menhaden: those age 1 or younger and those age 2 or older.

If only two ages are recognized, fish with no annuli can be aged by length. For each month, those below a certain fork length can be called age 1 or under, those above a certain length age 2 or older. Those in between cannot be individually aged, but the number in each length class can be apportioned to each age-group on the basis of the percentage of fish in each length class with one or two annuli. For example, in June 1971 (Table 3) all fish <165 mm may be called age 1, all >185 mm age 2. Of the 31 unaged fish 165-169 mm, 30 (97%) are age 1 and 1 (3%) is age 2; of the 45 between 170 and 174 mm, 37 (82%) are age 1 and 8 (18%) are age 2.

A question that may arise concerns the accuracy of previous aging methods. To shed some light on this question, we compared the percentages of fish at each age for methods 1 and 2. In method 1, fish ages had been based on a combination of factors: the general appearance of the scales, the number and location of rings, the fish length, and the time of year the fish was caught. In method 2, fish that had been aged by the number and location of scale rings, and fish that could not be aged, were grouped in 5-mm size classes. For each size class the number of unaged fish were apportioned to each age-group by the same percentage as fish that had been aged. We retained the age-3 group for comparative purposes, but could not differentiate between age-0 and age-1 fish.

The percentages at each age were remarkably similar, the differences between methods varying from only 0.1 to 2.7%. We concluded, therefore, that age compositions based on the previous method of aging are reliable and that valid inferences pertaining to population dynamics of Gulf menhaden can be based on them.

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VARIABILITY IN ZOOPLANKTON BIOMASS DISTRIBUTION IN THE NORTHERN SARGASSO SEA: THE CONTRIBUTION OF GULF STREAM COLD CORE RINGS[1]

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ABSTRACT

The scale and frequency of physical variability resulting from incursion of Gulf Stream cold core rings into the northern Sargasso Sea makes this faunal province more heterogeneous than previously recognized. At any one time such rings may cover between 6 and 13% of the surface area of the northern Sargasso Sea. They are more productive than the surrounding Sargasso Sea and have a zooplankton biomass intermediate between the Sargasso Sea and the slope water. Cold core rings may augment by 3 to 7% the primary productivity and by 8 to 16% the zooplankton standing crop of the northern Sargasso Sea. Compared with either the surrounding Sargasso Sea or their parent slope water, an unusually large percentage of the 0-800 m biomass in rings is found at depths greater than 200 m. This distribution may be related to hydrographic and biological changes associated with ring decay. Because of their higher productivity, differences in vertical biomass structure, and the possibility that ring food chain efficiency is lower than that of the Sargasso Sea, rings may provide a disproportionately large fraction of the total supply of organic matter to the northern Sargasso deep Sea.

A number of papers have characterized the zooplankton biomass of the northern Sargasso Sea (Menzel and Ryther 1961; Grice and Hart 1962; Bé et al. 1971; Deevey 1971; Deevey and Brooks 1971; and others). Because of the variety of methods employed in both sampling and processing, the results of these studies are not readily comparable. In general, previous authors have portrayed the Sargasso Sea as a remarkably homogeneous faunal province. The scale and frequency of regional variability resulting from incursions of cold core rings into the Sargasso Sea have not been generally appreciated. Cold core rings are mesoscale hydrological features 150 to 300 km in diameter and up to several thousand meters in depth. They form when southerly directed Gulf Stream meanders become so accentuated as to separate from the Stream and move south, enclosing a core of cold and relatively fresh slope water within a remnant of the Gulf Stream (Parker 1971; Fuglister 1972; Richardson 1976). It is likely that in the northern Sargasso Sea, at any one time, there are 10 to 15 such rings (Lai and Richardson 1977). Estimating the surface area of the northern Sargasso Sea as 32.9×10^5 km^2 (Jahn 1976), cold core rings may cover between 6 and 13% of this surface. (Throughout the ensuing sections, unless otherwise indicated, the terms ring, slope water, and Sargasso Sea denote hydrographic, not geographic, entities.)

An overview of the phytoplankton, zooplankton, and midwater fish populations inhabiting cold core rings has been given by Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). The results of that study indicated that mean zooplankton biomass in the upper 750-800 m of rings between 3 and 10 to 12 mo of age was consistently higher than that in the surrounding Sargasso Sea. In these preliminary data the fraction of biomass below 250-300 m in depth was particularly large while the near surface was more similar to the Sargasso Sea. We have now taken vertically stratified hauls in the same ring 3 mo apart. The data from these hauls confirm our initial interpretation.

The objective of this paper is twofold. First, we describe the zooplankton biomass distributions characteristic of the northern Sargasso Sea, of a cold core ring, and to a lesser extent of the slope water—the source of ring water. Second, we will attempt to relate the patterns observed to systematic variations in phytoplankton standing

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crop, primary productivity, and water temperature, and to explore the significance of ring biomass distribution.

METHODS

The major portion of the data to be presented in this paper was collected on RV *Chain* cruise 125 (August 1975) and on RV *Knorr* cruise 53 (November 1975). The ring sampled (designated Ring-D by the Naval Oceanographic Office), was formed in February 1975. It was, therefore, about 6 mo old when first sampled and 9 mo old when sampled again in November. In November the slope water was hydrographically complex. It is likely that some of our intended slope water tows (MOC 39 and MOC 40) may have been taken in the vicinity of a warm core ring (Saunders 1971). The upper 200 m of the water column at that station was warmer and more saline than is typical for the slope water. In addition, infrared satellite photographs clearly show the presence of this warm ring during the period of sampling. Other slope water stations may have been influenced by the passage of a warm core ring. In analyzing the data, MOC 39 and 40 are considered separately and designated warm core ring tows. Data corroborating specific points or conclusions have been drawn from collections made on RV *Atlantis* cruise 71, RV *Chain* cruise 111, and RV *Knorr* cruises 35 and 38 (Table 1).

Collections in Gulf Stream cold core rings, the northern Sargasso Sea, and slope water were made with three types of sampling gear: on the early cruises 1-m diameter ring nets or modified opening/closing 70-cm diameter bongo nets (McGowan and Brown 1966), on the two most recent cruises a multiple opening/closing net and environmental sensing system—MOCNESS (Wiebe, Burt, Boyd, and Morton 1976)—with a mouth area of 1 m × 1.4 m (effective area is 1 m^2). All nets were constructed from 0.333-mm Nitex[3] gauze; depth recorders and flow meters were used on all tows.

The 1-m nets were hauled obliquely, ideally to a depth of 800 m. On some cruises a second haul was taken to a depth of 300 m. Bongo nets were towed obliquely within the depth intervals 0-250, 250-500, and 500-750 m. With occasional exceptions, the MOCNESS sampled both from 800 m to the surface in 100-m intervals, and from 200 m to the surface in 25-m intervals. Sampling with 1-m and bongo nets was almost always done at night, while at most MOCNESS stations samples were taken both day and night. The types of tows taken on the five cruises are given in Table 1. All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium tetraborate. In the vicinity of all plankton hauls, hydrographic casts were made yielding nearly concomitant vertical profiles of temperature, salinity, oxygen, chlorophyll, nutrients, primary productivity, and phytoplankton species (see Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox 1976 for methods).

Zooplankton biomass was measured by the method of Ahlstrom and Thrailkill (1963) after removal of all organisms greater than 5 cm^3. Displacement volumes were measured 5 to 9 wk after a cruise. No attempt has been made in this paper to partition the biomass according to taxa. The species composition of those samples already examined appears similar to that reported for the region by Grice and Hart (1962), Deevey (1971), and Deevey and Brooks (1971).

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

TABLE 1.—Summary of slope water, ring, and Sargasso Sea zooplankton sample stations.

Cruise	Date	Age of ring (mo)	Number of samples (stations)			Type of net
			Ring	Sargasso Sea	Slope water	
Atlantis II 71[1]	21 Sept.-14 Oct. 1972	10-12	8(4)	28(15)	4(2)	1 m
Chain 111[1]	7 Feb.-18 1973	3.5	6(2)	5(2)	2(2)	1 m and bongos
Knorr 35[1]	23 Nov.-3 Dec. 1973	3.0	8(4)	1(1)	5(3)	1 m and bongos
Knorr 38[1]	12 Feb.-3 Apr. 1974	10-12				1 m
Chain 125[2]	4 Aug.-17 1975	6.0	48(1)	32(2)	48(2)	MOCNESS
Knorr 53[3]	17 Nov.-1 Dec. 1975	9.0	48(1)	40(2)	64(3)	MOCNESS

[1]Positions of stations illustrated in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976).
[2]Sargasso Sea: MOC 1,2 (35°37′, 68°31′), MOC 3,4 (35°22′, 68°17′), MOC 12 (34°11′, 71°40′), MOC 13,14,15 (34°10′, 71°34′); ring: MOC 5,11 (34°29′ 69°56′), MOC 6,7 (34°34′, 69°52′), MOC 8 (34°31′, 69°49′), MOC 10 (34°33′, 69°53′); slope water: MOC 16,17 (38°02′, 69°59′), MOC 18,19 (38°05′, 70°02′), MOC 20,21 (39°05′, 70°12′). All positions are north latitude and west longitude.
[3]Sargasso Sea: MOC 23,24,25 (32°44′, 71°10′), MOC 26 (32°52′, 71°08′), MOC 34 (34°12′, 70°30′); ring: MOC 27, 28, 29 (33°49′, 71°54′), MOC 31 (35°50′, 71°48′), MOC 32 (33°56′, 71°54′), MOC 33 (34°03′, 71°56′); warm core ring: MOC 39,40 (40°04′, 68°05′); slope water: MOC 35,36 (38°51′, 67°47′), MOC 37,38 (38°55′, 67°46′), MOC 41,42 (39°59′, 69°00′). All positions are north latitude and west longitude.

RESULTS

Regional Biomass

The biomass collections obtained in the same ring 3 mo apart in August and November 1975 corroborate differences already noted in 0-800 m zooplankton biomass between the Sargasso Sea, cold core rings, and slope water (Figures 1, 2). In both months the slope water 0-800 m biomass was larger than either the Sargasso Sea or ring 0-800 m biomass (Mann-Whitney U-test, $P<0.01$). In August, the contrast between slope water and the two other regions was particularly marked with average concentration in the upper 800 m approximately 10-12 times larger than in the Sargasso Sea and ring (Table 2, top). At several depths in the August slope water stations the zooplankton biomass was dominated by *Salpa aspera*.[4] Differences in abundance of this salp accounted for a large part of the variation between slope water stations. The high water content of these animals undoubtedly caused our estimate of biomass by displacement volume to be considerably higher than had we measured dry weight or organic carbon content. It is clear, nonetheless, that the standing stock of zooplankton was exceedingly large.

Relative to the Sargasso Sea, 0-800 m ring biomass was on the average 1.36 times larger in August and 1.33 times larger in November (Table 2, bottom). These differences are consistent with data from previous cruises; using paired regional biomass averages observed on all cruises to date (Table 3) we see that the mean zooplankton biomass in rings and in the Sargasso Sea is significantly different (Sign test, $P<0.05$).

TABLE 2.—Comparison of slope water, ring, and Sargasso Sea zooplankton biomass (cm^3/m^2) based on weighted averages of day and night samples collected at 0-800, 200-800, and 0-200 m depth intervals. Number of tows used to make average given in parenthesis.

	August 1975			November 1975		
Region	0-800	200-800	0-200	0-800	200-800	0-200
Sargasso Sea	16.6(4)	8.8(4)	8 1(8)	10.2(2)	5.6(2)	6.0(4)
Ring fringe				9 1(1)	4.3(1)	4 8(1)
Cold core ring	22.5(3)	15.6(3)	6.4(6)	13 6(4)	11.4(4)	3 4(5)
Slope water	256.2(4)	95.6(4)	121.8(6)	33.8(4)	23.0(4)	12.8(6)
Warm core ring				27.9(2)	17.2(2)	10.8(2)

	Ratio ring/Sargasso Sea		
Month	0-800	200-800	0-200
August	1.36	1.77	0.79
November	1.33	2.03	0.56

In November zooplankton standing crop was consistently lower than in August with the most pronounced change occurring in the slope water. Although *S. aspera* was still present at the slope water stations, it no longer dominated the biomass. Comparing August and November 0-800 m biomass averages, segregating day and night samples for each region, we see that the overall seasonal decline is statistically significant (Sign test, $P<0.05$, computed using cubic centimeters per square meter in Figures 1 and 2). Indeed only one November 0-800 m biomass value was as large as the smallest 0-800 m biomass in the same region in August.

[4]The significant biomass contribution of *S. aspera* is discussed in Wiebe, P. H., L. P. Madin, G. R. Harbison, L. R. Haury, and L. M. Philbin. 1977. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. Submitted to Mar. Biol.

TABLE 3.—Average zooplankton biomass in slope water, ring, and Sargasso Sea—dry weight (mg/m^3) in column ≈750 m deep. Numbers of stations per area and range of biomass values (after colon) given in parenthesis. This table is an expanded version of table 3 in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). Note that the biomass units in the original table were incorrectly presented as milligrams per square meter.

Cruise	Slope water	Ring	Sargasso Sea	Ring age (mo)	Ring ÷ Sargasso	Slope ÷ Sargasso
Atlantis II 71	7.43 (1)	2.24 (4:2.06-2.60)	1.68 (4:1.34-2.05)	10-12	1.33	4.42
Chain 111	4.21 (1)	4.95 ([1]2:2.21-7.68)	2.70 ([2]3:1.99-3.96)	3.5	1.83	1.56
Knorr 35	6.06 ([3]4:3.60-7.74)	3.67 ([4]3:3.15-4.33)	2.47 (1)	3.0	1.49	2.45
Knorr 38[5]	5.74 (4:2.2-9.14)	3.10 (6:2.56-4.98)	2.34 (4:1.76-3.21)	10-12	1.32	2.45
Chain 125[5]	9.10 ([6]2:6.85-11.35)	2.26 (3:1.73-2.57)	1.49 (4:0.90-1.97)	6	1.52	6.11
Knorr 53[5]	3.43 (4:2.77-4.03)	1.09 (4:0.72-1.35)	0.83 (2:0.80-0.86)	9	1.31	4.13
Mean				7.3	1.47	3.52

[1]Each of the two values is integrated for the water column based on three stratified bongo net tows.
[2]Two values are from oblique meter net tows; one is an integrated value based on three stratified bongo net tows.
[3]Two values are from oblique meter net tows; one is an integrated value based on three bongo net tows; one is an oblique bongo net tow
[4]One value is an integrated value based on three stratified bongo net tows; two values based on two stratified bongo net tows.
[5]Cubic centimeters per cubic meter converted to milligrams per cubic meter using equation 4 table 2 in Wiebe et al. (1975). Note that this conversion affects the regional biomas ratios (see Figure 2) because the relationship between displacement volume and dry weight is not linear.
[6]Salp-rich tows, MOC 39 and MOC 40, excluded.

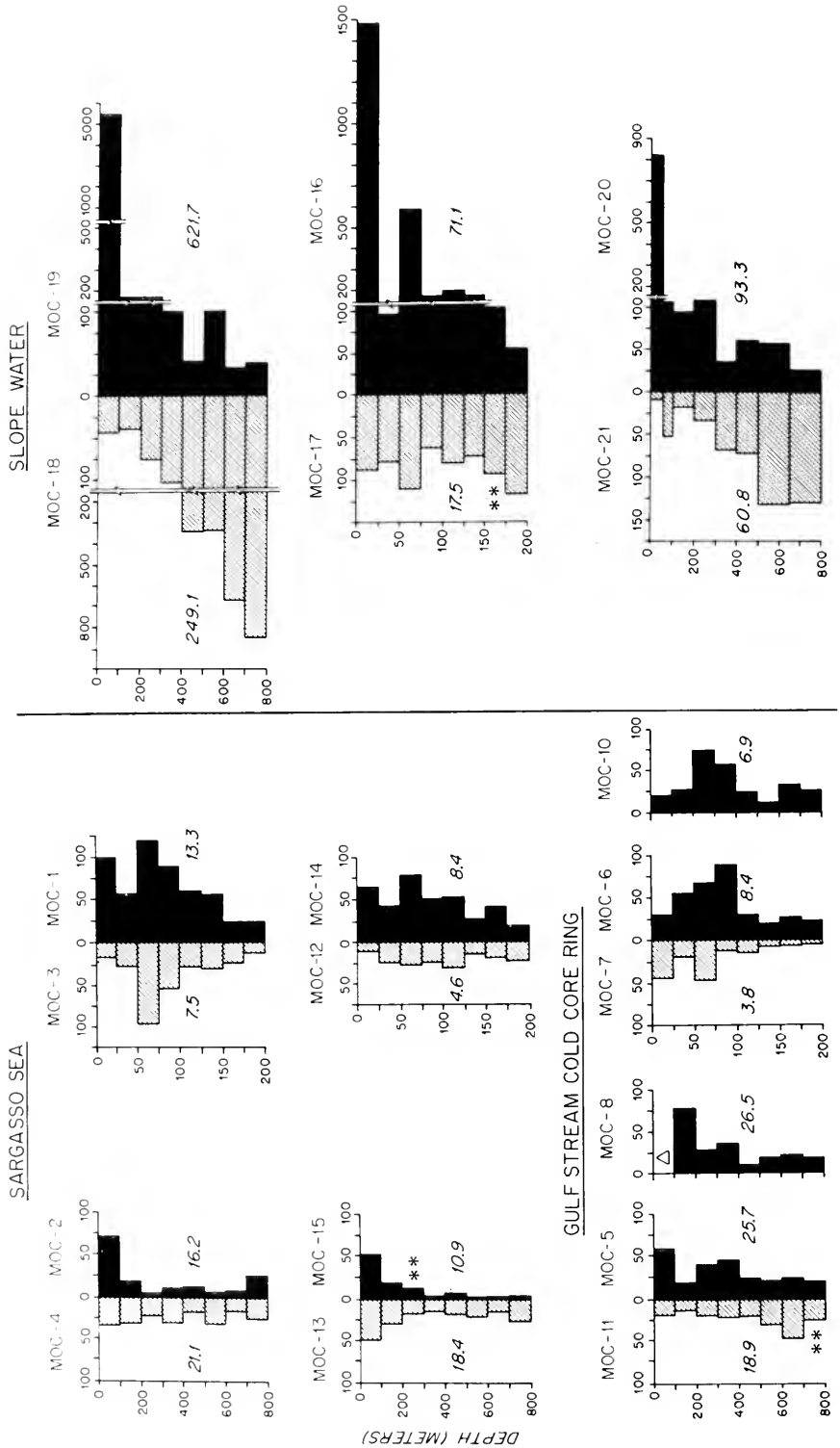

FIGURE 1.—Slope water, ring, and Sargasso Sea zooplankton biomass ($cm^3/1{,}000\ m^3$). August 1975—*Chain* cruise 125. Values associated with each profile are cubic centimeters per square meter for the entire portion of the water column sampled. Note that 0-200 m profiles have an expanded vertical depth scale.

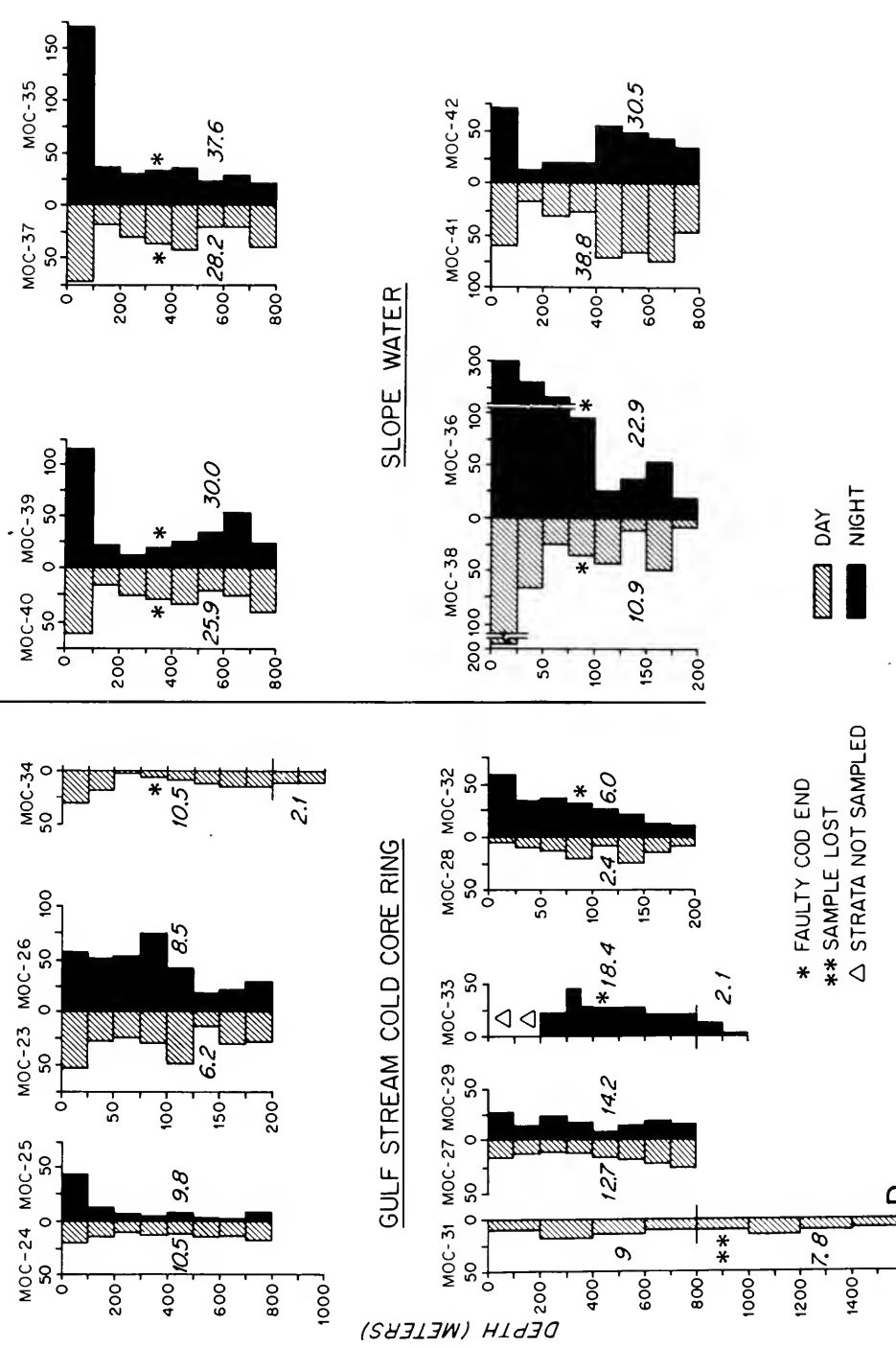

FIGURE 2.—Slope water, ring, and Sargasso Sea zooplankton biomass ($cm^3/1{,}000\ m^3$). November 1975—*Knorr* cruise 53. Values associated with each profile are cubic centimeters per square meter for the water column sampled except for MOC-31, MOC-33, and MOC-34, where values have been calculated for above and below 800 m. Note that 0-200 m profiles have an expanded vertical depth scale.

Average Vertical Structure

Comparing Ring-D biomass partitioned according to depth, the upper 200 m in the ring contained, on the average, less biomass during both sampling periods than did the Sargasso Sea (Table 2, top). This was true both day and night during the August and November cruises. In contrast, ring biomass between 200 and 800 m was higher both day and night (Figures 1, 2). The range of 200-800 m biomass values in the ring and in the Sargasso Sea does not even overlap. The combination of lower average surface biomass and higher average subsurface biomass in the ring is highly significant (Sign test, $P<0.01$, computed using sums of 0-200 m and 200-800 m $cm^3/1{,}000\ m^3$ derived from Figures 1 and 2). The regional weighted averages of percent 0-800 m biomass present in the upper 200 m in August were 51%, 34%, and 27% in the Sargasso Sea, slope water, and ring, respectively. In November these averages were 45%, 32%, and 25% (Table 4). Although very different sampling systems and tow strategies were employed, data from *Atlantis II* cruise 71 corroborate the direction of difference of these observations in that the percentages of 0-800 m biomass found at night in the upper 300 m were 64% and 52% for the Sargasso Sea and ring, respectively (Table 5). In addition, the 300-800 m biomass was 1.73 times larger in this latter ring than in the surrounding Sargasso Sea.

TABLE 5.—Ring and Sargasso Sea zooplankton biomass—*Atlantis II* cruise 71 (mg/m^2).

Area	0-300 m	0-800 m	$\frac{0\text{-}300}{0\text{-}800} \times 100$	
Ring	954	1,648	58%	52%
	963	2,080	46%	
	930	1,704	55%	
	828	1,728	48%	
Sargasso Sea	858	1,344	64%	64%
	798	1,072	74%	
	765	1,640	47%	
	921	1,304	71%	

Diel Migration

Complicating these general observations and contributing to sample variability are day/night differences in biomass distributions (Table 4). In all day/night sample pairs the fraction of 0-800 m biomass present in the 0-200 m interval is larger in the night sample (Sign test, $P<0.01$). This results from either diel migration or day/night differences in avoidance within the comparatively well-illuminated surface layers. Avoidance does not appear to be an important factor because at some stations the day 0-800 m biomass exceeds the night 0-800 m biomass. This is true in all Sargasso Sea 0-800 m sample pairs and at one slope water station (Figures 1, 2). Furthermore, some species of zooplankton taxa already enumerated, e.g., euphausiids and pteropods, exhibit strong diel migration patterns in all three areas.

Since we believe diel migration to be the appropriate explanation, the data further suggest that while essentially the same percentage of 0-800 m biomass was migrating into the surface layers of the Sargasso Sea (24-30% during both sampling periods), there was a reduced percentage migrating in the ring in November (21% in August versus 9% in November—Table 4). Although a smaller proportion of the biomass may have been migrating in the ring relative to the Sargasso Sea, there was a significantly greater (Mann-Whitney U-test, $P<0.05$) day/night biomass ratio in the

TABLE 4.—Percent of 0-800 m slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m (800 m tows only). D = Day; N = Night.

	August 1975					November 1975				
Region	Percentages of individual tows	D	N	N−D	(D + N)/2	Percentages of individual tows	D	N	N−D	(D + N)/2
Sargasso Sea	$D_1 = 32$	39	63	24	51	$D_1 = 30$	30	60	30	45
	$N_1 = 57$					$N_1 = 60$				
	$D_2 = 41$									
	$N_2 = 69$									
Ring fringe						$D_1 = 46$	46			
Cold core ring	$D_1 = 16$	16	37	21	27	$N_1 = 29$	20	29	9	25
	$N_1 = 32$					$D_1 = 21$				
	$N_2 = 42$					$D_2 = 19$				
Slope water	[1]$D_1 = 3$	7	61	54	34	$D_1 = 32$	23	41	18	32
	[1]$N_1 = 93$					$N_1 = 55$				
	$D_2 = 7$					$D_2 = 13$				
	$N_2 = 61$					$N_2 = 27$				
Warm core ring						$D_1 = 30$	30	46	16	38
						$N_1 = 46$				

[1]On this tow series, MOC 18 and 19, salps were extremely dominant. These tows are excluded from averages.

upper 200 m in the ring (Table 6). This apparent contradiction results from the fact, already noted, that the percentage of 0-800 m biomass present in the upper 0-200 m was very much greater in the Sargasso Sea. Day/night ratio of biomass in the upper water column is often used to measure intensity of diel migration; clearly the meaning of this ratio is highly dependent upon average vertical biomass distribution.

Slope water day/night sample pairs may be interpreted as documenting diel migration, but the data are extremely variable both within and between cruises (Table 4). There may have been a less well-developed migration in the fall, but the generality of this is questionable.

TABLE 6.—Day/night differences in slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m.

Region	Ratio night/day			
	August 1975		November 1975	
Sargasso Sea	[1]1.78	[2]1.37	[1]1.37	[2]1.86
	[1]1.84	[2]0.99		
Cold core ring	[1]2.01	[3]3.10	[1]2.48	[2]1.86
Slope water	[1]4.06	[2,3]68.33	[1]2.10	[2]2.27
		[2,3]14.82		[2]1.70

[1]Based on 0-200 m tows
[2]Based on 0-800 m tows
[3]Ratio affected by extreme salp dominance

Shallow Biomass Structure

In the 0-200 m biomass profiles, an intermediate biomass peak occurred between 50 and 100 m depth at nearly every station in August 1975 (Figure 1: MOC 1, 3, 6, 7, 10, 16, 17). At all but one of the Sargasso Sea and ring stations this intermediate peak is the highest observed value in the 0-200 m tows. At slope water stations of the same cruise this intermediate peak is the second highest observed value. If we rank each interval in a profile in order of zooplankton abundance, we can test the significance of this observation. For instance, the individual summer tows in the ring and the Sargasso Sea exhibit significant concordance as to which depth intervals have the larger and which the smaller zooplankton biomass (Friedman 2-way analysis of variance on ranks, $P<0.005$). Given this result, the best estimate of the differences between intervals is the order of their summed ranks (i.e., 50-75 m>75-100 m>100-125 m>25-50 m>0-25 m>150-175 m>125-150 m>175-200 m). Applying a procedure for testing differences between individual depth intervals (Nemenyi 1963), we see that concordance results from the fact that the 50-75 m biomass is significantly greater than the biomass in the intervals 125-150, 150-175, and 175-200 m, and the 75-100 m biomass is greater than the 175-200 m biomass ($P<0.05$). An intermediate peak is not a notable feature of any of the 0-200 m profiles taken on the fall cruise with the exception of the Sargasso Sea sample pair (Figure 2: MOC 23, 26).

DISCUSSION

Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have discussed the formation and decay of an idealized cold core ring. Initially conditions inside a ring core are identical to those in the slope water just northward of the Gulf Stream at the time of ring formation. Through time the ring decays; the isotherms deepen, the water becomes more saline, the O_2 minimum deepens, and the constituent flora and fauna either die off or become diluted by populations from the surrounding Sargasso Sea. Because zooplankton populations are generally suited to the environmental conditions they encounter within their normal range, this decay process may be viewed as the gradual imposition of a complex environmental stress upon an entire community. Wiebe, Hulbert, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have documented some of the intermediate stages in this idealized process. In fact, this process can be aborted when a ring is reabsorbed by the Gulf Stream (Fuglister 1972; Richardson et al. 1977). All biological and physical properties are not equally conservative so their decay rates would not be the same.

Regional Contribution of Cold Core Rings

PRIMARY PRODUCTIVITY.—It is well known that slope water is more productive than the Sargasso Sea. Ryther (1963) estimated that slope water is about twice as productive on an annual basis (120 g C/m^2 per yr versus 60 g C/m^2 per yr). Although our own data are scanty, rings on the average are intermediate between slope water and the Sargasso Sea (Table 7). A few simplifying assumptions permit budgetary computations to be made regarding the overall effect of rings on the carbon budget of the northern Sargasso Sea. Let us assume an average ring life of 1 yr and a linear rate of decay of productivity (i.e., that annual ring production is the arithmetic mean of annual Sargasso Sea and slope water production). Allowing 6 to 13% as the areal contribu-

TABLE 7.—Summary of slope water, ring, and Sargasso Sea primary productivity (mg C/m² per day), phytoplankton carbon[1] (mg/m²), and chlorophyll *a* (mg/m²) measurements.

Region	March 1974		August 1975		Phytoplankton carbon	November 1975		Phytoplankton carbon
	Productivity	Chlorophyll	Productivity	Chlorophyll		Productivity	Chlorophyll	
Sargasso Sea	228 5	46 4	[2]207	13 3	33 4	86.5		21
							12.0	
			100			252.2		
Cold core ring	440 1					483.2		
		73 0	83	17 3	45			28.2
	333 1		106			155.5	10.3	
						186.5		
Slope water	1,025 5		175			1,302 2		
		70 4		50.5				
	368 4		270		280	824.0	39	287
						376.2		
						363.7		

[1]Based on counts of cells larger than 4-5 μm
[2]The high value in average mg C·m² per day observed at this station is a consequence of one unusually high surface value.

tion of rings to the northern Sargasso Sea as explained earlier, and Ryther's estimate of a twofold difference in annual production, the net annual production of the geographic northern Sargasso Sea is then 3 to 7% higher than if it contained no rings (i.e., $6 \times 1.5 = 9$, $9 + 94 = 103$ and $13 \times 1.5 = 20$, $20 + 87 = 107$). Our assumption of linear decay is most certainly an oversimplification. In November 1975, the ring water column, like the slope water, began its winter overturn before the surrounding Sargasso Sea. Mixing eroded the seasonal thermocline that had been observed in Ring-D in August 1975. The decay we have assumed was reversed, and ring productivity was enhanced (Table 7).

ZOOPLANKTON STANDING CROP.—Similar calculations can be made regarding the relative contribution of rings to the mean zooplankton biomass of the geographic northern Sargasso Sea. Neglecting one station which had anomalously high values due to extreme salp dominance, the average of slope water biomass values is 3.5 times the observed Sargasso Sea biomass (Table 3). Given this ratio and the same linear [i.e., $(3.5 + 1) \div 2 = 2.25$] and areal assumptions made earlier, rings may augment the zooplankton standing crop of the geographic northern Sargasso Sea by 8 to 16% (i.e., $6 \times 2.25 = 14$, $14 + 94 = 108$ and $13 \times 2.25 = 29$, $29 + 87 = 116$). Our ratio of slope water to Sargasso Sea biomass may be compared with that of Grice and Hart (1962), who reported the slope water standing crop as three to four times that of the Sargasso Sea. They also excluded extremely salp-rich samples in making this comparison. Our assumption of 2.25 as an annual mean ring/Sargasso biomass ratio (i.e., linear decay) may be an overestimate considering the average biomass ratio obtained on all cruises to date and the average ring age sampled (Table 3). On the other hand some rings do last longer than a year and the lowest ring:Sargasso Sea ratios that we have observed are approximately 1.3 (i.e., >1.0).

We have noted a highly significant decline in 0-800 m biomass from August to November in slope water, ring, and Sargasso Sea both in data presented here and in data more recently collected.[5] This observation is consistent with those of Grice and Hart (1962) with respect to the slope water. They noted, however, no such decline in the Sargasso Sea. Neither is there a summer-to-fall decline in the Sargasso Sea data of Deevey (1971). The Sargasso Sea and slope water data of Fish (1954) exhibit irregular fluctuations in biomass throughout the summer and fall. Moore (1949) presented some Sargasso Sea data indicating a progressive decline of biomass from a spring maximum to a fall minimum. Their data substantiate that interseasonal fluctuations in the Sargasso Sea are less marked than in the slope water.

Vertical Structure

We have pointed out that, compared with either the Sargasso Sea or slope water, an unusually small percentage of 0-800 m biomass is present in the upper 200 m of a ring. We found a relatively large fraction of the 0-800 m zooplankton biomass above 200 m in the northern Sargasso Sea. The netting employed by Leavitt (1935, 1938) was relatively coarse (1.0 mm) so it is difficult to compare our results with his. Nonetheless, at his two Sargasso Sea stations (2462, 2463) the percentages of

[5]Some of this data is presented in figure 4 of Richardson, P. L., J. Schmitz, and P. H. Wiebe. 1977. Gulf Stream ring experiment. Polymode News 25:3. Unpubl. manuscr.

0-800 m biomass present in the upper 200 m were 42 and 49% which corresponds closely to our values (Table 3). Both of our results are virtually identical with those obtained by Menzel and Ryther (1961). From their table 1 we can calculate the percentages of 0-500 m biomass and 0-1,000 m biomass present above 200 m. Averaging the results, we find 44% of the 750-m biomass was present during the day above 200 m. Iashnov (1961) presented data for the Sargasso Sea in which 90% of the 0-1,000 m plankton was present above 200 m, but he used a relatively fine mesh net (0.180 mm). Unfortunately, Deevey and Brooks (1971) characterized 500-m depth intervals with horizontal tows at the midpoint of each interval to 2,000 m, while Grice and Hart (1962) sampled only the upper 100-200 m.

Several authors suggest that a vertical biomass structure similar to our slope water and Sargasso Sea observations is to be expected in temperate or subtropical oceanic environments relatively free of advective inputs. Vinogradov (1968: figure 47 and stations 3206 and 3829 in table 18) gave examples of oceanic regions with such a distribution. Zenkevich and Birstein (1956) agreed that zooplankton biomass in the North Pacific rather steadily decreases from the surface downwards, although the most marked reduction they discuss might be below our lowest standard sampling depth. The one very deep tow series we obtained in a ring, however, gave no indication of such a reduction (Figure 2, MOC 31).

Zooplankton biomass profiles obtained by Murano et al. (1976) in the northwest Pacific above the Sagami Trough exhibit the expected decrease with depth. Reanalyzed in our manner, the data of Marlowe and Miller (1975) for Station P in the North Pacific support the above generalization; the percentage of their 0-500 m biomass found at night in the upper 200 m was 57%. If one extrapolates their 500-m values as approximately applicable to the 500-800 m interval—a conservative approach for this argument—the resulting percentage becomes 49% (N). This is not unlike our average slope water percentage of 51% (N) and quite distinct from the average ring percentage of 33% (N) (Table 4). Station P is very different from Ring-D in respect to its vertical biomass distribution.

In slope water, the intermediate biomass peak in the upper 200 m approximately coincides with the depth of a nitrite maximum of the type discussed by Vaccaro and Ryther (1960). Our results and those of Marlowe and Miller (1975) appear to differ: they felt that the shallow nitrite peak of Station P was avoided by zooplankton. Since the levels of nitrite we have observed at the maximum are only slightly lower than those reported by Marlowe and Miller (0.2-0.5 μg A-N-NO_2/l versus 0.64 μg A-N-NO_2/l), our findings cast doubt on their speculation that nitrite toxicity might have been involved in the maintenance of the biomass minima they observed.

Explanations for Ring Biomass Structure

Given the relatively high zooplankton biomass of the slope water, it is clear why cold core rings have a higher average zooplankton biomass than the Sargasso Sea. Further, their higher average primary productivity appears responsible for this differential persisting 10-12 mo after ring formation. Our data suggest the decline in ring biomass takes place rather slowly; the oldest rings sampled (10-12 mo) had ring/Sargasso biomass ratios only 20% smaller than the same ratios in the newest rings sampled (3.0 and 3.5 mo, Table 3). Although physically and chemically intermediate between slope water and Sargasso Sea, rings appear to be unique in their vertical distribution of biomass.

We offer two logically distinct explanations for the small fraction of the 0-800 m biomass found within the upper 200 m of a ring. They are not mutually exclusive and the relative importance of these explanations is species dependent. The simpler argument stresses the importance of a physical factor—temperature. If a slope water animal were physiologically restricted to a particular temperature range, its habitat would descend as the ring decayed and isotherms sank. To the extent that the zooplankton population in the slope water exhibited this behavior, ring biomass distributions would deepen. This could apply only to a species which in its home range—the slope water—remains beneath the seasonal thermocline (i.e., moderately deep-living and exhibiting limited diel migration). Such a species would most likely have to be either carnivorous or omnivorous. Wiebe and Boyd (1978) have documented such a phenomenon for the slope water euphausid species, *Nematoscelis megalops*.

A more complex explanation stresses the importance of a biological factor—food resources. The kinds of changes that accompany ring decay must have a substantial effect upon zooplankton-phytoplankton interactions. Using unpublished

data obtained in August 1975 from 5 nine bottle hydrocasts, the number of phytoplankton cells per liter averaged 10,000 in the slope water, 2,500 in the ring, and 2,000 in the Sargasso Sea. Cells smaller than 4-5 μm were not enumerated and were, therefore, excluded from these computations. Values were integrated from 0 to 200 m—a conservative procedure tending to reduce slope water versus ring or Sargasso Sea differences. The species composition of the ring, while distinct, was more like that of the Sargasso Sea than that of the slope water. Again, considering the 0-200 m depth interval, the number of different phytoplankton species an animal would have encountered in a liter of water would, on the average, have been 6.0 (slope water), 9.6 (ring), and 10.4 (Sargasso Sea). Converting the mean cell volume of each species to carbon (Strathmann 1967) and multiplying by the number of individuals present, yielded values of average phytoplankton carbon of 1,400, 200, and 140 ng C/l. Thus, to acquire the same ration of food, a herbivore would have had to filter more than five times more water in the ring than in the slope water, and even more in the Sargasso Sea. In addition, the evenness of species' carbon equivalence was 0.46, 0.75, and 0.76. That is, the total carbon per liter was more evenly distributed among different species in the ring and the Sargasso Sea than in the slope water. (Evenness equals H/H_{max} (Pielou 1966) where H is the Shannon-Weaver diversity index computed upon species carbon equivalence rather than abundance and $H_{max} = \log_e S$ where S = number of species.) This last result implies that a herbivore capable of selecting by carbon content (i.e., particle size) would have found it less advantageous to concentrate on a particular species in the Sargasso Sea and the ring than in the slope water.

These properties of the phytoplankton population, i.e., species composition, carbon concentration, cell concentration, and cell carbon distribution, have profound effects on a filter-feeding herbivore's harvesting ability. We believe that early in ring evolution herbivorous slope water species are deleteriously affected and, therefore, may be replaced by Sargasso Sea forms more quickly than deeper living carnivorous or omnivorous slope water species. If we are correct, ring biomass distribution may deepen in part because a ring's 0-200 m biomass declines more rapidly than does its 200-800 m biomass.

Identification of some of the taxa in August 1975 samples, although limited, support the argument that in Ring-D epizooplanktonic herbivores were replaced before epizooplanktonic carnivores or omnivores. The species list of Ring-D thecosomatous pteropods, a largely herbivorous group, was quite similar to that of the surrounding Sargasso Sea.[6] Grice and Hart (1962) found that chaetognaths, a purely carnivorous group, were considerably more abundant in the Sargasso Sea than they are in slope water. In 6 nine-net fine-mesh tow series (12.5 cm diameter, Clarke-Bumpus nets with 67 μm mesh) taken in August, chaetognaths were five to ten times more abundant in the surrounding Sargasso Sea than they were in Ring-D. Other epizooplanktonic carnivores, e.g., *Stylocheiron suhmii* and *S. abbreviatum,* which are routinely found in the Sargasso Sea were not found in Ring-D August MOCNESS tows.

Organic Flux to Deep Sea

Rings may contribute a disproportionate fraction of the utilizable organic material available to the northern Sargasso deep sea. We feel this is likely both because of their generally higher productivity and because of their unique zooplankton biomass distribution and the factors that have resulted in that distribution. Ring zooplankton biomass below 200 m, in that it exceeds Sargasso Sea biomass and ultimately declines to a similar level, contributes to this augmentation. Differential seasonal mixing processes could also increase downward particulate flux. For example, in November 1975 we observed that winter mixing had proceeded further in Ring-D than in the surrounding Sargasso Sea water column. Herbivorous ring zooplankton (i.e., Sargasso forms) may have been unable to fully capitalize upon the sudden opportunity afforded by the increased primary production that accompanied the mixing (Table 7). If so, a larger fraction of this enhanced phytoplankton production would sink into the aphotic depths. Physical evidence obtained on two cruises undertaken to study rings during the summer has suggested to us that the seasonal thermocline may often be less stable in rings than in the Sargasso Sea.

Finally, there is a possibility of enhanced contribution of organic matter into the deep sea due to a lower overall trophic efficiency within the upper 200 m of rings (and slope water). If we divide

[6]John Wormuth, unpubl. data; cited with permission.

average 0-200 m zooplankton biomass (milligrams of carbon per square meter calculated using equation 4, table 2 in Wiebe et al. 1975) by 0-200 m phytoplankton carbon (milligrams of carbon per square meter from Table 5), excluding salp-rich MOC 18 and 19, we obtain the following ratios:

	Sargasso Sea	*Ring*	*Slope water*
Aug. 1975	253	138	84
Nov. 1975	332	131	28

Ratios in the ring are low, as are those in the slope water. Lower ratios suggest to us lower overall trophic efficiency within the upper 200 m. Although biased in that many cells are quite small, particularly in the Sargasso Sea, phytoplankton carbon of cells >5 μm is probably a reasonable estimate of the food available at the time of sampling to many of the herbivorous animals caught by our 0.333-mm mesh nets. The direction of difference noted above conforms with ideas expressed by Menzel and Ryther (1961), Heinrich (1962), and others who argued that especially close phytoplankton-zooplankton coupling may characterize oceanic tropical-subtropical waters.

The biomass data presented here illustrate the fact that geographic demarcation of oceanic faunal provinces is not sufficient. Hydrographic as well as faunal mapping is essential in explaining that portion of station-to-staion variability associated with mesoscale hydrographic variability resulting from phenomena like Gulf Stream cold core rings.

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RELATIVE CONTRIBUTION OF HUDSON, CHESAPEAKE, AND ROANOKE STRIPED BASS, *MORONE SAXATILIS*, STOCKS TO THE ATLANTIC COAST FISHERY

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ABSTRACT

Morphological characters were used in discriminant analysis to quantitatively estimate the relative contribution of striped bass, *Morone saxatilis*, stocks from various estuaries to the striped bass fishery along the Atlantic coast. Representative samples of the spawning stocks of the Hudson River, Chesapeake Bay system, and Roanoke River were collected and counts and measurements were taken on each specimen. Discriminant functions based on five morphological characters correctly classified approximately 75% of the specimens. The effectiveness of three types of estimates based on these functions in accurately estimating stock proportions was investigated in a simulation study. Results of the simulation study indicated which type of estimate was least biased. A sampling design using geographical and temporal strata was then employed to sample the Atlantic coastal fishery from Cape Hatteras, N.C., to Maine. Observations for the morphological characters were taken on collected fish and the resulting data entered into discriminant functions obtained from spawning-stock collections. The specimens were classified by area of origin and the three types of estimates of relative contribution of the Hudson, Chesapeake, and Roanoke stocks were obtained. Results indicated that the Chesapeake stock was the major contributor to the Atlantic coastal striped bass fishery and the Hudson and Roanoke stocks were minor contributors.

The striped bass, *Morone saxatilis*, is an important sport and commercial fish in the estuaries and coastal waters of the Atlantic seaboard from Maine to North Carolina (Koo 1970). Recruitment to the striped bass fishery is from various stocks of striped bass spawned and developed in rivers and estuaries along the Atlantic coast. Recapture locations of tagged striped bass indicate that individuals from all spawning areas north of Cape Hatteras, N.C., utilize much of the Atlantic coast north of their respective spawning areas during a northward migration in the spring and a southward migration in the fall (Merriman 1941; Raney et al. 1954; Alperin 1966; Schaefer 1968; Florence[3]; Texas Instruments[4]). The major spawning areas which potentially contribute individuals to the fisheries operating during the northward and southward migrations are the tributaries of Chesapeake Bay and the Roanoke and Hudson Rivers.

Although tagging data have not led to quantitative estimates of relative contribution, they have led to conflicting ideas as to which major stock of striped bass predominates in the fishery: the Hudson stock or the Chesapeake stock. Most published works have generally concluded that the striped bass stock from the Chesapeake Bay system is the major contributor to the fisheries north of Chesapeake Bay (Merriman 1941; Vladykov and Wallace 1952; Alperin 1966; Schaefer 1968; Porter and Saila[5]; Raney[6]). However, Clark[7] and Goodyear[8] concluded that the striped bass stock

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[7]Clark, J. 1972. Effects of Indian Point Units 1 and 2 on the Hudson River aquatic life. Testimony before USAEC Safety and Licensing Board for Indian Point, Unit no. 2. Docket no. 50-247, Oct. 30, 63 p.

[8]Goodyear, C. P. 1974. Origin of the striped bass of the middle Atlantic coast. Testimony presented to the Committee on Merchant Marine and Fisheries of the U.S. House of Representatives. Feb. 19, 40 p.

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from the Hudson River is the major contributor to the coastal fishery from New Jersey to Massachusetts because the number of striped bass tagged in Chesapeake Bay and recaptured outside the Bay was too low to indicate a large contribution of Chesapeake stock to that fishery.

Because of the controversy of which stock predominates, we conducted a study to obtain quantitative estimates of relative percentage of the major stocks in the coastal fishery. A previous study (Grove et al. 1976) demonstrated the feasibility of using discriminant analysis on morphological characters (counts and morphometric ratios) to distinguish among Hudson, Chesapeake, and Roanoke spawning stocks of striped bass. That study showed that adequate segregation of spawning stocks within the Chesapeake Bay system was not possible. Quantitative estimates of stock composition based on morphological characters and discriminant analysis have been obtained for sockeye salmon (Fukuhara et al. 1962; Anas and Murai 1969), pink salmon (Amos et al. 1963), and Atlantic herring (Messieh 1975). The present study establishes discriminant functions based on collections of spawning-stock specimens to classify striped bass collected in the Atlantic coastal fishery from southern Maine to Cape Hatteras. The percentage of specimens collected that were classified into each stock was used to estimate the relative contribution of that stock to the fishery.

METHODS AND MATERIALS

Collection of Spawning-Stock Specimens

During the spawning season of 1975, mature striped bass were collected from the natal rivers of major stocks along the Atlantic coast. These fish were assumed to have originated from the rivers (i.e., that striped bass, like salmon and other anadromous fishes, home to their natal stream to spawn). This assumption was supported by tagging studies in which striped bass tagged on spawning grounds were recaptured on the same spawning grounds in successive years (Mansueti 1961; Nichols and Miller 1967). Collections were composed of 232 mature striped bass from the Chesapeake Bay tributaries (70 from the Rappahannock River, 53 from the Potomac River, 52 from the Choptank River, and 57 from the Elk River and Chesapeake and Delaware Canal), 168 from the Hudson River, and 99 from the Roanoke River. Only 19 sexually ripe striped bass were collected from the Delaware River above the entrance to the Chesapeake and Delaware Canal, which confirms findings by Chittenden (1971) that spawning in the Delaware River is not substantial. Therefore specimens from the Delaware River were omitted from subsequent analyses. Collections were made primarily during April in the Chesapeake Bay tributaries, Delaware and Roanoke Rivers, and during May in the Hudson River. Most specimens were obtained fresh from commercial fishermen using pound nets, haul seines, and gill nets. Some were netted by study personnel.

To assure an adequate representation of the sexes and multiple year classes in spawning-stock collections, sampling was designed to obtain nearly equal numbers of male and female striped bass and a minimum of 10 individuals in each of the following length categories: $\leq$399, 400-549, 550-699, 700-849, and $\geq$850 mm. Discriminant functions based on male and female specimens from multiple year classes are needed to analyze an oceanic population which consists of a different sex ratio and broader age structure than that of the spawning stocks.

Processing of Spawning-Stock Specimens

Scale samples, counts, measurements, sex, and state of maturity were obtained from each specimen while in fresh condition. Scale samples from above the lateral line between the first and second dorsal fins were pressed on acetate cards. Ages were determined by the scale annulus method (Mansueti 1961). Measurements from the focus to the first and second annuli were made on magnified scale images. The following counts and measurements were taken: number of lateral line scales, left pectoral rays, right pectoral rays, second dorsal rays, anal rays, upper-arm gill rakers, fork length, snout length, head length, and internostril width. Methods used were those discussed by Hubbs and Lagler (1958) and Grove et al. (1976).

Counts, measurements, and age determinations were replicated by a second observer and a set of tolerances was established to reduce observation error. When differences between replicated observations exceeded tolerances, the observations were retaken. Means of the replicated counts and means of ratios of the replicated measurements were used in subsequent analysis.

Analysis of Spawning-Stock Specimens

Choice of morphological characters for segregation of Hudson, Chesapeake, and Roanoke spawning stocks followed three stages of statistical analysis: correlation analysis between each character and fork length (FL), analysis of the effects of sex and age on each character, and discriminant analysis. Analysis involved only specimens with observations on all counts and morphometric and scale-annulus measurements.

Since spawning stocks do not include immature specimens which occur in the coastal waters, we chose only those characters that were independent (i.e., not highly correlated) of fish size and could therefore be used to segregate specimens from the entire stock. Characters were considered to be independent of length when variations (r^2) attributable to length in any stock were ≤ 0.10. Characters not independent of length were used in further analysis when the distribution of character values had small overlap among spawning stocks since such characters help identify stock origin.

Multivariate statistical tests were made to determine the effect of sex and age on the characters used to determine the discriminant functions, since one assumption of discriminant analysis was that each stock was homogeneous. Differences in character values among ages for males or females and between sexes within each stock were tested with a procedure that combined tests of equality of means and equality of covariance matrices (Anderson 1958). Assuming equal covariance matrices, rejection of the null hypotheses of equal distributions indicated that one or more of the character means differed among ages or between sexes.

Multivariate discriminant analysis was used to gain maximum separation among stocks. Linear and quadratic discriminant functions (Anderson 1958; Kendall and Stuart 1968) for each spawning stock were determined from character values obtained from collections of that stock. A stepwise procedure on the linear function was used to indicate the subset of characters which best separated the stocks. The quadratic function based on this subset was formed if the assumption of a common covariance matrix among spawning stocks needed for the linear function was not met. The assumption in discriminant analysis that characters had a multivariate normal distribution was investigated with histograms.

Ability of the discriminant functions to separate stocks and accurately estimate stock proportions was assessed using functions based on total spawning-stock collections and functions obtained from a cross-validation procedure (Mosteller and Tukey 1968). In this procedure collections were randomly divided in half and discriminant functions were determined from one-half and applied to each half. Percentages of correct classification and estimates of stock proportion were obtained for each subset and compared with those from the total sample. Comparisons were also made between estimated and known spawning-stock percentages.

Although these estimates of stock percentages may accurately approximate true percentages in spawning-stock collections, they may deviate substantially from stock percentages in oceanic collections. Fukuhara et al. (1962) stated that the bias in these estimates increased as stock percentages became more disproportionate. Since stock percentages in oceanic collections may be more disproportionate than stock percentages in spawning-stock collections (i.e., 34% Hudson, 46% Chesapeake, and 20% Roanoke stocks), less biased estimates of stock percentages may be needed.

Adjusting Estimates of Stock Percentages

Two procedures were developed to obtain estimates of stock percentages that were less biased than the as-classified (i.e., classifications obtained directly from discriminant functions) estimates. The first procedure adjusted estimates using a technique described by Worlund and Fredin (1962) which generalized to the three population case methodology developed in Fukuhara et al. (1962). This procedure used percentages of specimens from each spawning stock that were misclassified into other stocks to correct as-classified estimates for bias due to misclassifications. When adjusted estimates were negative, as-classified estimates were modified by methodology developed by Schuermann and Curry.[9]

The second procedure iteratively reclassified specimens based on updated prior probabilities that specimens originated from each of the spawning stocks. The first stage of the procedure is the same as the as-classfied procedure; therefore as-

[9]Schuermann, A. C., and G. L. Curry. 1973. Notes on parametric programming. Unpubl. manuscr. Dep. Ind. Eng. Texas A&M Univ., College Station.

classified estimates of stock contribution are obtained at the end of this stage. However, these estimates are then used in the second stage as prior probabilities that specimens come from the three stocks. For example, the as-classified estimate of Hudson stock contribution obtained at the end of the first stage was used at the beginning of the second stage as our best guess of the proportion of specimens in the sample that originate from the Hudson. These prior probabilities are then used to weight the decision to classify each specimen into one of the stocks. Similarly, the proportion of specimens classified into each stock in the second stage were used as priors in the third stage. The procedure was carried out for nine stages.

The effectiveness of adjusted and iterative estimates in reducing bias in the as-classified estimate due to misclassification was investigated in a simulation study. Discriminant functions from the cross-validation study were used to classify a subset of specimens from the independent half of the spawning-stock collections, and each of the three types of estimates of relative percentage were obtained and compared with the known stock percentage. For percentages of Hudson stock ranging from 0 to 90%, the difference between each estimate of Hudson percentage and the known percentage of Hudson specimens in the subsample was obtained as a measure of bias in the estimate.

Collection, Processing, and Analysis of Atlantic and Hudson River Specimens

Assessment of the relative contribution of various stocks of striped bass to the Atlantic coastal fishery required a stratified sampling design that provided samples from the entire coastal fishery and considered the migratory nature of striped bass; therefore a geographically and temporally stratified sampling design was used. The geographical stratification consisted of 10 strata from southern Maine to Cape Hatteras, with 2 to 4 substrata within each stratum to compensate for variations in stock composition within the stratum (Figure 1). The Rhode Island stratum was not subdivided because of its small size. Temporally, the year was divided into six 2-mo periods to obtain estimates of stock composition by stratum throughout the year.

Collections of striped bass from the coastal fishery were obtained primarily from sport and commercial fishermen; however, in areas where adequate sport and commercial fisheries did not exist, study personnel used haul seines and gill nets to collect specimens. Collections were limited to striped bass caught during the same day (i.e., within 24 h) to assure freshness. In many instances the entire catch was used, but due to the size of some catches, a random sample proportional to the number of small (<550 mm), medium (550-850), and large (>850) striped bass caught was obtained.

Oceanic and overwintering specimens were processed in the same manner as spawning-stock specimens. Two replicates of 10 counts and measurements were taken from each specimen, and scale samples were obtained for subsequent age and growth rate determinations in the laboratory. A total of 2,737 oceanic specimens with a complete set of meristic, morphometric, and scale characters were processed (Table 1). Additionally, 79 striped bass overwintering in Croton Bay on the

TABLE 1.—Number of striped bass with complete character sets[1] collected by spatial stratum and period from Atlantic coastal fishery in 1975.

Spatial stratum	Locality	Legal/ sublegal[2]	Jan.-Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.	Total
1	S. Maine-N. Mass.	Legal			82	58	74		214
2	S. Mass.	Legal			91	90	82		263
3	Rhode Is.	Legal			60	43	56		159
4	E. Long Is. Sound	Legal			96		140	99	335
		Sublegal			5			1	6
5	W. Long Is. Sound	Legal	1	38	14	15	89		157
		Sublegal		2	42	85	10		139
6	E. Long Is. S. Shore	Legal		1	89	102	86	106	384
		Sublegal			8	17	19		44
7	W. Long Is. S. Shore	Legal		30	58	93	120	124	425
		Sublegal		4	11				15
8	N.J.	Legal		34	113	28	73	117	365
9	Del.-Md.-N. Va.	Legal		71	3		6	100	180
10	S. Va.-N.C.	Legal	27					24	51
Total			28	180	672	531	755	571	2,737

[1]Measurements and counts taken on all variables used in the character set.
[2]Sublegal-sized striped bass (< 406.5 mm FL) from New York waters (strata 4 to 7) were analyzed separately.

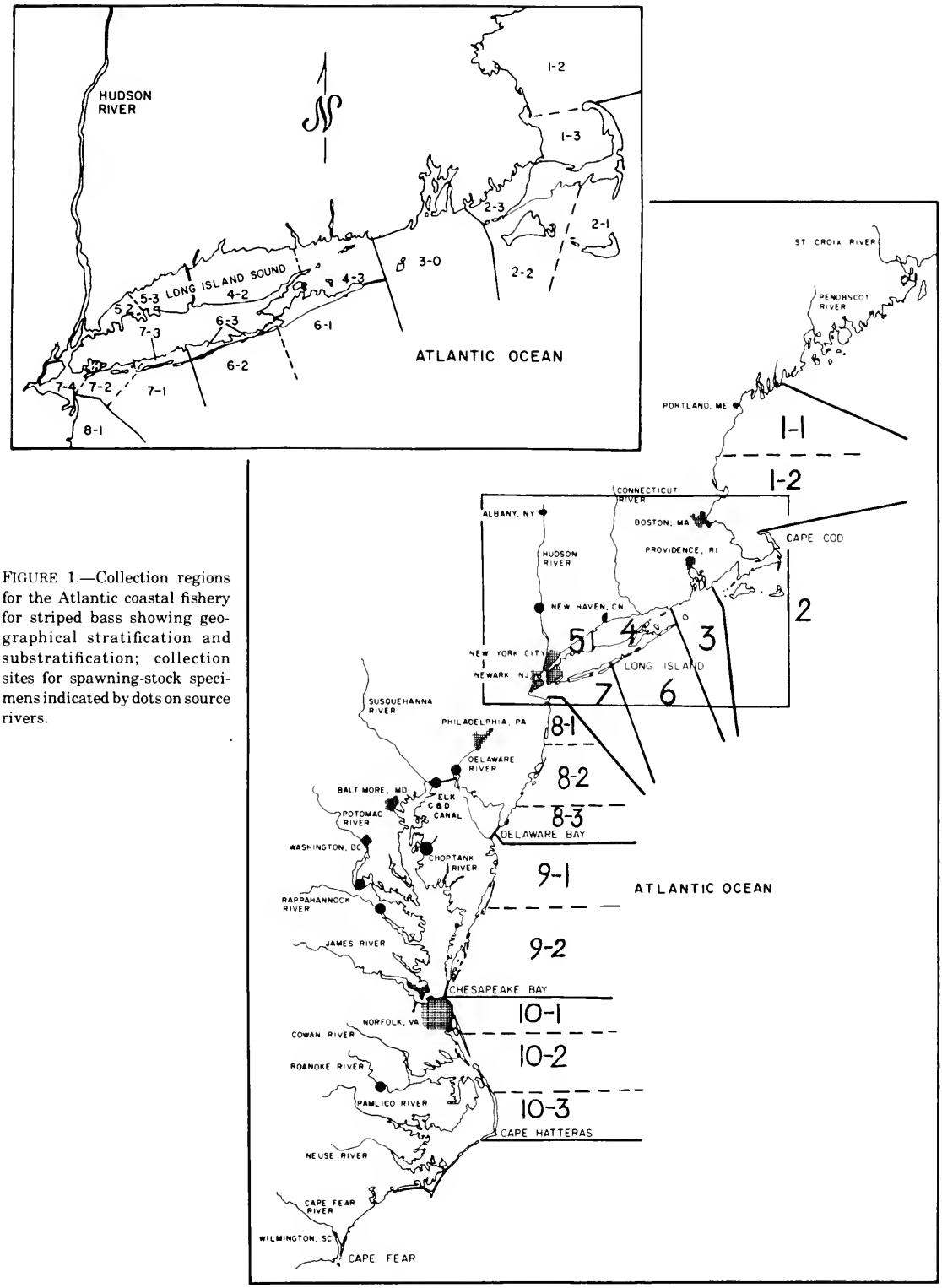

FIGURE 1.—Collection regions for the Atlantic coastal fishery for striped bass showing geographical stratification and substratification; collection sites for spawning-stock specimens indicated by dots on source rivers.

Hudson River from 6 December 1974 through 20 March 1975 were processed.

Three estimates of stock contribution, i.e., "as-classified," "adjusted," and "iterative" estimates, were calculated for collections of legal-sized, sublegal-sized, and overwintering striped bass by geographical and temporal strata. Sublegal-sized <406.5 mm or 16 in FL) and overwintering striped bass collected in New York waters were not considered to be a part of the coastal fishery and were analyzed separately. In each stratum, the percentage of striped bass allocated to a stock provided an estimate of that stock's relative contribution. Mean 1975 estimates of stock contribution of legal-sized striped bass were calculated by averaging strata estimates within periods then averaging across the six periods. Relative contribution estimates by age were also obtained.

The influence of the Hudson stock in coastal strata adjacent to the Hudson River was investigated by comparing the relative contribution of Hudson, Chesapeake, and Roanoke stocks within "inner" and "outer" zones designed by the U.S. Nuclear Regulatory Commission.[10] The inner zone encompassed western Long Island Sound (stratum 5), the New York Bight (stratum 7), and northern New Jersey (stratum 8-1), whereas the outer zone encompassed the remaining waters from Cape May, N.J., to Maine (strata 1 to 4, 6, 8-2, 8-3). Estimates of relative contribution for inner and outer zones were calculated for each period by summing the number of Hudson-, Chesapeake-, and Roanoke-classified fish within appropriate strata. Mean estimates of contribution within each zone were calculated for the year by averaging across temporal strata.

RESULTS AND DISCUSSION

Establishment of Discriminant Functions

Five characters were established as the character set best able to discriminate among Hudson, Chesapeake, and Roanoke stocks. They are, in order of importance (as established by stepwise linear discriminant analysis): 1) the ratio of snout length/internostril width, 2) the scale ratio of first to second annulus/focus to first annulus measure, 3) a character index (Raney and deSylva 1953), 4) the upper-arm gill raker count (which includes rudimentary rakers), and 5) the lateral line scale count. The character index, i.e., the sum of left and right pectoral, second dorsal, and anal fin rays, was used since Grove et al. (1976) demonstrated that individual fin ray characters did not add significant discriminatory ability.

The five characters satisfied the criterion for independence with fish length in each stock with only one exception. The snout length/internostril width ratio for the Roanoke stock has a coefficient of determination of nearly 0.20 but was retained because its distribution had the least overlap among spawning stocks of all characters, thus making it a potentially good discriminator.

Results of the test of homogeneity indicated that only the Hudson stock was homogeneous among ages and between males and females. Significant differences ($\alpha = 0.05$) were found among ages and between sexes in the Chesapeake spawning stock and among ages in the Roanoke spawning stock. Differences found in the Chesapeake spawning stock may have resulted from pooling collections from its four major tributaries.

Quadratic functions (Table 2) were used to discriminate among stocks as a result of the investigation of underlying assumptions of discriminant analysis. Significant differences ($\alpha = 0.05$) were found among covariance matrices of Hudson, Chesapeake, and Roanoke spawning stocks which suggested that quadratic functions would better discriminate among these stocks than linear functions. Histograms suggested that no radical departure of multivariate normality was evident, although normality of individual characters does not assure multivariate normality of the character set. Therefore multivariate normality of the character sets was assumed.

Percentage of spawning-stock specimens correctly classified by the quadratic functions and estimated stock percentages resulting from the use of these functions closely agreed with results obtained by the cross-validation procedure (Table 3). For the total set of collections, 76.8% of Hudson specimens, 67.7% of Chesapeake specimens, and 85.9% of Roanoke specimens were correctly classified, resulting in an overall correct classification of 74.4%. This was similar to overall percentages of 73.2 and 77.1 obtained for the cross-validation subsets. Estimated relative percentages for each stock varied <3 percentage points among the total set and cross-validated subsets, whereas varia-

[10]U.S. Nuclear Regulatory Commission. 1975. Final environmental statement related to operation of Indian Point Nuclear Generating Plant Unit no. 3 Consolidated Edison Company of New York, Inc. Office of Nuclear Reactor Regulation. Docket no. 50-286, Vol. 1:V-166-V-178.

TABLE 2.—Quadratic discriminant functions[1] based on Hudson, Chesapeake, and Roanoke spawning-stock specimens of striped bass and used to classify spawning-stock, oceanic, and overwintering specimens.[2]

Hudson:

$$F_{HUD} = -1{,}489.070559 - (0.077516U^2 + 0.256954W^2 + 1.171065X^2 + 2.536320Y^2 + 123.907000Z^2 - 0.019058UW + 0.015160UX - 0.007057UY + 0.090968UZ + 0.047441WX + 0.023246WY + 0.164200WZ + 0.457365XY - 2.799760XZ - 2.861250YZ) + 8.776221U + 28.127772W + 24.321052X + 7.985031Y + 381.695141Z$$

Chesapeake:

$$F_{CHES} = -1{,}368.946420 - (0.089560U^2 + 0.242459W^2 + 1.122690X^2 + 2.155850Y^2 + 117.554000Z^2 - 0.007099UW + 0.005302UX + 0.015500UY + 0.321075UZ - 0.092151WX - 0.000861WY - 2.363980WZ + 0.381082XY + 3.623860XZ - 1.590090YZ) + 11.316822U + 21.749040W + 25.294896X + 7.014936Y + 323.469441Z$$

Roanoke:

$$F_{ROAN} = -1{,}650.902863 - (0.107062U^2 + 0.316254W^2 + 2.063540X^2 + 0.842590Y^2 + 139.577500Z^2 - 0.062826UW + 0.015703UX + 0.043640UY + 0.228873UZ - 0.293615WX + 0.129292WY - 1.009790WZ + 0.106776XY - 0.606466XZ + 4.416000YZ) + 10.320202U + 27.000888W + 25.512087X + 22.351388Y + 469.422957Z$$

[1]Except for an additive constant ($-2.5 \ln 2\pi$) common to each function.

[2]F = discriminant score, U = lateral line scale count, W = character index, X = upper-arm gill raker count, Y = first to second annulus/focus to first annulus measurement ratio, and Z = snout length/internostril width ratio.

TABLE 3.—Comparison of correct-classification percentages and estimated and known stock percentages among the total set of spawning-stock specimens of striped bass and cross-validation subsets.

	Random set[1]			Independent set[2]			Total set[3]		
Spawning stock	Correctly classified (%)	Known stock (%)	Estimated stock (%)	Correctly classified (%)	Known stock (%)	Estimated stock (%)	Correctly classified (%)	Known stock (%)	Estimated stock (%)
Hudson	81.0	33.7	36.5	72.6	33.6	35.2	76.8	33.7	36.9
Chesapeake	69.8	46.6	40.2	68.1	46.4	42.4	67.7	46.5	40.3
Roanoke	87.8	19.7	23.3	86.0	20.0	22.4	85.9	19.8	22.9
Overall	77.1			73.2			74.4		

[1]Randomly sampled half of total spawning-stock collections used to determine quadratic functions for cross-validation.
[2]Remaining half of spawning-stock specimens classified by quadratic functions based on the random set.
[3]All specimens from spawning-stock collections classified by quadratic functions based on the total set.

tions between estimated and known stock percentages within sets was as much as 9 percentage points. The quadratic functions thus provided slightly biased estimates of stock percentages when applied to collections composed of 34% Hudson, 46% Chesapeake, and 20% Roanoke stocks.

Best Estimator of Relative Contribution

The best estimate of the percentage of Hudson River specimens in subsamples from the simulation studies was the estimate from the third iteration of the reclassification procedure (Table 4). On the average, this iterative estimate was less biased than estimates from other iterations, the as-classified estimated (i.e., estimate from the first iteration), and the adjusted estimate for most percentages of Hudson stock considered. In addition, the variance of the bias of the iterative estimate was often less than that of the other estimates. For percentages of Hudson stock $\leq 50\%$, the iterative and adjusted estimates closely agreed and the bias in each estimate was small (≤ 5 percentage points). The iterative estimate will, therefore, be used to estimate Hudson stock contribution in oceanic collections, and the adjusted estimate will be used to substantiate estimates of Hudson contribution $\leq 50\%$. The iterative estimate will also be used to estimate Chesapeake and Roanoke stock contributions.

TABLE 4.—Mean and standard deviation of absolute bias[1] of estimated relative percentages of Hudson River stock of striped bass in replicated random samples from spawning-stock collections.[2]

Known percent of Hudson River stock	Estimates of absolute bias					
	As-classified		Iterative		Adjusted	
	Mean	SD	Mean	SD	Mean	SD
[3]90	23.0	2.40	4.3	2.97	14.4	5.73
80	20.2	5.14	7.4	8.82	14.3	7.78
75	17.6	3.47	8.4	3.82	12.8	5.00
70	13.0	3.32	4.7	4.52	7.3	4.80
65	10.8	3.11	3.3	2.98	7.5	4.07
60	9.0	3.21	5.3	2.84	6.8	5.00
55	7.5	2.95	4.8	3.52	7.4	4.02
50	5.5	1.99	4.2	2.66	4.7	3.44
45	2.2	2.17	3.5	1.85	4.7	2.14
40	1.2	1.04	3.2	3.44	4.3	4.21
35	2.2	1.45	[4]4.2	[4]2.09	4.4	2.87
30	5.9	3.18	3.3	2.43	3.4	1.79
25	7.8	3.07	4.0	2.25	4.2	3.27
20	9.5	2.26	2.8	1.72	1.8	0.99
15	12.1	4.19	3.5	3.24	3.3	2.62
10	15.1	3.80	4.5	3.36	5.0	3.61
5	17.4	4.03	4.5	3.72	4.3	3.85
0	18.1	2.53	2.5	1.73	1.5	1.69
Overall mean	11.0		4.4		6.2	

[1]Absolute value of the difference between the true relative percentage of Hudson River stock in the subsample and the estimated relative percentage based on nine replicates of varying Chesapeake and Roanoke proportions in the subsamples.
[2]Estimates were based on random samples from one-half of spawning-stock collections which were classified as to area of origin by quadratic functions obtained from the other half of the collections.
[3]Based on two replicates.
[4]Based on eight replicates.

Estimates of Stock Contribution for Oceanic and Overwintering Collections

Iterative estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks indicated that the Chesapeake stock was the major contributor to the striped bass fishery along the Atlantic coast while the Hudson and Roanoke stocks were minor contributors (Table 5). The Chesapeake stock predominated in 34 of 35 geographical and temporal strata while the Hudson stock predominated in the remaining stratum. Iterative estimates of Chesapeake contribution to the fishery exceeded 80% in all strata not adjacent to the Hudson River. Iterative estimates of the Hudson stock were largest in western Long Island Sound and the New York Bight with values exceeding 20% during some periods. Although iterative estimates of Roanoke stock contribution never exceeded 20%, they were highest in North Carolina waters (stratum 10) and in strata from Massachusetts to Maine (strata 1, 2).

The Hudson stock contribution in strata from Massachusetts north to Maine and from New Jersey south to North Carolina (strata 8 to 10) should be low as indicated by iterative estimates (Table 5) and results of tagging studies. Zero estimates in northern waters do not necessarily indicate an absence of Hudson River striped bass since the simulation study has shown that such estimates may be obtained in situations where true contribution is low. In fact, data on adult striped bass tagged in the Hudson River during spawning season and recaptured in waters as far north as Boston Harbor, Mass., have indicated a northern migration of a portion of the Hudson stock (Texas Instruments see footnote 4). However, these data support near-zero estimates of Hudson contribution in southern waters since tagged striped bass were not recaptured south of northern New Jersey. Data (Chapoton and Sykes 1961) on adult striped bass tagged along the outer coast of North Carolina and recaptured on the spawning grounds of Chesapeake Bay and Albemarle Sound

TABLE 5.—Estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks of legal-sized striped bass[1] to 1975 oceanic collections by period and spatial strata. As-cl. = As-classified, Iter. = Iterative, and Adj. = Adjusted estimates.

Period	Stratum	Sample size[2]	Hudson			Chesapeake			Roanoke		
			As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.
Jan.-Feb.	10	27	25.9	3.7	6.7	63.0	92.6	90.7	11.1	3.7	2.6
Mar.-Apr	5	38	52.6	57.9	54.2	42.1	42.1	45.8	5.3	0.0	0.0
	7	30	23.3	3.3	0.0	73.3	96.7	100.0	3.3	0.0	0.0
	8	34	23.5	8.8	0.8	67.6	88.2	99.2	8.8	2.9	0.0
	9	71	8.5	0.0	0.0	77.5	97.2	98.9	14.1	2.8	1.1
May-June	1	82	11.0	0.0	0.0	68.3	90.2	88.5	20.7	9.8	11.5
	2	91	14.3	0.0	0.0	71.4	95.6	96.4	14.3	4.4	3.6
	3	60	30.0	3.3	13.9	60.0	96.7	84.5	10.0	0.0	1.6
	4	96	21.9	1.0	0.0	69.8	99.0	100.0	8.3	0.0	0.0
	5	14	35.7	28.6	23.0	57.1	71.4	77.0	7.1	0.0	0.0
	6	89	25.8	5.6	5.4	65.2	93.3	94.6	9.0	1.1	0.0
	7	58	41.4	25.9	33.7	51.7	70.7	66.3	6.9	3.4	0.0
	8	113	23.9	0.0	1.5	67.3	100.0	98.5	8.8	0.0	0.0
July-Aug	1	58	19.0	0.0	0.0	67.2	94.8	95.4	13.8	5.2	4.6
	2	90	7.8	0.0	0.0	72.2	96.7	90.8	20.0	3.3	9.2
	3	43	30.2	2.3	10.3	65.1	97.7	89.7	4.7	0.0	0.0
	5	15	26.7	0.0	5.1	66.7	100.0	94.9	6.7	0.0	0.0
	6	102	22.5	7.8	1.6	63.7	88.2	92.7	13.7	3.9	5.7
	7	93	33.3	15.1	13.4	65.6	84.9	86.6	1.1	0.0	0.0
	8	28	21.4	0.0	0.0	71.4	100.0	100.0	7.1	0.0	0.0
Sept.-Oct	1	74	13.5	0.0	0.0	77.0	98.6	100.0	9.5	1.4	0.0
	2	82	12.2	0.0	0.0	58.5	85.4	76.0	29.3	14.6	24.0
	3	56	25.0	3.6	7.5	58.9	94.6	83.3	16.1	1.8	9.2
	4	140	16.4	0.7	0.0	64.3	94.3	88.6	19.3	5.0	11.4
	5	89	41.6	40.4	37.2	46.1	57.3	56.5	12.4	2.2	6.4
	6	86	15.1	0.0	0.0	73.3	96.5	99.8	11.6	3.5	0.2
	7	120	23.3	1.7	2.9	63.3	95.0	91.6	13.3	3.3	5.2
	8	73	16.4	0.0	0.0	76.7	98.6	100.0	6.8	1.4	0.0
	9	6	16.7	0.0	0.0	66.7	100.0	92.2	16.7	0.0	7.8
Nov.-Dec	4	99	21.2	0.0	0.0	66.7	98.0	96.9	12.1	2.0	3.1
	6	106	16.0	0.0	0.0	69.8	99.1	95.9	14.2	0.9	4.1
	7	124	21.0	4.8	0.0	76.6	95.2	100.0	2.4	0.0	0.0
	8	117	21.4	0.0	0.0	72.6	100.0	100.0	6.0	0.0	0.0
	9	100	8.0	0.0	0.0	80.0	99.0	100.0	12.0	1.0	0.0
	10	24	12.5	0.0	0.0	62.5	83.3	82.0	25.0	16.7	18.0
Overall mean			23.0	6.5	6.6	66.0	90.8	90.2	11.0	2.7	3.2

[1]Not included are striped bass < 406.5 mm FL from New York waters.
[2]Sample sizes of five specimens or less in any stratum are not included

tributaries also support near-zero estimates of Hudson River contribution in waters off North Carolina.

Comparison between iterative and adjusted estimates indicated close agreement for each stock within the 35 strata. The largest difference between estimates was 12.2 percentage points, but differences of <5 percentage points occurred in 80% of the strata for the Hudson stock, 71% of the strata for the Chesapeake stock, and 86% of the strata for the Roanoke stock. The adjusted estimates therefore substantiate low iterative estimates of contribution of Hudson and Roanoke stocks.

Comparison of mean iterative and adjusted estimates of relative contribution indicated that the two estimates differed by <1 percentage point for each stock. Mean iterative and adjusted estimates were, respectively, 6.5 and 6.6% Hudson, 90.8 and 90.2% Chesapeake, and 2.7 and 3.2% Roanoke contribution.

The contribution of the Hudson stock to the coastal fishery was greater in strata adjacent to the Hudson River than in the remaining strata. Mean iterative estimates of relative contribution of the Hudson River stock to inner and outer zones were 16.0% (15.0% adjusted) and 2.8% (0.0% adjusted), respectively, for the year (Table 6). Although the Chesapeake stock was the predominant contributor to both inner and outer zones, the contribution of the Hudson stock exceeded that of the Roanoke stock in the inner zone but was less in the outer zone.

The Hudson stock predominated in collections of sublegal-sized striped bass in western Long Island Sound, the New York Bight, and in collections of specimens overwintering in Croton Bay on the Hudson River (Table 7). Iterative (and adjusted) estimates of the percentage of sublegal-sized fish classified into the Hudson stock in western Long Island Sound (primarily in Little Neck Bay) and the New York Bight were at least 80%, but were less than 40% along the southeastern shore of Long Island (stratum 6) from May through October. The iterative (and adjusted) estimated of contribution of the Hudson stock to the overwintering population in the Hudson River was greater than 95%.

This study has provided additional information in the importance of dominant year classes of striped bass. Approximately 52% of the specimens collected from the coastal fishery in 1975 were from the 1970 year class, and 77% of them were classified as Chesapeake fish. Schaefer (1972) stated that production of young-of-the-year striped bass in Chesapeake Bay during 1970 was the largest ever recorded and that this year class should provide excellent fishing in New York waters for 6 to 8 yr after recruitment. The presence of this dominant year class of Chesapeake fish confirms the rationale used by Merriman (1941) and Schaefer (1968) to conclude that the Chesapeake stock predominates in the coastal fishery. A summary of the occurrence of dominant year classes in the Atlantic coastal fishery has been given by Schaefer (1968).

TABLE 6.—Mean estimates[1] of relative contribution of Hudson, Chesapeake, and Roanoke stocks of legal-sized striped bass[2] to 1975 oceanic collections within USNRC zones.[3]

	Inner zone			Outer zone		
Estimate	Hudson	Chesapeake	Roanoke	Hudson	Chesapeake	Roanoke
As-classified	31.7	62.9	5.5	19.2	68.0	12.8
Iterative	16.0	83.1	0.9	2.8	94.2	3.0
Adjusted	15.0	84.2	0.8	0.0	96.4	3.6

[1]Average of five temporal strata since only one striped bass collected in inner zone during period 1 (Jan.-Feb.).
[2]Not included are striped bass <406.5 mm FL from New York waters.
[3]U.S. Nuclear Regulatory Commission inner zone corresponds to study strata 5, 7, and 8-1; the outer zone corresponds to study strata 1 to 4, 6, 8-2, and 8-3.

TABLE 7.—Estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks of sublegal-sized striped bass[1] to New York waters by period and spatial stratum and of legal-sized striped bass to the overwintering population in the Hudson River. As-cl. = as-classified, Inter. = iterative, and Adj. = adjusted estimates.

				Hudson			Chesapeake			Roanoke		
Population	Period	Stratum	Sample size[2]	As-cl.	Iter.	Adj.	As-cl.	Iter	Adj.	As-cl.	Iter	Adj
Overwintering			76	76.3	97.4	95.7	23.7	2.6	4.3	0.0	0.0	0.0
Sublegal	May-June	5	42	92.9	100.0	100.0	7.1	0.0	0.0	0.0	0.0	0.0
		6	8	12.5	0.0	0.0	50.0	62.5	64.3	37.5	37.5	35.7
		7	11	81.8	81.8	100.0	18.2	18.2	0.0	0.0	0.0	0.0
	July-Aug	5	85	88.2	100.0	100.0	11.8	0.0	0.0	0.0	0.0	0.0
		6	17	41.2	35.3	39.2	41.2	58.8	47.4	17.6	5.9	13.4
	Sept.-Oct	5	10	80.0	80.0	100.0	20.0	20.0	0.0	0.0	0.0	0.0
		6	19	26.3	15.8	20.8	36.8	47.4	41.9	36.8	36.8	37.3

[1]Striped bass <406.5 mm FL from New York waters.
[2]Sample sizes of five specimens or less in any stratum are not included. Three sublegal-sized specimens collected overwintering in the Hudson River were classified as Hudson fish.

SUMMARY AND CONCLUSIONS

A study was conducted to identify the origin of striped bass collected in the Atlantic coastal fishery and estimate the relative contribution of major stocks to the fishery. Quadratic discriminant analysis was applied to values of five morphological characters obtained from Hudson, Chesapeake, and Roanoke spawning-stock specimens to determine functions which best separated the stocks. Correct-classification percentages of 76.8, 67.7, 85.9% were obtained for the Hudson, Chesapeake, and Roanoke spawning stocks, respectively, resulting in an overall correct classification of 74.4% of the specimens.

A simulation study was conducted to investigate the bias in as-classified, iterative, and adjusted estimates of relative contribution due to misclassification error inherent in the discriminant functions. Results indicated that iterative estimates may best approximate the true contribution of the Hudson stock in oceanic collections.

A stratified sampling design was used during six 2-mo periods in 1975 to collect representative samples of striped bass in the Atlantic coastal fishery from southern Maine to Cape Hatteras. This provided estimates of stock composition by stratum throughout the year.

Oceanic samples were classified by discriminant functions and as-classified, iterative, and revised estimates of relative contribution of the major stocks were obtained. Mean iterative estimates of relative contribution for 1975 are 6.5% Hudson, 90.8% Chesapeake, and 2.7% Roanoke stocks. Iterative estimates of Hudson contribution for legal-sized striped bass exceeded 20% only in western Long Island Sound and the New York Bight during certain months. In collections from Western Long Island Sound and the New York Bight, iterative estimates of the percentage of sublegal-sized fish classified into the Hudson stock were at least 80% during the May through October periods. For Hudson River collections of overwintering striped bass, an iterative estimate of 97.4% Hudson stock was obtained.

The occurrence of a dominant year class was noted. Approximately 52% of the legal-sized specimens collected in the 1975 oceanic sampling program were from the 1970 year class, and 77% of these were classified as Chesapeake in origin.

Major conclusions drawn from the study are: 1) the Chesapeake stock is the major contributor to the Atlantic coastal striped bass fishery from southern Maine to Cape Hatteras; 2) the Chesapeake stock is also the major contributor of legal-sized striped bass in the vicinity of the Hudson River (western Long Island Sound and the New York Bight); 3) sublegal-sized striped bass collected in the vicinity of western Long Island Sound and the New York Bight are predominantly of Hudson origin; and 4) striped bass overwintering in the Hudson River are predominantly of Hudson origin.

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COPPER SENSITIVITY OF PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*, DURING ITS EARLY LIFE HISTORY

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ABSTRACT

Embryos and larvae of the Pacific herring, *Clupea harengus pallasi*, were exposed to copper, using a flow-through bioassay system. Herring embryos were exposed continuously from 12 h after fertilization until hatching, and larvae were exposed from the time of hatching until yolk sac absorption. Embryos were also exposed to 36-h duration pulses of copper in order to evaluate the sensitivy of different developmental stages of herring embryos to copper. Pulsed exposures started at 62, 98, or 136 h after fertilization. The following measurements were taken as indices of the toxic effects of copper: cumulative mortality, percent hatching, and larval length upon hatching.

The onset of mortality of herring embryos continuously exposed to copper began 90 h after fertilization, with deaths occuring over a short interval thereafter (response period). Significant embryo mortalities occurred at a copper concentration as low as 35 μg/l. Herring larvae continuously exposed to copper showed significant mortality at 300 μg/l copper, with no delay in the onset of mortality. Embryos exposed to 36-h pulses of copper during different developmental stages showed reduced sensitivity when exposed after the response period. Larvae that hatched from eggs exposed to a 36-h pulse of copper before the response period grew significantly less than those hatched from eggs exposed during later developmental stages.

Numerous studies have shown that many aquatic animals are adversely affected by increased levels of copper in water; most of the work on fishes has been restricted to freshwater species (Becker and Thatcher 1973; Brungs et al. 1976). Since 90% of the world's marine fish are taken from the continental shelf and nearshore upwelling areas (Waldichuk 1974), increases in copper pollution in coastal aquatic ecosystems are of particular concern.

The concentration of copper in unpolluted nearshore waters ranges from 0.3 to 3.8 μg/l (Chester and Stoner 1974). Increased concentrations of copper in coastal waters have resulted from the release of municipal waste waters (Mytelka et al. 1973; Mitchell and McDermott 1975) and of effluents from power plants (Hoss et al. 1975; Martin et al. 1977). In polluted waters, concentrations as high as 13,900 μg/l copper have been reported (Mitchell and McDermott 1975).

Examination of the toxic effects of copper on coastal marine fisheries is important for the establishment of water quality standards that will protect fishery resources of coastal zones. Eggs and larval stages of fish are reported to be the life history stages that are most sensitive to a variety of pollutants (Skidmore 1965; Pickering and Gast 1972; Struhsaker et al. 1974; Christensen 1975). The necessity of conducting toxicity tests during the most susceptible stage in the life history of an organism has been emphasized by Hynes (1970), and the sensitivity of vertebrate embryos to heavy metals has been suggested as a criterion for water quality by Birge and Just (1973).

While some work has been done to assess the toxicity of copper to the early life history stages of freshwater fishes (Mount 1968; Hazel and Meith 1970; McKim and Benoit 1971; O'Rear 1972; Gardner and La Roche 1973; Benoit 1975), little assessment has been made of toxic effects of copper on marine fishes. Such studies should be very important since mortalities that occur during the early life history stages of marine fish strongly influence the strength of a given year class of fish (May 1974; Bannister et al. 1974; Postuma and Zijlstra 1974; Cushing 1975; Vaughan and Saila 1976). Toxic effects that have an impact upon survival during early developmental stages would also act to reduce the strength of a given year class of fish. The embryos and larvae of the Pacific herring, *Clupea harengus pallasi*, represent a useful

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test organism for evaluating the toxic effect of copper upon the early life history stages of marine fish. The Pacific herring is a commercially important fish that spawns along both eastern and western Pacific coasts (Eldridge and Kail 1973; Hart 1973). Herring spawn great numbers of demersal, adhesive eggs on shallow intertidal substrates. The egg is relatively large, 1.3 to 1.6 mm in diameter, and is covered by a thick, three-layered, opaque chorion (Blaxter and Holliday 1963). Development of the embryo is comparatively slow, taking 7 to 9 days at 14°C (Alderdice and Velsen 1971). The tough chorion permits easy collection and handling, and the slow development of the embryo allows observation time not available in more rapidly developing species.

Three bioassays were conducted to evaluate the sensitivity of herring embryos and larvae to copper. The first two assays were designed to evaluate the sensitivity of embryos and larvae to continuous copper exposure, while the third examined the sensitivity of embryos to brief copper exposures. Since the form of copper to which the herring embryos and larvae were exposed may play a significant role in the toxic response (Pagenkopf et al. 1974), the partitioning of copper among the components of the water in the bioassay system was also determined.

MATERIALS AND METHODS

Collection and Handling of Test Organisms

Intertidal collections of Pacific herring eggs were made along the shore of Belvedere Island and the Tiburon Peninsula, San Francisco Bay, Calif. The eggs were collected directly into a 15-gal, insulated ice chest containing aerated seawater from the egg collection site and were transported to the laboratory within 2 h after collection. The water temperature at the collection site was 11.0°-11.5°C and upon arrival at the laboratory the temperature of the water increased to no more than 13.5°C. Only eggs deposited in single layers on *Fucus* sp., *Laminaria* sp., or *Gracilaria* sp. were chosen for testing. Before placing the eggs into exposure chambers, they were removed from the seaweed by bending the frond and then gently brushing them with a finger into a sorting dish containing seawater kept at 12°C. The eggs were examined with a microscope at 20×; only viable embryos at the same stage of development were chosen. No more than 51 embryos were placed in any exposure chamber. All transfers of embryos or larvae were carried out with a large-bore, polished glass pipette.

Embryos at two different stages of development were used for the tests. The age of the earlier stage embryos, collected 7 February 1975, was estimated to be 12 h after fertilization since they were undergoing epiboly (Ahlstrom's stage IV (Ahlstrom 1943)). These embryos were exposed to copper continuously, each of seven groups being exposed to a different copper concentration. The age of the later stage embryos, collected 26 February 1975, was estimated to be 48 to 50 h after fertilization (Ahlstrom's stage IX). These embryos were divided into four groups. Three groups were exposed for 36 h to the same copper concentration but during different developmental stages. The fourth group was maintained in flowing seawater from the time of collection to within 1 h after hatching, and then continuously exposed to different copper concentrations as larvae.

Bioassay System

The organisms were exposed to copper in 5-l clear plastic bowls (Figure 1). The exposure solution was introduced into each chamber by gravity flow from a mixing chamber into which seawater, at a rate of 11 ml/min, and copper chloride solution, pH 3, at a rate of 1 ml/h, were pumped continuously. Approximately 17 h was required for replacement of 90% of the water in the chamber. The height of water in the exposure chambers was maintained by a constant-level out-flow siphon. The diameter of the mouth of the out-flow siphon

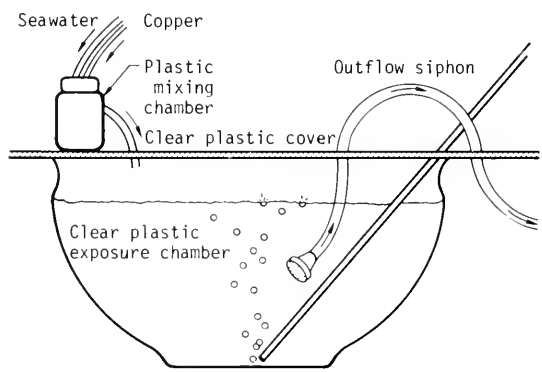

FIGURE 1.—Diagram of the exposure chamber and flow-through delivery system used to expose Pacific herring embryos and larvae to copper.

was greater than that of the tubing to reduce the flow velocity at the mouth of the siphon. The mouth of the siphon was covered with nylon netting (505-μm pore size) to prevent the loss of organisms from the chamber. A gentle stream of bubbles delivered to the bottom of the chamber provided aeration and mixing. All exposure chambers were immersed in a water bath whose temperature was monitored. Illumination was provided by the fluorescent lighting in the laboratory and followed the regular ambient photoperiod.

The exposure period, the nominal copper concentration, and the total number of embryos or larvae exposed during a typical experiment are given in Table 1. Each experiment was repeated at least once. All exposures were initiated by the addition of appropriate amounts of copper chloride to the chambers. The continuous exposure of the test organisms continued until all animals died or, in the case of embryos, until hatching occurred or, in the case of the larvae, until yolk sac absorption occurred. The pulsed exposures were terminated by transferring exposed embryos to an exposure chamber containing control seawater.

The following measurements were taken as indices of the toxic effect of copper: cumulative mortality with time, percent hatching, and larval length at hatching. The embryos or larvae were examined within the exposure chambers at each observation period with a 7× beam dissection microscope with a 21-cm depth of field. The criterion for embryo death was the lack of heart beat or body movement. Since the embryos were attached in clusters, dead embryos were not removed until the termination of a test. Larvae that hatched from pulse exposed embryos were collected, anesthesized with a 1% quinaldine solution, and preserved in 5% Formalin[2] in seawater. Measurements of the hatched larvae were made with an ocular micrometer and all obvious deformities noted. The criterion for larval death was a failure to respond to a gentle prod with a polished glass rod. Dead larvae were removed during each observation period and preserved in 5% Formalin in seawater.

Total copper concentrations were measured two

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

TABLE 1.—Experimental conditions and median lethal times for bioassays determining the sensitivity of Pacific herring embryos and larvae to copper.

Experiment	Exposure period (h)	Nominal copper concentration (μg/l)	Number of organisms exposed	Mean total copper concentrations (μg/l ± SD)	Number of water samples	Time to median lethal level (LT_{50} ± 95% confidence interval) (h)
Embryos, continuous exposure	180 (12 h after fertilization through hatching)	Control	150	4.3 ± 1.9	3	[1]
		25	48	27.9 ± 7.4	3	[1]
		35	49	38.1 ± 9.4	3	[2]144.9 ± 8.3
		45	50	44.1 ± 11.6	3	[2]134.4 ± 5.2
		55	49	51.2 ± 9.7	3	[2]134.8 ± 3.0
		100	53	127.9 ± 34.6	2	[2]115.4 ± 2.8
		200	49	235.5 ± 47.2	2	[2]98.7 ± 2.1
Larvae, continuous exposure	300 (Hatching through yolk sac absorption)	Control	100	2.5 ± 0.8	3	[1]
		300	49	274.0 ± 24.1	4	[1,3]
		600	49	572.1 ± 31.5	4	[1,2]
		1,400	50	1,349.0 ± 247.0	4	[2]41.7 ± 7.3
		2,000	51	1,969.0 ± 148.0	2	[2]23.8 ± 1.5
		2,500	49	2,425.4 ± 89.0	2	[2]20.9 ± 2.4
		3,500	51	3,430.5 ± 710.6	2	[4]15.6
						Time to median lethality following termination of pulse ± 95% confidence interval (h)
Embryos, pulsed exposures:						
Pulse I	36 (62 through 98 h after fertilization)	Control	49	3.0 ± 0.08	2	[1]
		100	44	93.8 ± 6.3	3	[2]38.4 ± 2.0
Pulse II	38 (98 through 136 h after fertilization)	Control	93	3.9 ± 1.6	3	[1]
		100	94	111.9 ± 13.7	4	[2]53.9 ± 6.1
Pulse III	36 (136 through 172 h after fertilization)	Control	46	6.1 ± 0.7	3	[1]
		100	48	101.6 ± 29.3	3	[1]

[1]50% mortality not achieved at this concentration.
[2]Slope significantly different from control slope ($P < 0.01$) (Snedecor and Cochran 1967).
[3]Slope significantly different from control slope ($P < 0.05$) (Snedecor and Cochran 1967).
[4]Determined according to the method of Litchfield and Wilcoxon (1949).

to four times during each bioassay to determine the actual concentrations to which the organisms were exposed. Water samples were collected in acid-washed polyethylene jars and acidified to pH 2 with concentrated HCl. Total copper was analysed by the APDC-DDDC-MIBK extraction method described by Kinrade and VanLoon (1974). The copper concentration in extracted MIBK solutions was determined with a model 303 Perkin Elmer atomic absorption spectrophotometer, using an HGA-2100 graphite furnace with a deuterium background corrector.

Since the chemistry of copper in seawater is complex, more than one form of copper may be present in the bioassay water. To examine the form of the copper in the bioassay system water, out-flow samples were collected from the bioassay system before organisms were introduced to determine the particulate-bound fractions (>0.45μm), ionic fraction (bound by Chelex-100 resin (Riley and Taylor 1968)), and complexed fraction (not bound by Chelex-100 resin). The analysis scheme is summarized in Figure 2. To monitor the partitioning of copper into each of these fractions, copper-64 was equilibrated with water samples after they were withdrawn from the bioassay system. The partitioning of stable copper in the seawater of the bioassay system was indicated by the percentage of the initial activity recovered in each of the described fractions.

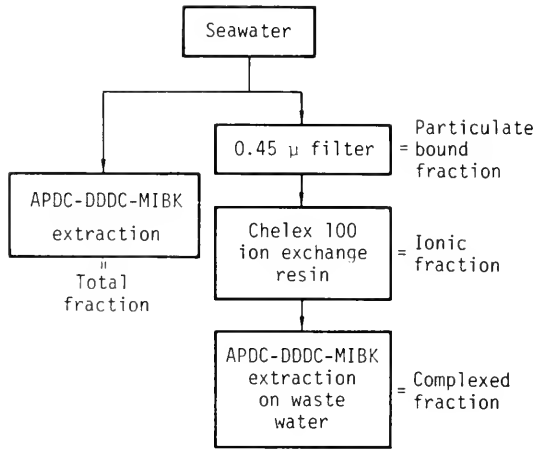

FIGURE 2.—Analysis scheme for the separation of copper fractions recovered from the bioassay system used to expose Pacific herring embryos and larvae to copper.

Statistical Analysis

The measures of toxicity determined in this study were the time to 50% mortality at each concentration of copper tested (median lethal time, LT_{50}) and the concentration of copper resulting in 50% mortality over a given time (median lethal concentration, LC_{50}). These toxicity measures were deterimed by performing a weighted linear regression analysis on the sets of cumulative mortality data using the logistic function. The straight line transform of the logistic function is: logit $P = \ln P/Q = \alpha + \beta x$, so that if logit P is plotted against x, the points will fall on a straight line with α as the intercept and β as the slope (Berkson 1953). In our calculations of LT_{50}, x represented the time from the onset of the reaction period in the case of continuous embryo exposures, from hatching in the case of continuous larval exposures, and from the termination of a given pulse in the case of pulsed embryo exposures. In our calculations of LC_{50}, x represented concentration, and our method followed that outlined by the American Public Health Association (1976) with logit analysis used in place of probit analysis.

A computer was used to calculate the LC_{50} and LT_{50} values, and for each fitted line the program determined: the LT_{50} or LC_{50}, the 95% confidence limits associated with the LT_{50} or LC_{50}, Pearson's rho (ρ), the slope (β) and the intercept (α), and the mean square error (EMS); no assumptions of homogeneity were made and the EMS was calculated in every case, rather than assuming an EMS of 1 for homogeneous data (Finney 1964).

In the case of embryos that were exposed continuously or exposed to pulses of copper, deaths prior to the delayed reaction period or the onset of the pulsed exposure, respectively, were not used in the data analysis. In no case were mortalities during these periods greater than 6%.

The relationship between time to 50% mortality during continuous exposure of both embryos and larvae and concentration was determined following the method outlined in the American Public Health Association (1976). The resulting toxicity curve was used to estimate the lethal threshold concentration (incipient LC_{50}) (Sprague 1969).

RESULTS

Physical Parameters of the Bioassay System

Mean copper concentrations measured during each test are reported in Table 1. The partitioning

of copper-64 among particulate-bound, ionic, and complexed fractions of copper recovered from the bioassay water indicates that the copper was primarily in the ionic form (Table 2). The mean pH of the water in exposure chambers in all tests was 8.08 (SD = ±0.024). The mean temperature for all tests was 13.3°C (SD = ±0.8°C).

TABLE 2.—Percentages of copper-64 in fractions of seawater recovered from the bioassay system used to expose Pacific herring embryos and larvae to copper.

Nominal copper concentration (μg/l)	Particulate bound	Ionic	Complexed	Total[1]
10	5.2	83.6	4.3	93.7
50	4.2	88.3	3.7	96.5
100	1.1	89.9	2.1	94.0
500	0.7	93.8	1.7	97.0
1,000	0.6	91.8	1.1	96.9
2,000	1.0	96.4	1.0	99.9

[1]Total includes copper-64 remaining in Chelex-100 resin after elution.

Continuous Exposures to Copper

Survival of embryos continuously exposed to copper was high at all concentrations of copper tested until 90 h of exposure, at which time dose-related mortalities occurred (Figure 3). The period during continuous exposure when embryo deaths begin is termed the reaction period. Mortalities of developing embryos at copper concentrations of 35 μg/l and higher were significantly different from controls ($P<0.01$). Virtually no hatching occurred at concentrations above 45μg/l copper. Developmental features observed in the control embryos during the onset of the reaction period included the appearance of eye pigmentation, the onset of coordinated body movements, and the initiation of heart beat. Embryos continuously exposed to copper concentrations of 100 μg/l copper and higher developed an opaque cast to the chorion, which was followed later by whitish discoloration of the body. Embryos continuously exposed to 200 μg/l copper developed an opaque change in the chorion at 60-72 h from fertilization, with body discoloration, spasmodic contractions, quiverings, and reduced fin fold development occurring at 84-96 h from fertilization.

Herring larvae continuously exposed to copper were many times less sensitive to copper than herring embryos. Larval mortalities differed significantly from controls at concentrations of 300 μg/l copper and higher ($P<0.05$) (Figure 4). Prior to death the larvae sank to the bottom of the exposure chamber and patches of whitish discoloration were observed over the bodies. Spasmodic quivering and whole body contractions were observed in larvae at concentrations of 1,400 μg/l copper and above.

The toxicity curves for continuously exposed herring embryos and larvae are shown in Figure 5. Median lethal times for each copper concentration tested and 95% confidence limits are detailed in Table 1.

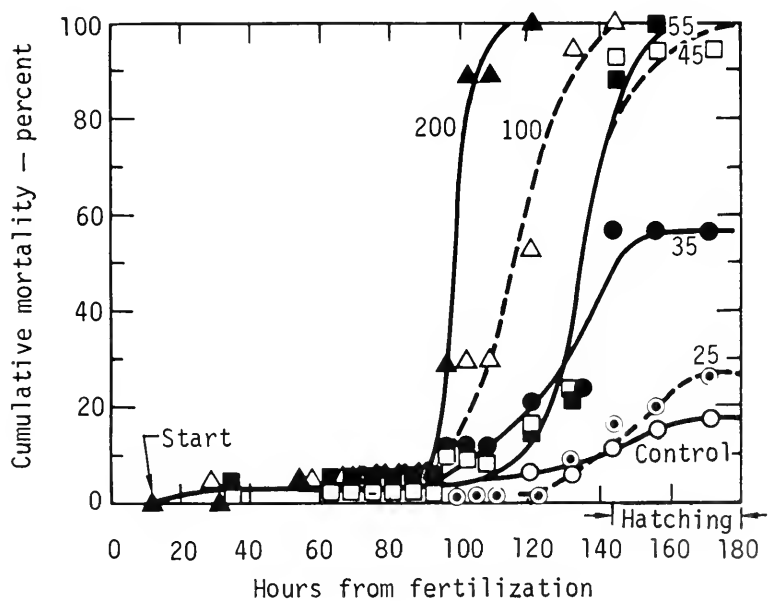

FIGURE 3.—Percent cumulative mortality of Pacific herring embryos continuously exposed to copper (micrograms per liter). Mortality curves shown are the fitted logit curves used to establish median lethal times.

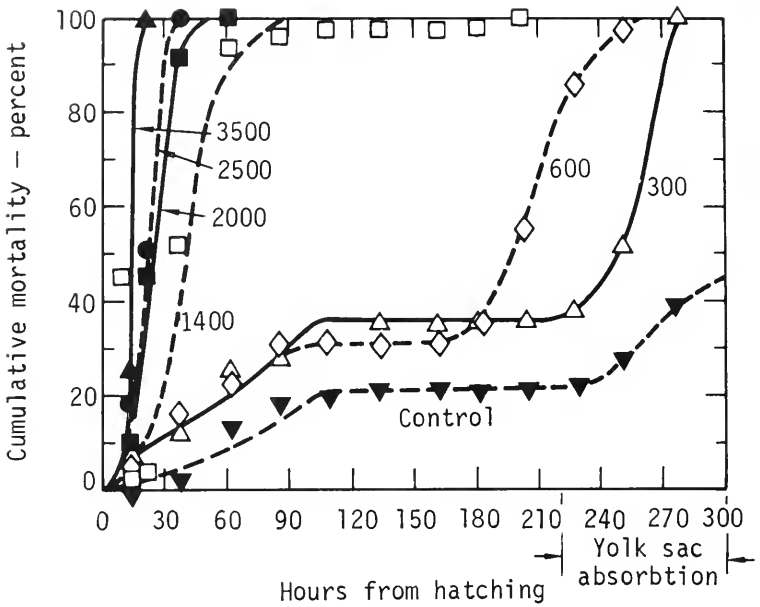

FIGURE 4.—Percent cumulative mortality of newly hatched Pacific herring larvae continuously exposed to copper (micrograms per liter). Mortality curves shown are the fitted logit curves used to establish median lethal times.

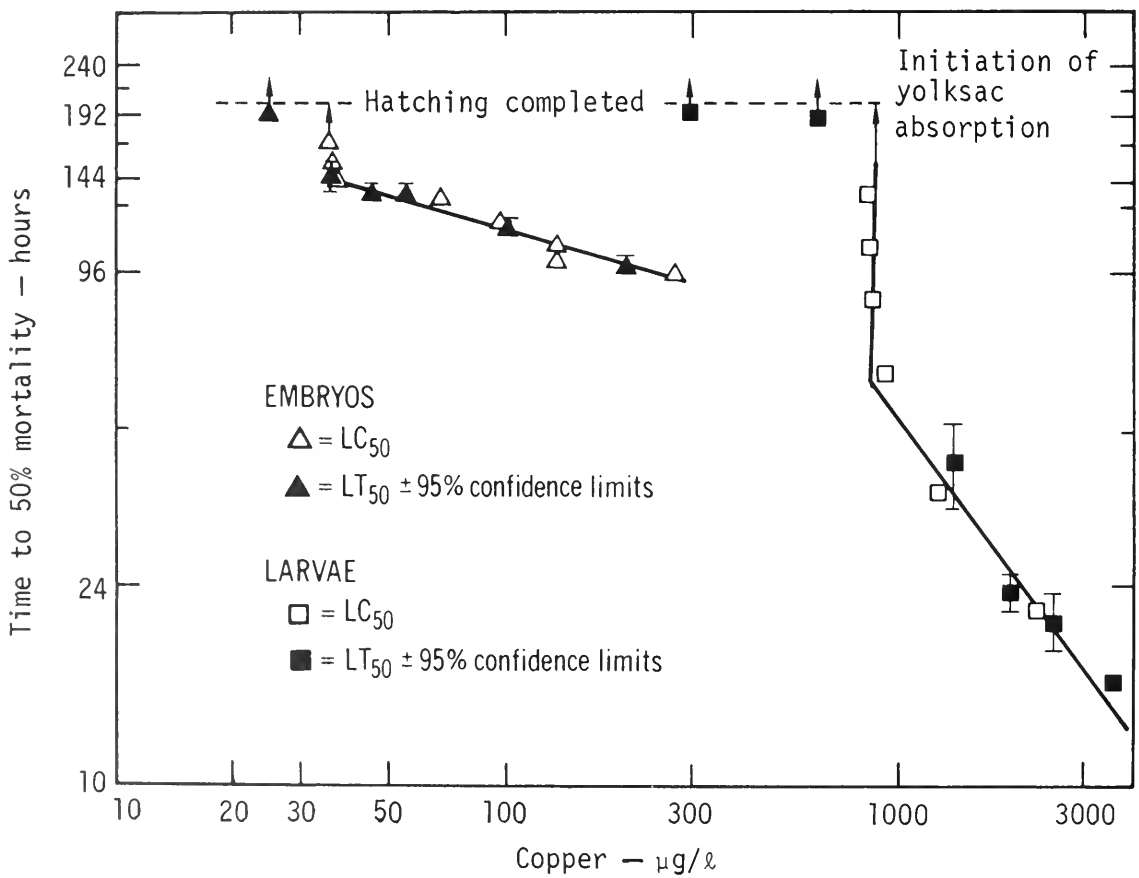

FIGURE 5.—Toxicity curves for Pacific herring embryos and larvae continuously exposed to copper.

The toxicity curve for herring embryos is presented for the purpose of discussion only, since the 90 h delay until the onset of mortality, regardless of concentration, biases the toxicity curve for comparison with other organisms without a reaction period. Sprague (1969) recommended that a concentration that killed 50% of the population during an exposure sufficiently long that acute lethal action has ceased (incipient LC_{50}) be used as the single most useful criterion for toxicity. The incipient LC_{50} is not influenced by the bias introduced by the reaction period. The estimated incipient lethal level for herring embryos was found to be 33 μg/l copper.

Only larval deaths earlier than 100 h after hatching were considered in the construction of the larval toxicity curve since larvae surviving beyond approximately 200 h after hatching have begun yolk sac absorption, and the apparently synergistic effects of copper stress and starvation can be observed in the larval time vs. percent mortality curves (Figure 4). The estimated incipient lethal level for herring larvae was found to be 900 μg/l copper.

Thirty-six Hour Pulsed Embryo Exposures

Pulses of copper exposure for 36 h showed that the sensitivity of herring embryos to copper changed as the embryos developed (Figure 6, Table 1). A 36-h pulse of 100 μg/l copper delivered during the reaction period (Pulse I) had the greatest effect upon hatching and the length of larvae at hatching (Table 3). A 36-h pulse of 100 μg/l copper delivered just before hatching (Pulse III) had a signficant effect on larval length at hatching, but the percentage of embryos hatching was actually greater than controls.

TABLE 3.—Percent Pacific herring embryos hatching and mean larval length at hatching for three groups of Pacific herring embryos exposed to 36-h pulses of 100 μg/l copper. Each group received a pulse at a different time during development.

Item	Mean larval length (mm ± SD)	Percent hatching
Controls	6.10 ± 0.47	92
Pulse 1	3.77 ± 0.2*	6
Pulse 2	4.23 ± 0.31*	47
Pulse 3	5.75 ± 0.62*	98

*Significantly different from controls ($P<0.01$) (Snedecor and Cochran 1967).

DISCUSSION

Several features of the toxic response of herring at various stages of their early life history are of interest. Previous tests examining the sensitivity of other fish embryos and larvae to copper have found that the larval stage is the more sensitive stage (Hazel and Meith 1970; McKim and Benoit 1971, O'Rear 1972; Gardner and La Roche 1973;

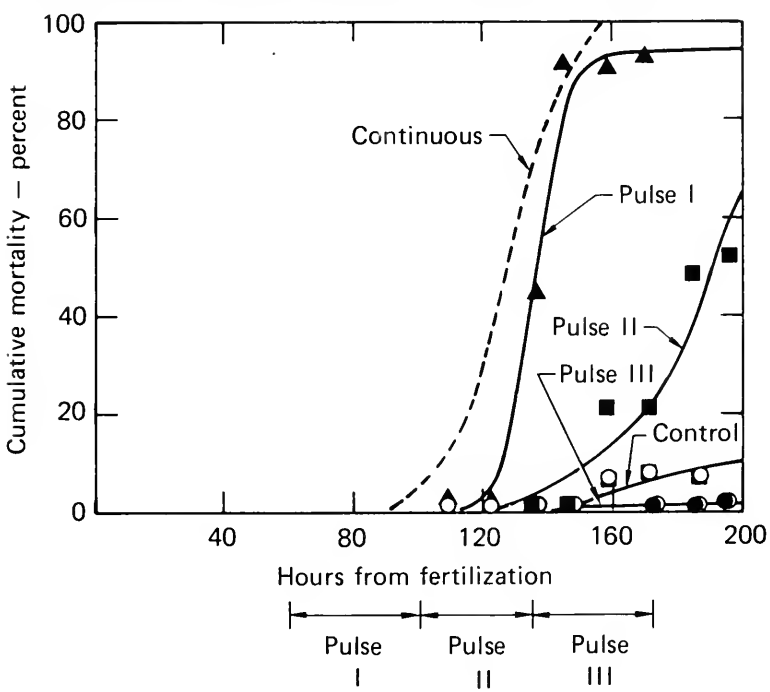

FIGURE 6.—Percent cumulative mortality of three groups of Pacific herring embryos exposed to 36-h pulses of 100 μg/l copper. Each group received a pulse at a different time during development. The cumulative mortality observed for Pacific herring embryos continuously exposed to 100 μg/l copper (See Figure 3) is shown for comparison.

Benoit 1975). Contrary to these findings, we found that embryos of the Pacific herring appear to be the stage that is more sensitive to copper. It should be noted that the fishes examined in previous studies spawn in fresh or brackish waters and cannot be considered true marine species as is the herring.

Another interesting feature of the toxic response of the herring embryos and larvae was that the behavior prior to death was similar to that of adult fish exposed to copper. Jerky, uncoordinated, and spontaneous movements were noted by Baker (1969) in the winter flounder, *Pseudopleuronectes americanus,* acutely exposed to 3,200 and 1,000 μg/l copper. Bluegill, *Lepomis macrochirus,* chronically exposed to 162 μg/l copper showed periodic involuntary spasms several weeks prior to death (Benoit 1975). The spasmodic contractions and quiverings noted in herring embryos and larvae prior to death might be of a similar nature. Baker noted that these symptoms are similar to those of Wilson's disease which also manifests spasmodic muscle contractions and quiverings in mammals. Wilson's disease is the result of an inborn error of metabolism that results in an excess of unbound copper in the blood stream (Adelstein and Vallee 1962). Goldfish, *Carassius auratus,* subjected to doses of 1,000 μg/l copper exhibit severe neurotoxic symptoms and accumulate copper in nervous tissues at levels similar to those seen in Wilson's disease (Vogel 1959).

Some of the toxic effects observed in herring embryos and larvae were similar to those reported for other heavy metals. Striped bass, *Morone saxatilis,* embryos exposed to copper or zinc (O'Rear 1972) and Baltic needlefish, *Belone belone,* exposed to cadmium (Dethlefsen et al. 1975) developed opaque discoloration of the chorion during exposure. In the present study, the chorion of the herring embryos became increasingly opaque as exposure to copper continued. Wedemyer (1968) found that in coho salmon, *Oncorhynchus kisutch,* 70% of the total zinc-65 uptake during exposure was firmly bound to the chorion, 26% was bound in the perivitelline space, and only 2% reached the yolk and 1% reached the embryo. Wedemyer (1968) also demonstrated that copper is bound by the salmon embryo's chorion. The opaque discoloration noted in herring embryos with continued exposure to copper may well be a reaction resulting from copper uptake by the chorion.

The observation of a reaction period during bioassays with herring embryos has been noted previously. A reaction period for herring embryos continuously exposed to cadmium (Rosenthal and Sperling 1974) and high temperatures and salinities (Alderdice and Velsen 1971) occurred at about the time of the onset of heart beat. The sensitivity of this developmental period in the herring was further borne out by our findings in which 36-h pulses of 100 μg/l copper during the reaction period caused higher mortalities than 36-h pulses during later developmental periods.

Pacific herring embryos may be vulnerable to toxic effects from effluents now being discharged into coastal environments. A survey of 108 municipal waste effluents on the Atlantic coast showed that 50% of the waste effluents contained >100 μg/l copper; some discharges were as high as 5,900 μg/l copper (Mytelka et al. 1973). A survey of six municipal waste discharges along the southern California coast revealed concentrations ranging from 74 to 13,900 μg/l copper with an average annual mass emission rate of 532 t of copper during 1971-74 (Mitchell and McDermott 1975). While the amount of copper discharged in the ionic form was not reported, the potential for environmental exposure levels approaching the incipient LC_{50} of 33 μg/l copper found for herring embryos in the present study should be considered in establishing water pollution control standards.

Frequently authors conducting bioassays using copper or other heavy metals have not examined the chemical state of the metal in their bioassay system. Such characterizations are important since different chemical forms of metals may have different toxic effects (Lee 1973). The method outlined in this work for examining the particulate bound fraction, the ionic fraction, and the complexed fraction of metals in seawater provides a means of examining the important chemical forms of copper in aquatic bioassay systems. With the use of appropriate isotopes this method could easily be applied to other metals. In the case of the system used to expose Pacific herring embryos and larvae it appears that the ionic form of copper predominated. In freshwater the ionic form of copper seems to be the most toxic (Pagenkopf et al. 1974). This is probably also the case for Pacific herring embryos and larvae exposed to copper in seawater.

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ESTIMATED ZOOPLANKTON PRODUCTION AND THEIR AMMONIA EXCRETION IN THE KUROSHIO AND ADJACENT SEAS

TSUTOMU IKEDA[1] AND SIGERU MOTODA[2]

ABSTRACT

Production and ammonia excretion of zooplankton in the Kuroshio and adjacent seas were estimated from field data of biomass, size distribution, and habitat temperature of zooplankton, and from experimental data of respiration and ammonia excretion rates as functions of body size and temperature. Winberg's basic balanced equations were applied to calculate production from respiration data. Further, mortality related to the lifespan and the ratio of herbivores to carnivores in the zooplankton community were estimated from theoretical assumptions.

In this study, 18-72% of primary production was grazed by herbivorous zooplankton, and production of herbivorous zooplankton (= secondary production) was 10-60 mg C/m^2 per day. The ecological efficiency between primary and secondary production was 5-22%. Ammonia-nitrogen excreted by zooplankton was 4-24 mg N/m^2 per day, which can support 11-44% of the nitrogen requirements of primary production.

In marine ecosystems solar energy photosynthetically fixed as organic matter by phytoplankton is channelled through zooplankton to nektonic fishes and crustaceans at higher trophic levels. Important features of the roles of zooplankton in this scheme are their extremely high conversion efficiency of phytoplankton organic matter (in contrast with terrestrial ecosystems, see Wiegert and Owen 1971; Steele 1974) and the simultaneous regeneration of nutrients through their excretory activities. The latter role is considered an important mechanism in maintaining constant primary production levels in the seas, especially in oligotrophic areas (Ketchum 1962; Corner and Davies 1971).

These dynamic functions of zooplankton have seldom been quantitatively evaluated in the field. One difficulty lies in the fact that the zooplankton community includes animals belonging to a variety of phyla and a number of species which differ geographically. Information from detailed studies on one or a few species is not adequate for this purpose, and collection of all necessary data on each component species in the community is not practical. Therefore, the development of some alternative approach is needed to overcome this problem.

METHODS

In this study, we treat the zooplankton community as an assemblage of different sizes of animals and use body size-related constant functions for respiration and ammonia excretion from laboratory experiments to estimate feeding, production, and ammonia regeneration in the Kuroshio and adjacent seas. A systematic survey of the study area had been carried out by Japanese participants in the CSK (Co-operative Study of the Kuroshio and adjacent region) organized by UNESCO during 1965-67 (Motoda et al. 1970; Irie and Yamazi 1972).

Biomass, Habitat Temperature, and Size (= Weight) Distribution of Zooplankton

Zooplankton were sampled vertically from 150 m with a NORPAC standard net (mesh aperture, 0.35 mm) in summer (June-October 1965 and 1966) (Figure 1A) and winter seasons (December-April 1965, 1966, and 1967) (Figure 2A). From the average biomass of zooplankton summarized by Yamazi (1971) for 0-150 m, the present study area was divided into four density classes (<10, 10-50, 50-100, and >100 mg wet weight/m^3). The isopleth for 100 mg wet weight/m^3 shifted northward in the cold season and southward in the warm season, especially in the east China Sea (Motoda et al. 1970; Irie and Yamazi 1972). Seasonal difference in the composition of

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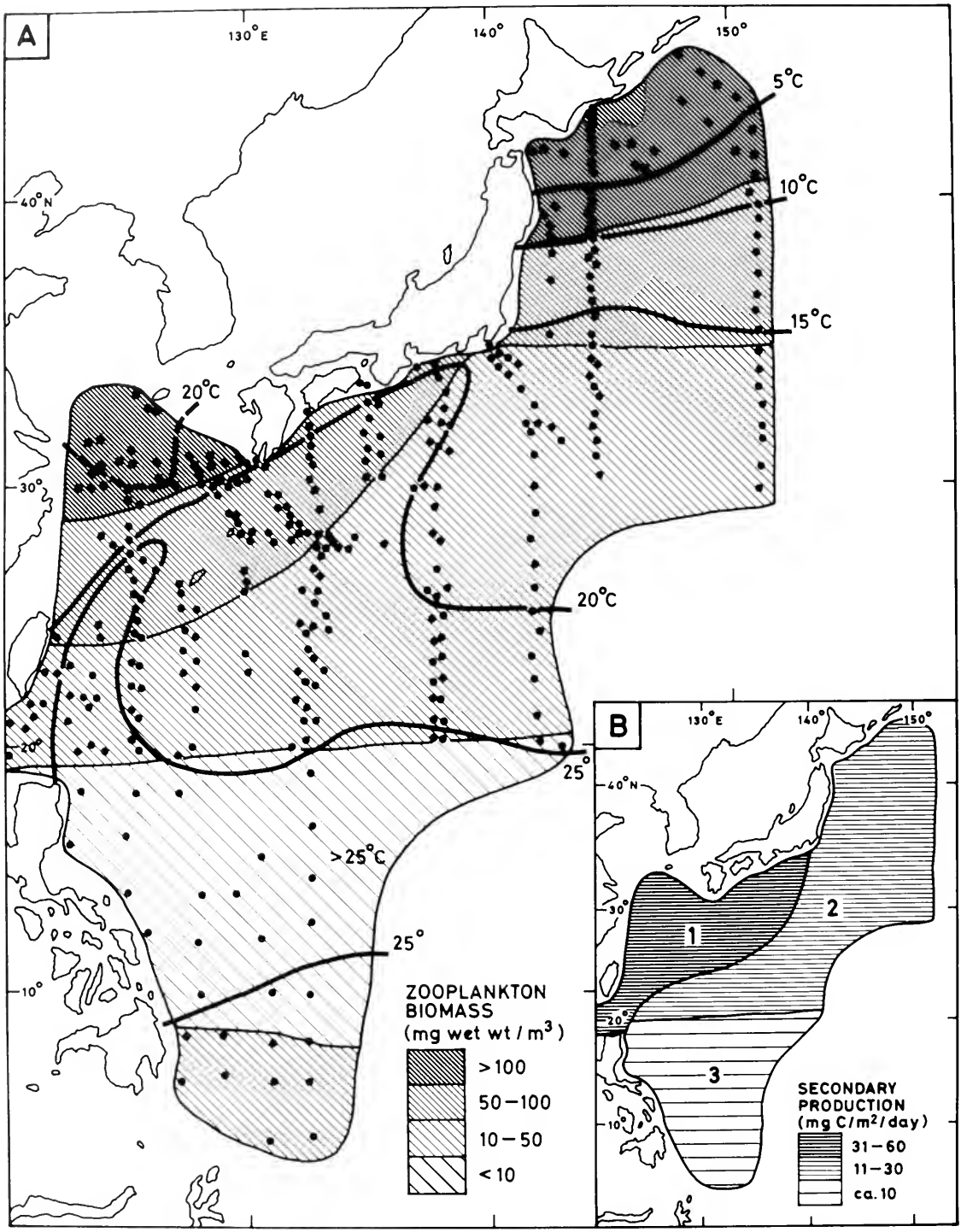

FIGURE 1.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the warm season (June-October) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

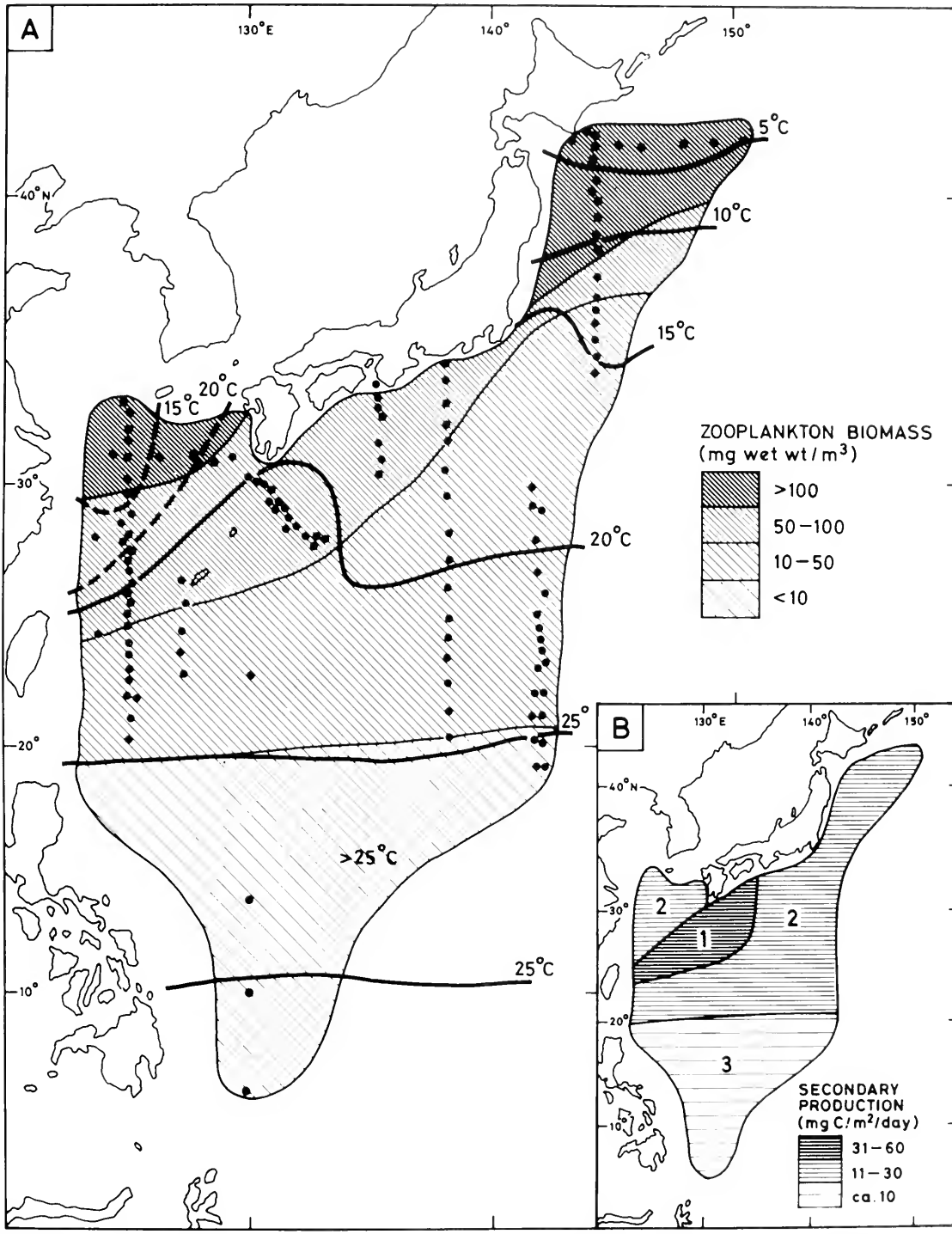

FIGURE 2.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the cold season (December-April) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

zooplankton taxonomic groups among stations was less pronounced, with copepods dominant (56-65% of total individual number), followed by *Noctiluca* (8-15%), appendicularians (6-7%), and chaetognaths (4-5%) (Yamazi et al. 1972). Biomass expressed per cubic meter was converted to per square meter by multiplying by depth of sampling.

The habitat temperature of zooplankton from 0-150 m was represented by that at 100 m (Japanese Oceanographic Data Center 1967, 1969). In the east China Sea, which is shallower than 150 m, the temperature at 50 m was taken as the habitat temperature (Figures 1A, 2A).

From data summarized by Yamazi (1971), the biomass of zooplankton per haul was divided by total number of individuals per haul to obtain average body weight. Values thus obtained at all sampling stations were grouped into warm or cold season, and assumed as a general size distribution in each season (Figure 3). The highest frequency was observed in the range 0.1-0.2 mg wet weight/animal in both seasons. Faunal differences south and north of the subarctic boundary (ca. lat. 40°N) reported by Motoda and Marumo (1965) were ignored here, because no systematic difference was found in average body size of zooplankton between these areas. The skewed size distribution was converted to a normal distribution curve by logarithmic transformation (base 10). Fitness to the curve was tested primarily by the normal probability paper (Harding 1949) and finally confirmed by chi-square test (warm season: $\chi^2 = 17.85$, df = 6, $P<0.01$; cold season: $\chi^2 = 7.24$, df = 6, $0.25<P<0.5$). The normal distribution curves of log body size thus obtained were $\mu = -0.8033$ (SD = 0.2856) for the warm season and $\mu = -0.7350$ (SD = 0.3705) for the cold season.

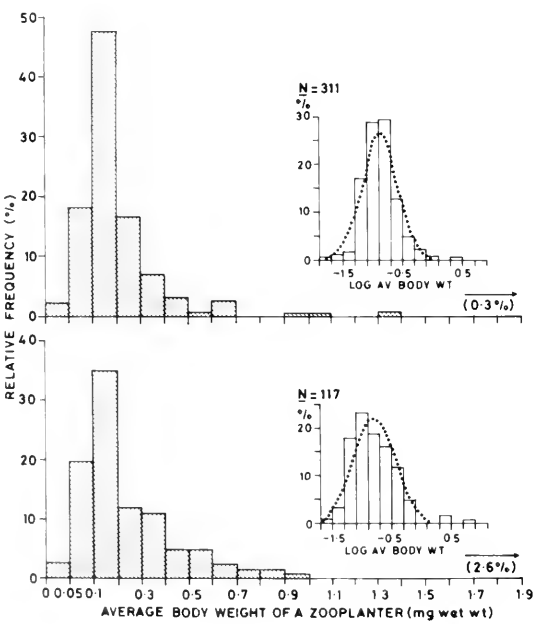

FIGURE 3.—Relative frequency of average size of zooplankton (biomass/number of zooplankton at each sampling station) in warm (June-October) (upper figure) and cold (December-April) (lower figure) seasons in the Kuroshio and adjacent seas. A normalized frequency distribution fitted by logarithmic transformation of body weights is superimposed on the right side of each figure. N is number of sampling stations.

Respiration and Ammonia Excretion

From measurements of respiration and ammonia excretion rates on various zooplankton species from tropical to boreal seas, Ikeda (1974) found that the body weight and habitat temperature are most important factors which affect rates. As a result of stepwise regression analyses, the relationship among these parameters was expressed as:

$$R \text{ or } E = aW^b \quad (1)$$

$$\text{or } \log_{10}R \text{ or } \log_{10}E = \log_{10}a + b \log_{10}W \quad (2)$$

where R is respiration rate (μl O_2/animal per h); E, ammonia excretion rate (μg N/animal per h); and W, body dry weight (mg/animal). Constants, a and b, are given as a function of habitat temperature (°C) (Ikeda 1974 amended the bias introduced by logarithmic transformation),

$$\text{for } R\text{: } b = -0.01089T + 0.8918$$
$$\log_{10} a = 0.02538T - 0.1259$$
$$\text{for } E\text{: } b = -0.00941T + 0.8338$$
$$\log_{10} a = 0.02865T - 1.2802.$$

Combining the normalized body size distribution of zooplankton obtained above and the values in Table 1, total respiration and ammonia excretion rates were estimated from the sum of the rates of six classes of the normal distribution curve equally divided by the SD, i.e., −3 to −2, −2 to −1, −1 to 0, 0 to 1, 1 to 2, and 2 to 3, which covers over 99% of the total area under the curve. In each class, body size of zooplankton was represented by the median value, i.e., SD = −2.5, −1.5, −0.5, 0.5,

TABLE 1.—Analysis of body size distribution of zooplankton in the Kuroshio and adjacent seas from a normalized catch distribution curve. Warm season (June-October): $\mu = -0.8033$, SD = 0.2856; cold season (December-April): $\mu = -0.7350$, SD = 0.3705. The interval of $\mu \pm 3$ SD of the normal curve was equally divided by the SD class intervals (1-6), and median value in each class interval was taken as the representative body size ($W_1 - W_6$) for that class interval.

Class interval No.	Class interval SD	Median body size Wt	Median body size SD	Median body size equivalent (mg wet wt animal) Warm	Median body size equivalent (mg wet wt animal) Cold	Theoretical frequency (%) f
1	−3 to −2	W_1	−2.5	0.030	0.020	2.15
2	−2 to −1	W_2	−1.5	0.058	0.051	13.59
3	−1 to 0	W_3	−0.5	0.113	0.120	34.13
4	0 to 1	W_4	0.5	0.218	0.282	34.13
5	1 to 2	W_5	1.5	0.422	0.662	13.59
6	2 to 3	W_6	2.5	0.815	1.553	2.15
				$\Sigma Wf = 19.63$	26.79	$\Sigma f = 99.74$

TABLE 2.—Respiration and ammonia excretion rates per unit biomass of zooplankton in warm (June-October) and cold (December-April) seasons as derived from calculations in the text.

Habitat temp (°C)	Respiration rate (μg C/mg dry wt per h) Warm	Respiration rate (μg C/mg dry wt per h) Cold	Ammonia excretion rate (μg N/mg dry wt per h) Warm	Ammonia excretion rate (μg N/mg dry wt per h) Cold
5	0.790	0.735	0.162	0.148
10	1.300	1.183	0.270	0.242
15	2.144	1.911	0.450	0.396
20	3.538	3.091	0.750	0.648
25	5.849	5.011	1.252	1.065

1.5, and 2.5. Then, total respiration (R_{tot}) and total ammonia excretion rates (E_{tot}) became

$$R_{tot} = R_1 f_1 + R_2 f_2 + \ldots + R_6 f_6 \quad (3)$$

$$E_{tot} = E_1 f_1 + E_2 f_2 + \ldots + E_6 f_6 \quad (4)$$

where $R_1, R_2, \ldots, R_6$ and $E_1, E_2, \ldots, E_6$ are the respiration rates and ammonia excretion rates of zooplankton with body weight $W_1, W_2, \ldots, W_6$, respectively, and $f_1, f_2, \ldots, f_6$ are respective theoretical frequencies (= individual number) in each weight category. A wet weight:dry weight conversion factor of 10 was assumed (Wiebe et al. 1975). Frequency $f_1, f_2, \ldots, f_6$ of a given zooplankton biomass (ΣW) was calculated by multiplying $f/\Sigma Wf$. To facilitate calculation, respiration and ammonia excretion rates per unit biomass of zooplankton characterized by the size distribution curve in warm and cold seasons were computed as functions of habitat temperature (Table 2). Respiration was expressed as carbon units assuming $RQ = 0.8$ (protein metabolism).

Feeding and Production Estimates From Respiration

Winberg (1956) proposed the following basic balanced equations for fishes:

$$0.8F = P + R \quad (5)$$

$$K_1 = P/F \cdot 100 \quad (6)$$

$$K_2 = P/(0.8F) \cdot 100 \quad (7)$$

where F is feeding; P, growth (= production); R, respiration; K_1, gross growth efficiency; K_2, net growth efficiency; and 0.8, digestion efficiency for fishes. From these equations F and P are derived by knowing R and K_1,

$$F = 100R/[0.8(100 - K_2)] = 100R/(80 - K_1) \quad (8)$$

$$P = K_2R/(100 - K_2) = K_1R/(80 - K_1). \quad (9)$$

Apparently both digestion efficiency and gross growth efficiency (K_1) of marine zooplankton differ to a great degree, not only among zooplankton species but also within a single species (Table 3). Marshall and Orr (1955a) observed that the digestion efficiency of *Calanus finmarchicus* changed with a variety of food phytoplankton species offered. Apparently K_1 can be affected by developmental stages (Mullin and Brooks 1970b; Paffenhöfer 1976; Harris and Paffenhöfer 1976), feeding rate (Mullin and Brooks 1970b; Harris and Paffenhöfer 1976), kinds of food (Paffenhöfer 1976), and method of estimation (Butler et al. 1969, 1970). Moreover, both quality and quantity of foods used in these experiments are not necessarily the same as those that zooplankton will meet in the field. Although we have little information about the exact nature of foods of zooplankton in the field, their digestion efficiency is assumed to be quite high, because zooplankton have an ability to select suitable foods (Lasker 1966; Marshall 1973). The value of K_1 has a tendency to increase with a decrease in food concentration (Mullin and Brooks 1970a; Harris and Paffenhöfer 1976). In the field, food concentration is much lower than in laboratory experiments so that a higher K_1 value would be expected.

For these reasons we finally chose values of 70% for digestion and 30% for K_1 as realistic values of zooplankton in the field, regardless of species and food habit. Then, Equations (8) and (9) for fishes were rewritten for zooplankton, as

$$F = 100R/(70 - 30) = 2.5R \quad (10)$$

TABLE 3.—Digestion efficiency and gross growth efficiency (K_1) of marine zooplankton species obtained from laboratory experiments. Methods of estimation are with radioactive isotopes (^{14}C, ^{32}P, and ^{35}S), elemental analyses (C, N, and P), calories, weight, and ratio method of Conover (1966a). (Means in parentheses.)

Zooplankton species	Digestion efficiency and method of estimation		K_1 and method of estimation		Sources
Calanus finmarchicus	26-99	^{32}P			Marshall and Orr (1955a)
Calanus finmarchicus	53-78	^{14}C			Marshall and Orr (1955b)
Euphausia pacifica			11-74(32)	^{14}C	Lasker (1960)
Calanus helgolandicus	74-91	dry wt			Corner (1961)
Temora longicornis	52-98	^{32}P			Berner (1962)
Calanus hyperboreus	44-65 (55)	ratio method	4-36(21)	weight	Conover (1964)
			5-50(30)	calories	
Calanus finmarchicus and *C. helgolandicus*			36	N	Corner et al. (1965)
Calanus hyperboreus	39-86(69)	ratio method			Conover (1966a)
Mixed zooplankton	18-92(63)	ratio method			Conover (1966a)
Calanus hyperboreus	40-87	ratio method			Conover (1966b)
Euphausia pacifica	46-95(84)	^{14}C	6-46(26)	^{14}C	Lasker (1966)
Calanus finmarchicus and *C. helgolandicus*	54-68(62)	N	14-34	N	Corner et al. (1967)
Metridia longa	54-57	ratio method			Haq (1967)
Metridia lucens	35-94(70)	ratio method			Haq (1967)
Calanus finmarchicus			21-38	N	Butler et al. (1969)
and *C. helgolandicus*			19-35	P	
Calanus finmarchicus	77	P	17	P	Butler et al. (1970)
and *C. helgolandicus*	62	N	27	N	
Calanus helgolandicus			34-35	C	Mullin and Brooks (1970a)
Rhincalanus nasutus			30-45	C	Mullin and Brooks (1970a)
Sagitta hispida			36	N	Reeve (1970)
Lucifer chacei	8-22	^{35}S	7-14	calories	Zimmerman (1973)
Chiridius armatus	81-97	ratio method			Alvarez and Matthews (1975)
Calanus helgolandicus			3 7-35	C	Paffenhöfer (1976)
Pseudocalanus elongata			14-18	C	Harris and Paffenhöfer (1976)
Temora longicornis			17-27	C	Harris and Paffenhöfer (1976)

$$P = 30R/(70 - 30) = 0.75R. \quad (11)$$

Mortality Loss During Production

Production calculated as in Equation (11) assumes zero mortality. But production is always accompanied by mortality, caused mainly through predation by other animals and natural physiological mortality. We considered only mortality from the latter source.[3]

Assuming that 1 ml of oxygen is required to combust about 1 mg of organic matter (Jörgensen 1962), the instantaneous growth rate of zooplankton is expressed as follows from Equations (1) and (11),

$$dW/dt = (0.75/1{,}000)aW^b \quad (12)$$

where W is body dry weight (milligrams) and t, time (hours). The time required to grow from egg (W_0 in milligrams) to adult (W in milligrams) is derived from the integrated form of Equation (12),

$$t = 1{,}000\,(W^{1-b} - W_0{}^{1-b})/(0.75(1 - b)). \quad (13)$$

Chiba (1956) measured egg size in 55 species of copepods. From his data and the body length-weight relation of copepods developed by Krylov (1968) the W_0:W ratio was calculated as 0.0001:1 to 0.01:1. A similar range of the ratios is also found in the data of euphausiids, reviewed by Mauchline and Fisher (1969). The lifespan of zooplankters was defined arbitrarily as $1.5t$ (duration of adult stage is one-half that of the preadult). Daily mortality (M) caused by the length of life span becomes

$$M = 24/(1.5t). \quad (14)$$

Total mortality (M_{tot}) of the zooplankton community in terms of percent of biomass is given in the following equation:

$$M_{tot} = 100(M_1f_1W_1 + M_2f_2W_2 + \ldots + M_6f_6W_6) \div (f_1W_1 + f_2W_2 + \ldots + f_6W_6) \quad (15)$$

where $M_1, M_2, \ldots, M_6$ are daily mortalities of zooplankters with body weight $W_1, W_2, \ldots, W_6$,

[3] In addition to natural physiological mortality, molting loss by copepods, the most dominant group in zooplankton community, was included in the original calculations of Ikeda and Motoda (1975). Here we ignore the molting loss because neither molting intervals nor body size at molting were known. Therefore, present production estimate (10-60 mg C/m² per day) is slightly higher than original one (9-57 mg C/m² per day; Ikeda and Motoda 1975).

TABLE 4.—Daily mortality related to the lifespan of zooplankton in warm (June-October) and cold (December-April) seasons as derived in the text.

Habitat temp (°C)	Season	Weight ratio of egg to adult 0.01:1	0.001:1	0.0001:1	Average (% of biomass)
5	Warm	0.68	0.53	0.46	0.51
	Cold	0.63	0.49	0.43	
10	Warm	1.24	1.01	0.91	0.96
	Cold	1.13	0.92	0.83	
15	Warm	2.27	1.92	1.77	1.81
	Cold	2.03	1.71	1.58	
20	Warm	4.14	3.60	3.39	3.37
	Cold	3.63	3.15	2.96	
25	Warm	7.51	6.69	6.40	6.21
	Cold	6.45	5.74	5.49	

respectively. For M_{tot} as a function of habitat temperature and W_0:W ratio (0.0001:1, 0.001:1, and 0.01:1) see Table 4.

Ratio of Herbivores to Carnivores in Zooplankton Community

Although zooplankton include both herbivores and carnivores, this distinction of food habits is probably of little importance regarding ammonia excretion by zooplankton. However, the difference is essential when production is considered, especially secondary production.

We assumed that the zooplankton community at any trophic level is represented by a similar size distribution, same digestion efficiency (70%) and same K_1 value (30%). Assuming that the daily production of herbivores ($0.75a\Sigma W_i^b (b_i/B_0)B_0$) equals the daily consumption by the primary carnivores ($2.5a\Sigma W_i^b (b_i/B_1)B_1$) (derived from Equations (1), (3), (10), and (11)) the relation can be simplified to

$$B_1 = (0.75/2.5)B_0 \qquad (16)$$

where B_0 and B_1 are the total number of herbivores and primary carnivores, respectively, in a community, and b_i is the number of zooplankters of a given body size. Assuming that the daily production of carnivores in the lower trophic level is equal to the daily feeding of carnivores at the next trophic level, the number of carnivores at trophic level n becomes

$$B_n = (0.75/2.5)^n B_0 . \qquad (17)$$

The total number of zooplankters from the primary carnivore level to the carnivore trophic level n becomes

$$B_1 + B_2 + \ldots + B_n = B_0((0.75/2.5) + (0.75/2.5)^2 + \ldots + (0.75/2.5)^n)$$
$$= B_0 ((0.75/2.5)(1 - (0.75/2.5)^n))/(1 - 0.75/2.5).$$

If the number of trophic levels of carnivores is simply taken as 2, then the number of primary and secondary carnivores can be calculated to be

$$B_1 + B_2 = 0.39B_0.$$

This value does not differ greatly from the value obtained when an infinite number of carnivorous trophic levels are considered

$$B_1 + B_2 + \ldots + B_\infty = 0.43B_0.$$

Therefore, the value 0.4:1 seems appropriate for the ratio of numbers of carnivorous zooplankton to all herbivorous zooplankton.

RESULTS AND DISCUSSION

Distribution of estimated production of herbivorous zooplankton (i.e., secondary production) is summarized for warm and cold seasons in Figures 1B and 2B. Table 5 summarizes our estimates for grazing, production, and natural physiological mortality of herbivorous zooplankton and ammonia-nitrogen excretion of zooplankton (herbivores plus carnivores).

Production

The present use of Winberg's balanced equations to estimate productivity (growth) from data on respiration is not new. Shushkina (1968) estimated the production of the copepod, *Haloptilus longicornis*, in the Fiji Sea from an indirectly calculated respiration rate for this species and K_2 values from the literature including zooplankton species. In order to determine whether zooplankton in the field were supplied adequate food, we used a set of values for digestion efficiency, and gross growth efficiency (K_1), instead of a single value of net growth efficiency (K_2), to obtain feeding requirements and production simultaneously (which is not possible when K_2 is used, see Equation (8)). When the feeding requirements of zooplankton exceed food availability (i.e., food shortage), any estimate of production from Winberg's equation is unrealistic. However, our data indicate that feeding requirements of herbivorous zooplankton was 18-72% of primary production (Table 5).

TABLE 5.—Estimates of grazing, production (corrected for natural physiological mortality), and ammonia nitrogen excretion of zooplankton collected from 0 to 150-m depth with NORPAC net (0.35-mm mesh) in the Kuroshio and adjacent seas, together with primary production values from the literature (Anonymous 1967, 1968, 1969; Saijo et al. 1972). For designation of subareas, see Figures 1B and 2B.

Item	Subarea 1	Subarea 2	Subarea 3	Range
Zooplankton:				
a. Herbivorous zooplankton grazing (mg C/m² per day)	107-214	36-107	ca. 36	36-214
b. Herbivorous zooplankton production (mg C/m² per day)	31-60	11-30	ca. 10	10-60
c. Herbivorous zooplankton natural physiological mortality (mg C/m² per day)	1-4	0-2	ca. 1	0-4
d. Zooplankton excretion (mg N/m² per day)	12-24	4-12	ca. 4	4-24
Phytoplankton:				
e. Primary production (mg C/m² per day)	200-500	50-500	50-200	50-500
f. Phytoplankton nitrogen requirement (mg N/m² per day)	35-88	9-88	9-35	9-88
Phytoplankton:zooplankton relation:				
g. Ratio of herbivorous zooplankton grazing to primary production (a/e) (%)	43-54	21-72	18-72	18-72
h. Ecological efficiency from primary production to secondary production (b/e) (%)	12-16	6-22	5-20	5-22
i. Ratio of zooplankton nitrogen excretion to phytoplankton nitrogen requirement (d/f) (%)	27-34	14-44	11-44	11-44

Engelmann (1969) summarized annual production (P_a) and respiration (R_a) of animal populations (mostly terrestrial invertebrates and vertebrates) and found that $\log_{10}P_a$ was proportional to $\log_{10}R_a$. His findings were further confirmed with a large amount of data by McNeill and Lawton (1970). For comparatively short-lived poikilotherms (generation time <2 yr) the relation is expressed in the following equation (McNeill and Lawton 1970),

$$\log_{10}P_a = 0.8262 \log_{10}R_a - 0.0948$$

or

$$P_a = 0.804\ R_a^{0.8262}$$

This empirical equation resembles $P = 0.75\ R$ (Equation (11)) that we derived from Winberg's equations for marine zooplankton in this study.

Mullin (1969) reviewed production estimates for marine zooplankton and gave 5-224 mg C/m² per day as a summary value for zooplankton production at various sea areas, exclusive of values on a single species. Our estimate of secondary production (10-60 mg C/m² per day) falls in these ranges. It is noted, however, that some data cited by Mullin (1969) are on mixed zooplankton (herbivores plus carnivores) so that these are not comparable to our results which referred only to herbivorous zooplankton. For the same reason, the ecological efficiency between primary production and secondary production obtained in our study (5-22%) is not necessarily comparable to the ratio of zooplankton production to primary production (9-58%) in Mullin (1969).

Ammonia Excretion

The Kuroshio and its adjacent region in the Pacific Ocean (south of the subarctic boundary at ca. lat. 40°N) are oligotrophic (Reid 1962). Taniguchi (1972) studied geographical variation of primary production in the western Pacific Ocean and suggested that nutrients are the most important factor limiting the primary production level in the Kuroshio region. In situ primary production reported in this area is in the range of 50-500 mg C/m² per day (Anonymous 1967, 1968, 1969; Saijo et al. 1972) which is equivalent to 9-88 mg N/m² per day from a C:N ratio of 5.7:1 on phytoplankton (Redfield et al. 1963). Our estimate of ammonia-nitrogen regeneration through zooplankton excretion which can support 11-44% of the nitrogen requirement for primary production was 4-24 mg N/m² per day. Eppley et al. (1973) estimated that 40-50% of nitrogen demand for primary production was supplied by zooplankton excretion in the nutrient depleted subtropical gyre of the northern Pacific Ocean. A significant contribution of zooplankton excretion (up to 77-90% of the nitrogen requirement for primary production) was reported in Long Island Sound (Harris 1959) and offshore waters off the Washington and Oregon coasts in summer (Jawed 1973). The importance of ammonia as a nitrogen source for phytoplankton is further substantiated by its preferential utilization by phytoplankton (cf. Dugdale 1976).

Future Aspects

The production and ammonia regeneration models presented here are advantageous for understanding the marine zooplankton community which includes diversified species and widely divergent body sizes, like those inhabiting subtropical and tropical seas. Models require basically

three parameters: zooplankton biomass, size distribution, and habitat temperature. Although we obtained size distribution indirectly it should be obtainable directly. The fitting of zooplankton size distribution data to the normal distribution curve may not be necessary in some instances but this will facilitate calculations. To estimate production from respiration data, constant values of digestion efficiency and K_1 were used in this study, but these can be used as variables. From morphological characteristics of feeding organs, Timonin (1971) reported that 50-80% of zooplankton biomass in the Indian Ocean were carnivores and Motoda and Minoda (1972) reported that 20-27% of zooplankton numbers in the Kuroshio region were herbivores. These values are below the herbivore:carnivore ratios we calculated.

Since only zooplankton data were collected with 0.35-mm mesh nets and smaller zooplankters pass through this mesh size, we probably underestimated zooplankton biomass. According to Beers and Stewart (1971) biomass of microzooplankton including copepod nauplii, ciliates, foraminiferans, and radiolarians was 12-71% (24% on average) of total zooplankton collected in 202-μm nets in the eastern tropical Pacific Ocean. The important role of microzooplankton as a secondary producer and nutrient regenerator in pelagic marine ecosystems is anticipated but suitable data are yet unavailable for modeling.

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GROWTH RATE OF THE SAND CRAB, *EMERITA ANALOGA*, (HIPPIDAE) IN TWO DIFFERENT ENVIRONMENTS

CRAIG FUSARO[1]

ABSTRACT

The field growth rate of *Emerita analoga* was estimated under two different sets of environmental conditions. One beach location on the southern California coastline near Santa Barbara was compared with a beach on Santa Cruz Island, only 42 km distant. The island population of *E. analoga* experienced colder water which contained less suspended solids than the mainland population studied. The crabs on the island beach were found to grow at about one-third the rate of those on the mainland, as measured by the "instantaneous growth rate" technique.

The growth rate of a crustacean species is of considerable ecological interest for at least two reasons. First, the usual positive relationship between body size and fecundity means that an increased growth rate may increase reproductive output. Second, the proportion of animals which are mature within any specified population will depend on the growth rate (to maturity) of its members. These relationships indicate that a measure of individual growth, averaged for a population, may give information about reproductive success and, therefore, about the persistence of a population under its particular set of environmental circumstances. Further, comparison of the growth rates for populations of the same species under differing environmental regimes may indicate how the species responds to its environmental conditions in terms of growth.

The proximity of the Channel Islands to the mainland near Santa Barbara provides excellent opportunity for comparative studies. The differing oceanographic conditions between some beaches of Santa Cruz Island and nearby Goleta Bay on the mainland allow an analysis of growth as a function of different environmental characteristics. This is the intent of the present work.

This study is an analysis of the growth rate in two nearby populations of the sand crab, *Emerita analoga*. It is an anomuran crab which inhabits beaches of the eastern North Pacific from southern Canada to central Baja California. There also are populations of the species in the Gulf of California and the eastern South Pacific, but these populations are not considered here. The crab normally lives between high and low tide marks buried in sand on sandy beaches, and follows the water's edge up and down the beach with the tides. The crab is somewhat unusual for its family in that it procures its food by filtering seawater that washes over its finely setose second antennae as waves rush onto and ebb from the beach face. *Emerita analoga* can often be found in dense aggregations on beaches of southern California during spring and summer. This species was chosen for comparative growth study because: 1) it is seasonally very abundant and easily captured in great numbers; 2) it is of a size which facilitates the handling and treatment of such numbers; and 3) it inhabits beaches of the mainland and beaches on nearby Santa Cruz Island.

Several methods have been used in the past to measure the incremental type of growth experienced by crustaceans, all of which have merits and drawbacks. These methods include: field caging, laboratory confinement, mark and recapture methods, and modal size class analysis. The best of these for the estimation of field growth rate is field caging. This method, unfortunately, cannot be applied to sand crabs living in their shifting sand habitat. For reasons presented in detail in the methods, a different approach has been used to measure growth for *E. analoga* The "instantaneous growth rate" method used here takes advantage of certain aspects of the crustacean molt cycle to minimize handling effects while estimating field growth rate. Both molt increment and molt frequency measures are taken, which are combined to give an instantaneous growth rate for an average individual of each population. By this method the response of growth to different en-

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vironmental conditions in the field can be observed for this species.

METHODS

Several alternatives for the measurement of growth for *Emerita analoga* were possible, including all those mentioned above. Field caging did not seem practical, and laboratory impoundment does not provide information on the growth rate in the field situation. Mark and recapture techniques are adaptable to the species (Dillery and Knapp 1970), but considerable time and effort can be expended for very little data return. The usual recapture rate is low, 10% or so at best, unless unusual circumstances, e.g., a fishery, exist. Modal size class analysis can give an index of average growth, but can be misleading without corroborative evidence from the laboratory or some other method of growth measurement. Unfortunately, no such corroborative data exist for *E. analoga*. As a result of these considerations, an instantaneous growth rate method was chosen to estimate growth for this species. This method as applied to *E. analoga* is described in the following sections.

Localities

Two locations were chosen on the basis of their proximity and on preliminary observed differences in their environmental conditions. One site, the beach of Goleta Bay adjacent to the University of California Santa Barbara campus, is bathed in relatively warm water (mean surface temperature for 1974 and 1975: 13.7°C) that is relatively turbid (average lateral visibility: <1 m).

The second site, a bay on the northwest corner of Santa Cruz Island, is about 42 km (25 mi) south of the coast of Santa Barbara, and experiences much different water conditions. At this location, water clarity is almost always excellent (10-20 m of lateral visibility), indicating a relative lack of suspended materials. In addition, Neushul et al. (1967) described current patterns in the vicinity which indicate that this site is bathed in a colder water mass originating in the north. The mean surface temperature measured at the Santa Cruz Island site during 1974 and 1975 was 12.1°C.

Sampling

Sand crabs were gathered and separated into size classes by methods described fully in Wenner et al. (1974). The use of an automatic size sorting sieve permitted measurement of a large number of live crabs rapidly. Samples were taken approximately biweekly at Santa Cruz Island and Goleta in 1974 and monthly at Goleta in 1975. The crabs, separated into size classes, were then placed in screen compartments in sand in a continuous flow seawater table for a period of 5 days. Every day each compartment was checked for molts, and the number of molts and molt increments were recorded. Where multiple molts occurred in any size class on 1 day, premolt and postmolt carapace length were paired by rank from least to greatest measure. This procedure might tend to reduce the variance in molt increment slightly, but no significant differences were found between single molt and multiple molt records for 20 molt increment observations during May-July at Goleta in 1974 ($0.5<P<0.6$, $t = 0.667$, df = 36).

Water temperature data were taken at the time of sampling, and water temperature was monitored throughout the 5-day holding period. Water samples were also taken monthly from July to October 1975. The water was filtered through preashed, preweighed Whatman[2] GF-C glass fiber filter paper under 4-5 lb vacuum, after coarse filtration through a 2-mm screen. Efford (1966) suggested that *E. analoga* can handle particles between 5 μm and 2 mm. The filter paper filtered particles down to approximately 5 μm in size. Thus an approximation of the range of particle sizes utilized by *E. analoga* was filtered from the water. Filterable solids (grams/liter) were measured in this way from both sites.

Instantaneous Growth Rate Rationale

Given that two parameters of crustacean growth, i.e., molt increment and molt frequency, are the factors which need be estimated, a method is required which minimizes handling effects but which still allows observation of size-specific changes in these measures.

Prolonged impoundment in a laboratory situation tends to affect both the molt increment and molt frequency; however, aspects of the crustacean molt cycle provide an advantage if crabs are held in the laboratory for a short period of time. Drach (1939) described the molt cycle of *Cancer*

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

pagurus. From this description it is clear that a crustacean actually spends a great deal of its time involved with the molting process. Once the specific stimulus to molt has occurred, environmental changes seem to have little effect in modifying the process (Green and Neff 1972). In other words, a crab which is about to molt will molt. In fact, keeping *E. analoga* in running seawater tables for a very short portion of their molt cycle does not alter a relatively high value for molt frequency and increment. For example, Table 1 shows data from a 14-day period in which *E. analoga* were kept in running seawater tables. These data suggest that for a period of 5 days or so *E. analoga* may be relatively unaffected by impoundment in running seawater tables, but that confinement for longer periods reduces both the increment at molt and molt frequency.

From the above, it follows that keeping *E. analoga* in running ambient seawater tables for a period of 5 days generates relatively accurate "instantaneous" estimates of field growth rate for these crabs. This allowed me to collect sand crabs from the field, place them in seawater tables within 2 or 3 h after collection, and monitor them daily. Molt increment was measured directly as animals within each size class molted, and molt frequency was calculated by the formula: $f_m = t/p_t$ where f_m = molt frequency in days, t = total number of days held, and p_t = proportion of animals which molted in t days. For instance, if half the crabs molted in 5 days, the average molt frequency would be 10 days.

TABLE 1.—Molt records for *Emerita analoga* kept in running seawater tables for 14 consecutive days.

Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]	Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]
1	13	1.2	8	4	0.8
2	11	1.3	9	8	0.9
3	19	1.2	10	6	—
4	27	1.0	11	5	—
5	17	1.2	12	2	—
6	9	0.8	13	3	—
7	7	0.9	14	2	—

[1]At 5.9 mm premolt carapace length.

RESULTS

Environmental Differences

Water temperature showed a consistent annual difference between Goleta Bay and Santa Cruz Island for 1974 and 1975 (Figure 1), though the peak water temperature for 1975 was the same for both locations. During June-October 1974, the mean surface temperature difference between sites was 2.9°C. Peak water temperature was maintained for about 2 mo (mid-June to mid-August) at Goleta Bay in 1974 while Santa Cruz Island experienced peak temperature for a month or less.

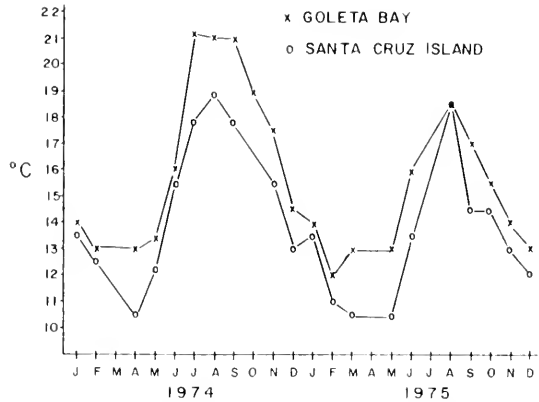

FIGURE 1.—Annual surface temperature variation at Goleta Bay and the western tip of Santa Cruz Island for several years. Data from March to October 1974 are from direct observation. All other data are from U.S. Coast Guard sea surface isotherm charts for Point Conception south.

Four water samples, taken at each location monthly between July and October 1975, showed a large significant difference ($P<0.001$, $t = 6.36$, df = 14) between the amount of filterable solids in the water washing onto the two beaches. Goleta Bay averaged 0.11321 ± 0.02933 g/l of filterable solids while Santa Cruz Island averaged 0.04416 ± 0.00925 g/l. This means that about 2½ times as much filterable material was potentially available for *E. analoga* at Goleta Bay as at Santa Cruz Island. Unfortunately, organic content of these samples was not measured. This would have been a more reliable index of food availability than filterable solids.

Growth

Comparison of data from Goleta Bay in 1974 and 1975 indicates that the instantaneous growth rate method produces repeatable results and that the growth rates at Goleta Bay for the two time periods were about the same (Table 2). Comparison of data from Goleta Bay and Santa Cruz Island in 1974 indicates that sand crabs from the island site were molting about half as often, on the average, as those crabs from Goleta Bay during the

TABLE 2.—Summarized growth data for sand crabs from Goleta Bay and Santa Cruz Island in 1974 and 1975. Mean ± SD is given for each measure.

Item	Goleta Bay		Santa Cruz Island, 1974		
	1974	1975	All samples	First 3	Last 3
Molt increment (mm):					
Sample size	581	629	188	118	70
$\bar{x}$ increment	0.9 ± 0.3	1.0 ± 0.4	0.6 ± 0.3	0.8 ± 0.3	0.4 ± 0.2
$\bar{x}$ premolt carapace length	7.3 ± 1.8	7.4 ± 4.2	7.5 ± 2.7	8.0 ± 3.0	7.4 ± 1.8
Molt frequency (days):					
Sample size	1,785	1,334	1,703	717	986
$\bar{x}$ frequency	26 ± 19	18 ± 11	50 ± 24	36 ± 18	63 ± 22
$\bar{x}$ premolt carapace length	7.7 ± 1.8	7.0 ± 3.4	7.7 ± 3.1	8.8 ± 3.5	7.0 ± 1.6

sampling period. Also, the island site crabs gained about a third less in carapace length at each molt than the mainland animals (Table 2). Thus, sand crabs at the island beach would take about three times as long as the Goleta Bay crabs to reach a given size, growing at the observed rates. Calculation of the instantaneous rate of growth (molt increment ÷ intermolt period) for the two beaches in 1974 gives values of 0.035 mm/day for Goleta Bay and 0.012 mm/day for Santa Cruz Island

Separation of the Santa Cruz Island samples into two equal time periods (May-early July, late July-September) yielded an interesting observation. The later group of samples showed a much lower growth rate than did the earlier, which can be explained by the steady decline in molt increment (Figure 2). The relatively high value (0.9 mm) in late May could represent a peak, but the island site was not sampled prior to May. The pattern of molt increment vs. time for Goleta Bay (Figure 2) was different, showing peaks in July and September. The decrease in August may reflect changes in the number of maximum size males, which decrease in molt increment as they approach maximum size, and also may reflect an influx of juvenile crabs into the population in August. The first peak corresponds in time with the peak water temperature for the sample period (Figure 1). This may be a result of a physiological response to temperature by *E. analoga*. Crabs observed in the laboratory at different temperatures fed at different rates. Those in warmer water fed most often (Fusaro 1977).

At both locations, molt increment was positively correlated with size (Figure 3). The difference between means of molt increment from the two locations was 0.3 mm, amounting to about one-half of an average molt increment for the Santa Cruz Island beach population.

Molt frequency data could not be correlated with carapace length at either location, although a generally similar trend existed in most samples. A

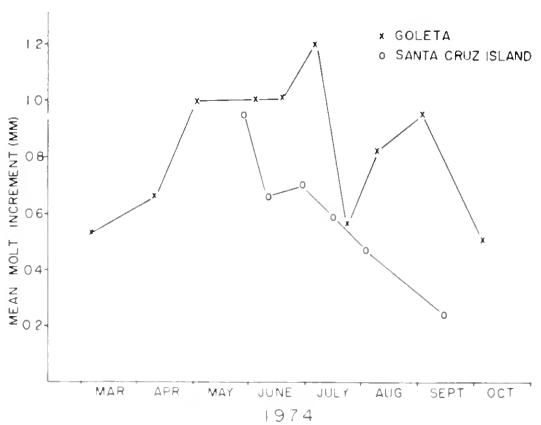

FIGURE 2.—Molt increment vs. time for sand crabs from Goleta Bay and Santa Cruz Island. Each point is a mean for that sample date.

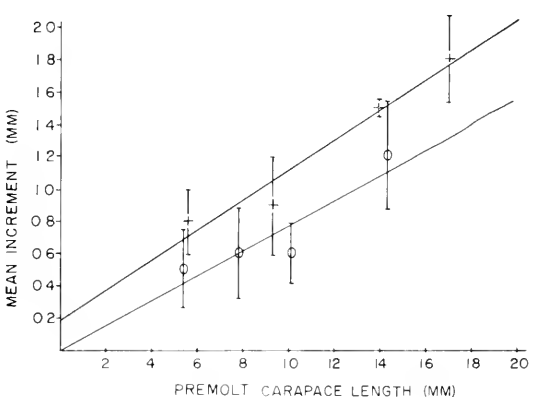

FIGURE 3.—Regression of mean molt increment on premolt carapace length for grouped size class data of sand crabs from Goleta Bay (+'s) and from Santa Cruz Island (0's). Regression line equations are $Y = 0.0932X + 0.1829$ for Goleta Bay and $Y = 0.0776X - 0.0041$ for Santa Cruz Island. Correlation coefficients are 0.98 for Goleta Bay and 0.92 for Santa Cruz Island. Vertical bars at each point represent ± 1 SD.

relatively high molt frequency was observed at smaller sizes (about every 7-12 days/molt at 5 mm carapace length), and this value increased generally in larger size classes (to about every 80-90 days/molt at 20 mm carapace length). Molt frequency averaged over a similar range of premolt carapace lengths did reveal, however, a large difference between the populations on the two different beaches (Table 2).

Population structure data reveal differences in several measures which relate to the growth rate of *E. analoga* (Table 3). The mean size of both males and females was reduced at the Santa Cruz Island site. The proportion of females larger than the mean minimum size of ovigerous females was drastically reduced at the Santa Cruz Island site (2.7% compared with 21.1% at Goleta). In addition, the overall proportion of females which were ovigerous was much smaller at the island site (1.1% compared with 19.4% at Goleta).

TABLE 3.—Population structure data from pooled samples of *Emerita analoga* between June and September 1974. All size values are in millimeters carapace length and sample sizes are in parentheses.

Item	Goleta Bay	Santa Cruz Island
Mean size ♂	7.5 (8,956)	6.0 (6,951)
Mean size ♀	9.7 (6,347)	7.5 (7,730)
Mean % ovigerous ♀	19.4 (6,347)	1.1 (7,730)
Mean min size ovigerous ♀	13.8 (6,347)	13.8 (7,730)
% ♀ >13.8 mm carapace length	21.1 (6,347)	2.7 (7,730)

DISCUSSION

Methods for Measuring Growth

The growth rate of crustaceans in nature, though of considerable research interest, has been difficult to measure for several reasons. Primarily, all of the hard parts of the animal are cast off with the molt, making the marking of them all but impossible until recent years. Wenner et al. (1974) discussed the problems associated with measuring growth for crustaceans, and their table 1 summarized possible patterns of growth for the Crustacea. That table stressed the relative contribution of two factors in crustacean growth: molt increment and molt frequency. Both of these may be responsive to different environmental parameters, altering the growth pattern of a species.

The standard methods for measuring field growth rate for crustaceans (caging, mark and recapture, and analysis of modal size classes without corroborative data) are unsatisfactory to compare field growth rates for different populations of *E. analoga*. Since none of these methods alone suffices for this kind of comparative measurement with *E. analoga*, the instantaneous growth rate approach was used in this comparative analysis. The method has qualities common to some of the other methods mentioned, but avoids some of the inherent problems of those methods. This technique allows direct observation of size-specific molt frequency and molt increment, while minimizing the handling effects normally associated with laboratory impoundment. It is likely that molt frequency estimates by this method are more accurate for the larger crabs, for which the 5-day holding period is a relatively smaller proportion of the intermolt period. The method has allowed comparison of growth factors (molt increment and frequency) in detail for *E. analoga* and gave repeatable data such as that found for Goleta Bay in 1974 and 1975. Thus a technique for measurement of crustacean growth has been developed here which may hold promise for such comparative studies as this, where field caging is impractical.

Growth of *Emerita analoga*

The large difference in the growth rate of *E. analoga* between beaches of Goleta Bay and a Santa Cruz Island bay is remarkable in view of their proximity (about 42 km apart) but not in view of the different environmental conditions found at each beach. The combination of colder water and reduced filterable material in suspension in the water appears to have slowed the growth of *E. analoga* on Santa Cruz Island. This difference is evidence of the sensitivity of these two factors of sand crab growth to variation in environmental qualities.

It is tempting to construct growth curves from such data on molt increment and molt frequency, having arrived at estimates for these. Both of these factors, however, have been shown to be highly responsive to environmental conditions. In fact, they vary widely in time and space with no clear pattern emerging as yet. A growth curve constructed from these data would apply only under a specific set of environmental conditions. Certainly these large differences in growth rate in nearby beaches precludes the use of modal size classes from several beaches for the determination of growth for *E. analoga*, as Efford (1967) did earlier.

Efford (1967:84, figure 3) presented a growth curve for *E. analoga*, constructed from data taken from 22 beaches on the Pacific coast between Ensenada, Mexico, and Tofino, Canada (a 2,400 km distance). Three-fourths of the data presented were gathered over a period of only 2 mo (between 17 June and 17 August 1961). The remaining data were collected in 1959 and 1963. Where size-frequency data were bimodal, the author assumed that two year classes were present. To construct a growth curve from his data, Efford also had to assume that: 1) growth rate was the same year to year (temporally stable, at least during the growing season); and 2) longshore migration did not take place for *E. analoga*.

Dillery and Knapp (1970) demonstrated that an average *E. analoga* individual of about 26 mm carapace length travels about 15 m/day alongshore in an easterly direction on local beaches in Santa Barbara. This implies that the individuals in inhabiting a particular location may change from day to day. Barnes and Wenner (1968) suggested that the interpretation of size-frequency data is considerably simplified if sex reversal is assumed for this species, and some direct evidence (Wenner 1972) supports this assumption. However, recent laboratory data (Fusaro 1977) suggest that a differential growth rate for males and females between 9 and 14 mm carapace length may account for the observed size-frequency distributions and sex ratio patterns, rather than protrandry.

Combining data from different beaches, as Efford (1967) did, also carries with it the assumption that the growth rate is relatively the same for the various parts of the range of *E. analoga* (spatially stable). However, in an analysis of *E. talpoida* data presented by Wharton (1942), Efford suggested that the growth pattern of this latter species may differ in the southern part of its range. It is likely that temperature was responsible for the difference, as it is likely that temperature has an effect on the growth of *E. analoga* in different parts of its Pacific coast range.

Wenner et al. (1974) presented data (their figure 5) which suggested that for *E. analoga*, even different local populations may display different growth patterns, at least as indicated by size at sexual maturity. Data presented in this report imply that molt increment and molt frequency are indeed different in different environmental regimes in nature. Growth curves constructed for such different areas would likely differ. To combine these sets of data would be to obscure the real differences in growth rate observable in such local, proximate populations.

The instantaneous growth rate estimate, though, may be used as an index of how well a population fares under a given set of environmental conditions. Consider this instance. It has been shown that a population of *E. analoga* on a beach at Santa Cruz Island grew about one-third as fast as a population in Goleta Bay (molt increment depressed by one-third and molt frequency depressed by one-half). Assuming a fixed number of molts to maturity (e.g., Wenner et al. 1974, table 1), the island population would reach maturity at a smaller size and in about twice as long a time. In fact, population structure data (Table 3) shows that sand crabs from the island population reached maturity at about the same size as those from Goleta Bay. If a fixed size at maturity is assumed, the island population sampled would take about three times as long to reach that fixed size.

The third possible assumption, that there is a fixed length of time to maturity, is argued against by all available data. In any of these cases, however, the population of sand crabs inhabiting the beach of the Santa Cruz Island bay location was at a distinct disadvantage in terms of reproductive success when compared with the population of *E. analoga* inhabiting the Goleta Bay beach. This reproductive disadvantage was brought about at least in part by the large observed differences in molt frequency and molt increment at the two locations. A much smaller percentage of females were of reproductive size, probably due to the differential growth rate (see Table 3).

Cox and Dudley (1968) also reported large variations in the size of the smallest egg bearing female *E. analoga* found in their collections. Data presented here may account for such previously problematical observations, in that differences in growth rate may affect the size distribution and abundance of mature females.

As these data suggest, then, the growth rate of a crustacean population plays an important role in the life history of that species in its particular environmental situation. Of course, when dealing with a species which has pelagic larval stages, it becomes difficult to study local populations under the assumption that they are genetically different. Recruitment patterns are not generally well known for species with pelagic larvae (see Thorson 1950; Efford 1970; Mileikovsky 1971; Strathmann

1974), thus confounding the issue of reproductive success for a population in a particular habitat. Thus "relative reproductive success" may not be as good a criterion between populations such as these as it is between species. Measurement of differences in such life history factors as growth rate may, therefore, take on added significance in the comparison of two populations or species in differing environments, inasmuch as they do not depend on the assumption of genetic isolation but concern themselves more with the relationship of the population to its particular environmental circumstances.

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TIME-DEPENDENT SOLUTIONS AND EFFICIENT PARAMETERS FOR STOCK-PRODUCTION MODELS

R. IAN FLETCHER[1]

ABSTRACT

The time-dependent formulations of the Graham-Schaefer and Pella-Tomlinson systems are restructured so as to accommodate directly the critical-point parameters of their respective governing graphs; the resulting parametric system accounts for the behavior of either model wholly in terms of its management components. The indeterminate exponent and the coefficients of the Pella-Tomlinson equations are uncoupled and the dual formulations associated with the conventional casting of the system are eliminated; the governing equations and corresponding solutions are cast into composite forms and the sign changes of coefficients become automatic. The previously obscure relationships between management parameters and variable graph curvature in the Pella-Tomlinson model are expressly formulated; maximum sustainable yield is shown to be independent of the indeterminacy of the system. Time-delay estimators for both systems are formulated.

We analyze here, in a deterministic setting, certain of the transient, nonlinear mechanisms employed in the modelling of stock and yield during periods of imbalance between fishing removals and stock productivity. The general method of analysis, which appeals primarily to the direct parameterization of critical points, will apply to any nonlinear scheme of exploitation and gross production, but it applies in particular to the Graham-Schaefer hypothesis (Graham 1935; Schaefer 1954) and to the "generalized" model of Pella and Tomlinson (1969). Since control of either system rests ultimately with the control of critical points, we restructure the parametric definitions accordingly and the governing equations for both systems are then controlled directly by parameters of management significance.

Typically, either system reflects the deterministic premise that a stock of fishes, otherwise held by exploitation at levels below a prior abundance, will constantly strive to recover its numbers in accord with some innate, self-regulating, and repeatable mechanism of restoration. Any such restoration must accrue from the productivity of the stock, and by Graham's hypothesis, the inherent or latent capacity for productivity in a stock of fishes depends jointly on the current size of the stock (in numbers or biomass) and the difference between the current and potentially maximum sizes. Whence, in terms of time-dependent biomass B, and with the proportionality coefficient defined as the ratio of "intrinsic" growth rate k and b_∞, Graham's formula for latent productivity $\dot{P}$ takes on the familiar form

$$\dot{P}(B) = kB - \frac{k}{B_\infty} B^2. \qquad (1)$$

Of the two expanded terms, the first governs the intrinsic, exponential capacity for growth of the population's biomass, while the negative, nonlinear term provides the damping that ultimately slows growth as $B(t)$ approaches its asymptotic maximum B_∞. The two terms, in their algebraic sum, govern the latent productivity of the stock at any stock size between zero and B_∞. Parameter k, as we shall see, is coupled analytically and phenomenologically to parameter B_∞, but the dependence of k on root B_∞ in Equation (1) can be supressed in favor of the direct parameterization of maximum productivity (which, in the complete exploitation model, we identify with maximum yield rate).

In the Pella-Tomlinson model, the parametric controls for latent productivity exceed by one the total number of such parameters in Graham's formulation, an increase in freedom that comes at considerable cost to tractability, both analytical and statistical. The differential equation that governs latent productivity in the Pella-Tomlinson system has the indeterminate form

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$$\dot{P}(B) = c_1 B + c_2 B^n, \quad (2)$$

with exponent n the additional parameter, but with the signs of the coefficients now dependent on the range of definition of n. As before, the combined terms describe, at any stock size B, the stock's latent capacity for productivity. With n undetermined (its determination being a part of the empirical demonstration), solutions of Equation (2) constitute infinitely many growth laws. By setting $n = 2$, and with $c_1 > 0$, $c_2 < 0$, Equation (2) reduces to the Graham equation (Equation (1)). Pella and Tomlinson (1969) attribute Equation (2) to Richards (1959). For a detailed analysis of (2) as a general growth form, see Fletcher (1975); the anticedents of this analysis appear there.

In either of the two systems, exploitation enters the formulation for productivity by the direct difference $\dot{P} - \dot{Y}$, with $\dot{Y}$ signifying the rate of biomass removal owed to exploitation and $\dot{P}$ the latent productivity of the stock. Wherefore, in writing

$$\dot{B}(B) = \dot{P}(B) - \dot{Y}(B), \quad (3)$$

we interpret $\dot{B}(B)$ as being the resultant productivity, at stock size B, that nets to the stock for its growth. The net may be positive, negative, or zero accordingly as $\dot{P}$ and $\dot{Y}$ vary with B. That is

$\dot{P} > \dot{Y}$ implies $\dot{B} > 0$: the stock's latent productivity exceeds the rate of exploitation; a positive net productivity remains to the stock and the stock so tends to a higher level of biomass.

$\dot{P} < \dot{Y}$ implies $\dot{B} < 0$: the rate of biomass removal exceeds the stock's capacity for growth; the stock adjusts to the deficit in net productivity by tending to a lower level of total biomass.

$\dot{P} = \dot{Y}$ implies $\dot{B} = 0$: the exploitation rate just balances latent productivity, and biomass trajectory $B(t)$ exhibits an extremum. Should $\dot{B} = 0$ over finite time, stock biomass remains stationary and the state called "equilibrium" prevails.

Although the detailed time course of any real stock biomass is actually determined by variations in renewal, survival, member growth, and the age- or size-dependent probabilities of capture, such effects are not usually separated in the models of interest here, and yield rate $\dot{Y}$ customarily takes the form

$$\dot{Y}(t) = F(t) \cdot B(t), \quad (4)$$

with the implication that all fish of the fishable stock are presumed to share, in equal measure, the force of fishing mortality F, irrespective of age or size. By admitting Equation (4) into Equation (3), our general form for net productivity becomes

$$\dot{B} = \dot{P} - F \cdot B, \quad (5)$$

where the time variation of F is usually prescribed by average effort f on the assumption that $F = qf/\tau$, quantity q being the individual probability of capture per unit of effort and τ the averaging interval measured in fractions of the dimensional time unit of F.

ANALYSIS OF THE GRAHAM SYSTEM

Figure 1 illustrates the phase-plane graph of Equation (1), the latent productivity of a Graham stock. Maximum productivity m occurs at stock size p. And regardless of the conventions employed in the formulation of Equation (2), essential parametric control in the equation resides specifically with its nonzero root B_∞ and with coordinate m of the critical point (p, m). Parameter m and B_∞ constitute a complete, minimum set of analytically independent parameters for latent

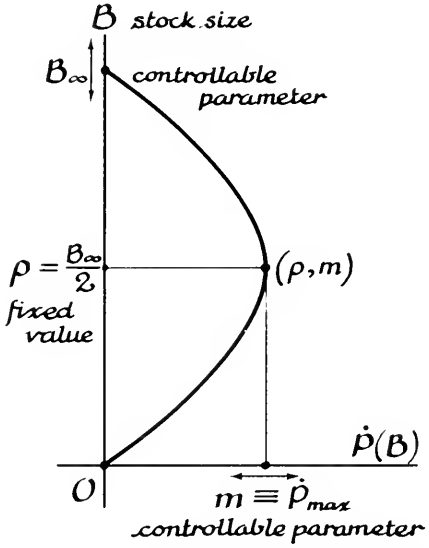


FIGURE 1.—Latent productivity $\dot{P}$ as a function of stock size B, the Graham model. See Equations (1) and (1a).

productivity in the Graham system, and they represent the whole extent of available control over the graph of Equation (1). Coordinate p of the critical point has the fixed value $B_\infty/2$, and the graph of Equation (1) has a fixed curvature of second degree.

Wherefore, productivity Equation (1), cast directly in terms of analytical parameters m and B_∞, takes on the form

$$\dot{P} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2, \qquad (1a)$$

and intrinsic rate k, as it turns out, bears a proportionality dependence on maximum productivity and maximum biomass in the relationship

$$k = \frac{4m}{B_\infty} \left[\equiv 4\frac{P_{\max}}{B_{\max}}\right]$$

And with the substitution of Equation (1a) into Equation (5), the formula for the net productivity of a Graham stock becomes

$$\dot{B} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2 - FB. \qquad (6)$$

In the integrated, equilibrium versions of the Graham system, maximum latent productivity m becomes maximum sustainable yield (MSY), hence parameter m may be directly interpreted as MSY in any optimization procedure on Equation (6).

If we restrict the time-dependence of F to abrupt changes so that any solution of Equation (6) corresponds on its interval of validity, however brief, to some constant value of F, then the time-dependence of B in Equation (6) becomes

$$B(t) = \frac{B_*}{1 + C_0 e^{-(4m/B_\infty - F)t}}$$
$$B_* = \left[1 - \frac{FB_\infty}{4m}\right] B_\infty, \qquad (7)$$

and with initial time t_0 set arbitrarily to zero, the integration constant in Equation (7) becomes

$$C_0 = \frac{B_* - B_0}{B_0}.$$

Figure 2 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) for cases where

$$F < \frac{4m}{B_\infty}.$$

As indicated in the figure, root B_* becomes the adjustment level to which biomass trajectory $B(t)$ will trend when F is less than critical quantity $4m/B_\infty$ (and obviously, $B(t)$ trends to B_∞ in Equation (7) when F is zero). The system is governed by the positive branch of Equation (6) when $\dot{Y} < \dot{P}$ (in which case, $\dot{B} > 0$), and by the negative branch of Equation (6) when $\dot{Y} > \dot{P}$ (in which case, $\dot{B} < 0$). But this partitioning of F into subranges for negative or positive $\dot{B}$ is a density-dependent process. Although we must have $F < 4m/B_\infty$ for positive B_*, the values of F on that range that drive the stock either up or down will depend on initial stock size B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (6), mortality F must have a value such that

$$0 < F < \frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right],$$

in which case $B(t)$ increases from initial value B_0 towards a higher adjustment level B_*. But for any value of F on the interval

$$\frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right] < F < \frac{4m}{B_\infty},$$

then $\dot{Y} > \dot{P}$ and $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Figure 3 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) when

$$F \geq \frac{4m}{B_\infty},$$

in which case the adjustment level of biomass corresponds to the zero root of Equation (6). As indicated by the figure, any mortality F so great as to equal or exceed the quantity $4m/B_\infty$, if maintained, will fish a Graham stock to extinction.

Since Equation (6) governs the relationship between transient biomass and nonequilibrium removal, we look to its solution (Equation (7)) for time delays between equilibria. But the asymptotic behavior of Equation (7) is a minor analytical annoyance to be circumvented here. Let us

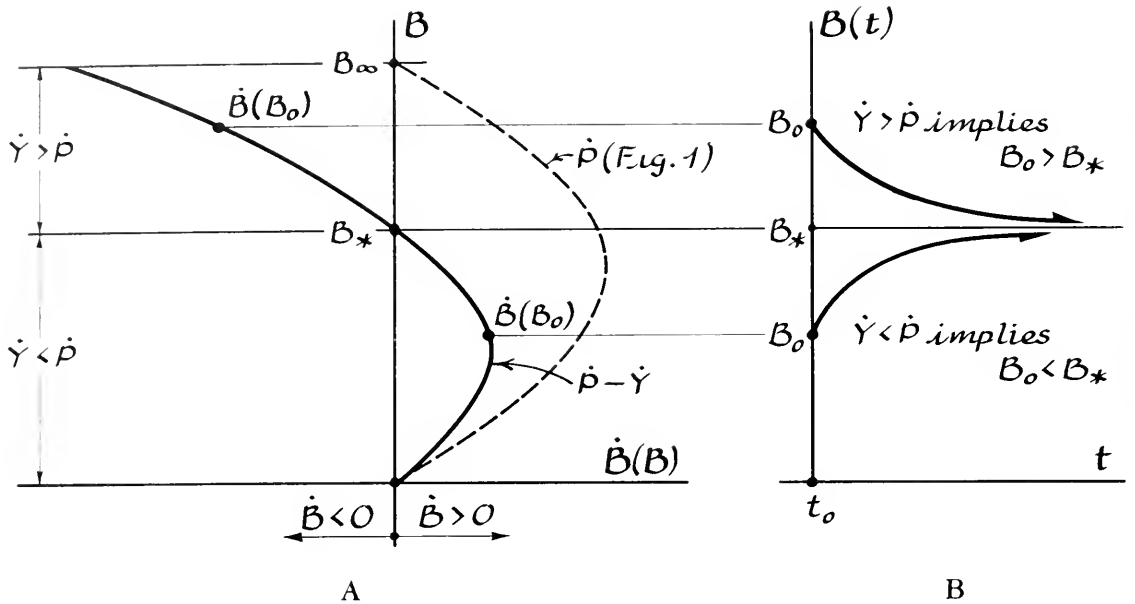


FIGURE 2.—A. Typical phase-plane graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality F constrained to the interval $0 < F < 4m/B_\infty$. When removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$ then $\dot{B} < 0$ and the negative branch of Equation (6) applies. When productivity $\dot{P}$ exceeds removal rate $\dot{Y}$ then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (7). When $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. When $\dot{Y} < \dot{P}$, biomass increases from initial value B_0 towards adjustment level B_*.

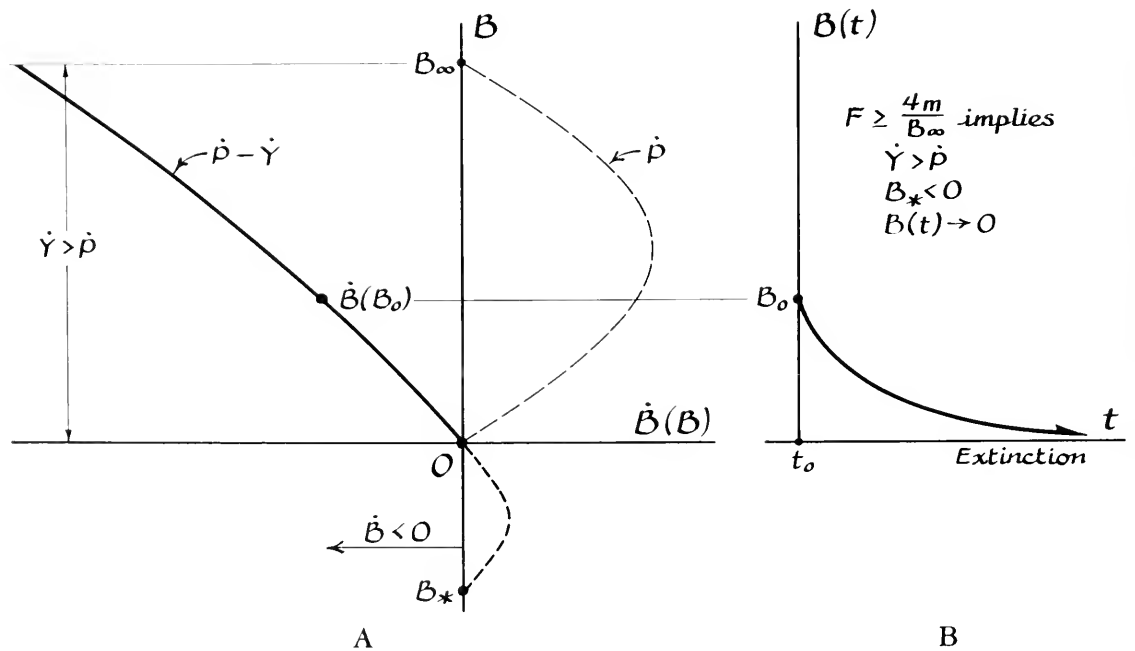


FIGURE 3.—A. Typical graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality $F \geq 4m/B_\infty$. For any such value of F, the zero root of Equation (6) applies, removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$, and $\dot{B} < 0$. B. Typical solution trajectory $B(t)$ of Equation (7) when $F \geq 4m/B_\infty$. Biomass declines from initial value B_0 towards extinction level $B = 0$.

presume that no practical technique of estimation will have a precision of resolution better than some assignable percentage of true stock size, and let us reflect that practical uncertainty in our analysis by expanding the asymptotic bound of Equation (7) to a region of radius $\epsilon \cdot B_*$ around the analytical value of the bound (ϵ being the measure of the uncertainty). Whence, with B_0 and B_1 now signifying initial and adjustment levels, and by supposing that F changes abruptly at time t_0 from value F_0 to some new value F_1, Equation (7) becomes

$$(1 \pm \epsilon) = \frac{1}{1 + C_0 e^{-(4m/B_\infty - F_1)t}},$$

the plus sign applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$. By setting initial time t_0 arbitrarily at zero,

$$C_0 = \frac{B_1 - B_0}{B_0},$$

and the transition time between initial level B_0 and the ϵ-region at adjustment level B_1 becomes

$$t_{\text{lag}} = \frac{1}{4m/B_\infty - F_1} \ln \left[\frac{(1 \pm \epsilon)(B_1 - B_0)}{-(\pm \epsilon B_0)} \right]. \quad (8)$$

In few commercial fisheries do we expect to see exploitation rates constant over intervals equal to transition times t_{lag}, and in any case we anticipate considerable variation in stock size along the way, owing to chance events. Nevertheless, Equation (8) serves a purpose; it will give us some idea, in a management strategy, of the time delays to be expected in bringing a stock from one general state of exploitation to another through the regulation of mortality F.

To illustrate the particularization of Equation (8), we follow an adaptation by Ricker (1975: 312-315) of Graham's work on demersal stocks of the North Sea. To accommodate our formulation here, parameters for Ricker's adaptation would be

B_∞ = 220,000 tons,
m = 40,300 tons yr^{-1} (the MSY of the model).

With reference to Ricker's illustrations (1975: 312-315), we first calculate the time delay that accompanies a reduction in mortality from F_0 = 0.40 yr^{-1}, corresponding to a stock level of B_0 = 100,000 tons, to a new mortality commencing at reference time zero, of F_1 = 0.20 yr^{-1}. The adjustment level to which $B(t)$ will trend in the transition period is B_1 = 160,000 tons (by setting, in Equation (6), $B = 0$, $F = F_1$ and $B = B_1$. If we now specify the uncertainty in estimation precision as being, say, 5% of true stock size, then Equation (8), with $F_1 < F_0$ and ϵ = 0.05, gives the estimated delay in adjustment as

$$t_{\text{lag}} = \frac{1}{0.533} \ln \left[\frac{(1 - 0.05)(160{,}000 - 100{,}000)}{0.05(100{,}000)} \right]$$
$$= 4.6 \text{ yr}.$$

When the model stock declines between similar levels, the time delay is longer. That is, stock at level B_0 = 160,000 tons, corresponding to the fishing mortality F_0 = 0.20 yr^{-1}, declines to the adjustment level B_1 = 100,000 tons following an increase at $t_0 = 0$ to the new mortality F_1 = 0.40 yr^{-1}. Transition time t_{lag} now becomes

$$t_{\text{lag}} = \frac{1}{0.333} \ln \left[\frac{(1 + 0.05)(100{,}000 - 160{,}000)}{-0.05(160{,}000)} \right]$$
$$= 6.2 \text{ yr}.$$

Yields from transient periods differ considerably from the removals associated with equilibrium states. Obviously, an increase in fishing mortality increases the yield temporarily, and a decrease in fishing mortality decreases the yield temporarily, but the ensuing trends of adjustment will depend, in the context of the Graham system, on the following relationships:

$F < 4m/B_\infty$; stock size $B(t) \to B_*$ (Figure 2), which implies that $\dot{Y} \to FB_*$.
$F \geq 4m/B_\infty$; root $B_* < 0$ and $B(t) \to 0$ (Figure 3) which implies that $\dot{Y} \to 0$.
$F = 2m/B_\infty$; stock size $B(t)$ implies p (p being the biomass level $B_\infty/2$ where maximum latent productivity occurs; Figure 1), which implies that $\dot{Y} \to m$. Accordingly, we may identify parameter m, in any of the rate equations here, with MSY (which, we should remember, is itself a yield rate).

Since, by Equation (4), instantaneous removal varies in time as $\dot{Y}(t) = F(t)B(t)$, then over the course of the adjustment interval that follows an abrupt change in F, yield from a Graham stock will accumulate as

$$Y(t) = (B_\infty - B_*) \ln \left[1 + \frac{B_0}{B_*}\left(e^{(4m/B_\infty - F)t} - 1\right)\right] \quad (9)$$

$$B_* = \left[B_\infty - \frac{F B_\infty^{\,2}}{4m}\right].$$

ANALYSIS OF THE PELLA-TOMLINSON SYSTEM

As noted in the foregoing section, the maximum latent productivity m of a Graham stock always occurs at a biomass value exactly one-half the unexploited maximum B_∞. In turn, MSY of the equilibrium model must also occur at the stock level $B_\infty/2$. So as to gain control over the locations of those extrema, Pella and Tomlinson (1969) modify the Graham system by writing the differential equation for latent productivity $\dot{P}$ essentially in the form of Equation (2), which, by the customary treatment, has a troublesome, dual formulation owing to the sign changes at $n = 1$ of coefficients c_1, c_2. On the interval $0 < n < 1$ latent productivity in the Pella-Tomlinson system takes the basic form

$$\dot{P} = aB^n - bB \quad (10)$$

(where, for the sake of emphasis, $c_1 = -b$, $c_2 = a$, with a and b positive), but on the interval $n > 1$ latent productivity takes on the basic form

$$\dot{P} = bB - aB^n \quad (11)$$

(where $c_1 = b$, $c_2 = -a$, with a and b positive). In either case, the bound B_∞, the maximum productivity m, and the ordinate p (which governs the biomass level where m occurs), all depend on the numerical value assigned to exponent n. That is, root B_∞ is given by

$$B_\infty = \left[\frac{a}{b}\right]^{1/(1-n)},$$

the ordinate p is determined by

$$p = \left[\frac{an}{b}\right]^{1/(1-n)},$$

while maximum productivity m, by the conventional casting of the model, must be determined from the formula

$$m = \pm \frac{b(1-n)}{n}\left[\frac{an}{b}\right]^{1/(1-n)},$$

the plus sign applying to Equation (10) and the minus sign to Equation (11).

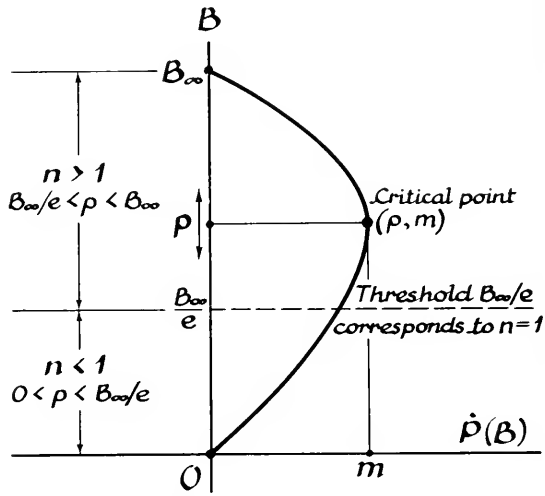


FIGURE 4.—Typical graph of Equation (12), latent productivity $\dot{P}$ as a function of stock size B, the Pella-Tomlinson system.

Coordinate p, in its location with respect to root B_∞, directly reflects the value assigned to exponent n, as indicated by Figure 4. When n takes any value between zero and unity, coordinate p falls on the range between zero and B_∞/e ($\approx 0.3679\, B_\infty$), in which case Equation (10) applies. When n takes any value greater than unity, coordinate p falls on the range between B_∞/e and B_∞, in which case Equation (11) applies. But the coordinate m has no essential dependence on exponent n, and its apparent coupling with n (as indicated by the formulation above) is merely an inconvenient artifact of the conventional analysis. With parameters m and n uncoupled (see Fletcher 1975), the Equations (10) and (11) that govern latent productivity in the Pella-Tomlinson system can be consolidated into the single governing equation

$$\dot{P} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right]^n, \quad (12)$$

with γ a purely numerical factor wholly prescribed by n as

$$\gamma = \frac{n^{n/(n-1)}}{n-1}. \qquad (13)$$

With the coefficients so cast, the sign reversals at turning point $n = 1$ become automatic. In consequence, the consolidated interval of definition for n becomes $0 < n < \infty$ (the point $n = 1$ being a removable singularity). With parameter m thus separated from n in Equation (12), the undetermined exponent n can be defined solely by the fraction p/B_∞ in the relationship

$$\frac{p}{B_\infty} = n^{1/(1-n)}. \qquad (14)$$

Consolidated Equation (12) now takes on the role in the Pella-Tomlinson system that Equation (1a) takes on in the Graham system. In fact, when $n = 2$, Equation (12) reduces to Equation (1a), in which case $\gamma = 4$ and $p/B_\infty = \frac{1}{2}$. As an interesting aside here, we note that Equation (12), at the turning point $n = 1$, takes on the form

$$\dot{P} = -e\,m\left[\frac{B}{B_\infty}\right]\ln\left[\frac{B}{B_\infty}\right]$$

(e being Napier's constant), while ratio (14), in the limit as $n \to 1$, has the value

$$\frac{p}{B_\infty} = \frac{1}{e}.$$

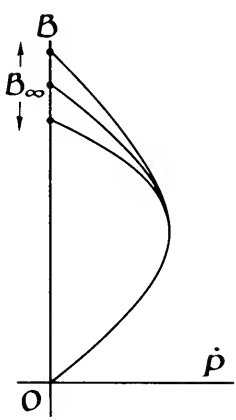
In fact, Fox (1970) constructed a stock-production model around this special case, but since the ratio p/B_∞ has the fixed value $1/e$, Fox's model "has as rigid a form as the Graham model" (Ricker 1975: 331).

Quantities m, p, and B_∞ constitute a complete, minimum set of independent parameters for latent productivity in the Pella-Tomlinson system. Collectively they control the behavior of governing Equation (12), but the influence of any one parameter remains independent of the remaining two. Figure 5 illustrates their separate effects on the graph of Equation (12).

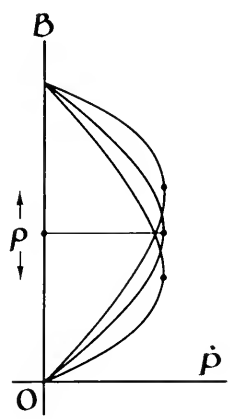
By appealing to the same piecewise constraints that enter the Graham productivity equations, we substitute Equation (12) into the general productivity formula (Equation (5)) and net productivity in the Pella-Tomlinson system becomes

$$\dot{B} = \gamma m\left[\frac{B}{B_\infty}\right] - \gamma m\left[\frac{B}{B_\infty}\right] - FB. \qquad (15)$$

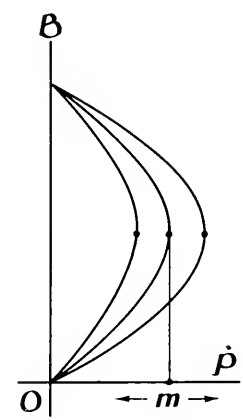
And over any time interval, however brief, that mortality F might be presumed to have a fixed value, biomass variable B in Equation (15) has the general time-dependent solution



B_∞: unexploited stock level [the nonzero root of Equation (12)].



p: biomass level for maximum productivity [the coordinate of B in Equation (12) where m occurs].



m: maximum productivity [the extremum coordinate P_{max} in Equation (12)].

FIGURE 5.—The graph of Equation (12), latent productivity in the Pella-Tomlinson system, as controlled by independent parameters m, p, and B_∞.

$$B(t) = \left[B_*^{1-n} + C \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right]^{1/(1-n)}, \tag{16}$$

$$B_* = \left[\frac{\gamma m}{\gamma m - F B_\infty}\right]^{1/(1-n)} B_\infty.$$

By setting initial time t_0 arbitrarily at zero, the integration constant C in Equation (16) becomes

$$C = B_0^{1-n} - B_*^{1-n}.$$

Biomass Equation (16) will apply immediately upon a change in F and remain valid thereafter for the time that F remains constant. Over such time, population biomass will trend up or down in accord with Equation (16) from initial size B_0 towards adjustment level B_*. Should nonzero root B_* be negative (which is possible only when $n > 1$), then the adjustment level corresponds to the zero root of Equation (15) and the population tends to extinction by Equation (16).

The critical relationships between fishing mortality, productivity, and time-dependent yield rate in the Pella-Tomlinson system are considerably more complex than the relationships between F, $\dot{P}$, and $\dot{Y}$ in the Graham system. Figure 6 illustrates the behavior of $\dot{P} - \dot{Y}$ when $n < 1$, and Figures 7 and 8 illustrate $\dot{P} - \dot{Y}$ when $n > 1$. The ratio $\gamma m/B_\infty$ becomes the critical quantity in the Pella-Tomlinson system ($4m/B_\infty$ being its counterpart in the Graham system).

As indicated by Figure 6, the biomass level p where maximum productivity occurs must lie on the range $0 < p < B_\infty/e$ when $0 < n < 1$. And when n takes any such value, the corresponding Pella-Tomlinson stock will exhibit nonzero adjustment levels of biomass for all values of fishing mortality however large; such a stock cannot be fished to extinction. That is, nonzero root B_* of Equation (15) will always have a positive value when $0 < n < 1$, its range of variation being $0 < B_* \leq B_\infty$ for F unrestricted on $0 \leq F < \infty$. But F is partitioned into subranges accordingly as $\dot{Y} < \dot{P}$ or $\dot{Y} > \dot{P}$. And those values of F, for which $B(t)$ either increases or decreases to B_*, depend on the critical ratio $\gamma m/B_\infty$ and initial biomass value B_0. To insure, for arbi-

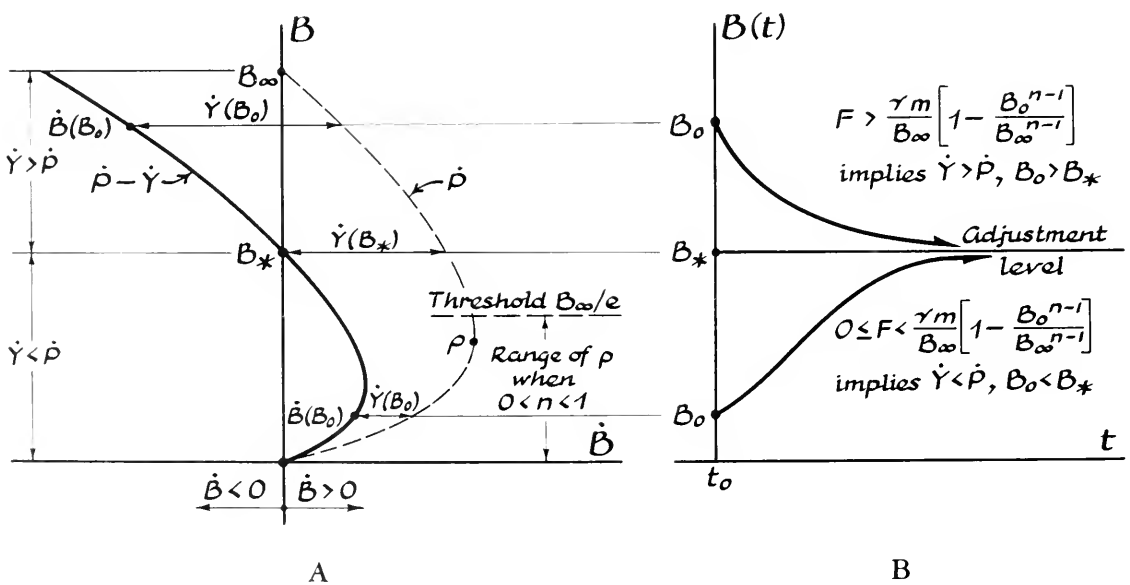


FIGURE 6.—A. Typical phase-plane graph of net productivity Equation (15), the Pella-Tomlinson system, for values of n where $0 < n < 1$. For any such value of n, root B_* of Equation (15) is always positive irrespective of the magnitude of F. Should removal rate $\dot{Y}$ exceed latent productivity $\dot{P}$, then $\dot{B} < 0$ and the negative branch of Equation (15) applies. Should $\dot{P}$ exceed removal rate $\dot{Y}$, then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (16), when $0 < n < 1$. Should $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. But when $\dot{Y} < \dot{P}$, biomass increases from B_0 towards B_*.

trary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must have a value such that

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right],$$

in which case $\dot{B} > 0$ and the positive branch of Equation (15) applies. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*. But for any value of F such that

$$F > \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right],$$

then $\dot{Y} > \dot{P}$ and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Although the sign of $\dot{B}$ and the consequential course of $B(t)$ is a density-dependent process for given F, we should note here that when

$$F = \left[\frac{n-1}{n}\right]\frac{\gamma m}{B_\infty}, \qquad (17)$$

then $B(t) \rightarrow \dot{Y}$ and $\rightarrow m$, irrespective of initial conditions. Accordingly, we may identify parameter m with MSY in any of the (reformulated) rate equations of the system.

As indicated by Figures 7 and 8, the biomass level p where m occurs must lie on the range $B_\infty/e < p < B_\infty$ when $n > 1$. And with n so prescribed, root B_* of Equation (15) may have positive or negative values accordingly as F has a value less or greater than the critical ratio $\gamma m/B_\infty$. Figure 7 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$0 \leq F < \frac{\gamma m}{B_\infty}$$
$$0 < B_* \leq B_\infty,$$

in which case, root B_* of Equation (15) becomes the adjustment level such that $B(t) \rightarrow B_*$ by Equation (16). But whether $B(t)$ trends up or down to B_* depends on the further partitioning of F with respect to initial biomass value B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must be further constrained to the interval

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right];$$

thus $\dot{B} > 0$ and the positive branch of Equation (15) applies as indicated by Figure 7a. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*, as indicated by the lower curve of Figure 7b. But for any value of F on the interval

$$\frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right] < F < \frac{\gamma m}{B_\infty},$$

then $\dot{Y} > \dot{P}$, $\dot{B} < 0$, and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_* as indicated by the upper curve of Figure 7b.

Should mortality F equal or exceed the critical ratio $\gamma m/B_\infty$ in a Pella-Tomlinson system where n exceeds unity, the corresponding stock, over sufficient time, will trend to extinction. Figure 8 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$F \geq \frac{\gamma m}{B_\infty}$$
$$B_* \leq 0,$$

in which case the zero root of Equation (15) applies, and we have $\dot{B} < 0$ and $B(t) \rightarrow 0$, irrespective of initial conditions.

By expanding the asymptotic bound of Equation (16) to a region of radius $\epsilon \cdot B_*$, and by appealing to arguments similar to those that led to the delay estimate (Equation (8)) of the Graham system, we calculate from Equation (16) the transition times for a Pella-Tomlinson stock as being

$$t_{\text{lag}} = \frac{B_\infty}{(1-n)(\gamma m - F_1 B_\infty)} \ln\left[\frac{1-(1 \pm \epsilon)^{1-n}}{1-(B_0/B_1)^{1-n}}\right] \qquad (18)$$

where ϵ represents the imprecision of stock-abundance estimates, and where B_0 and B_1 signify initial and adjustment levels as they correspond to mortality values F_0 and F_1. Again we suppose that F changes abruptly at zero reference time from value F_0 to the new value F_1, the plus sign of Equation (18) applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$.

By Equation (4) and the assumption that F varies in time by taking on fixed values of finite duration, we can write the transient yield rate for the Pella-Tomlinson system in the consolidated form

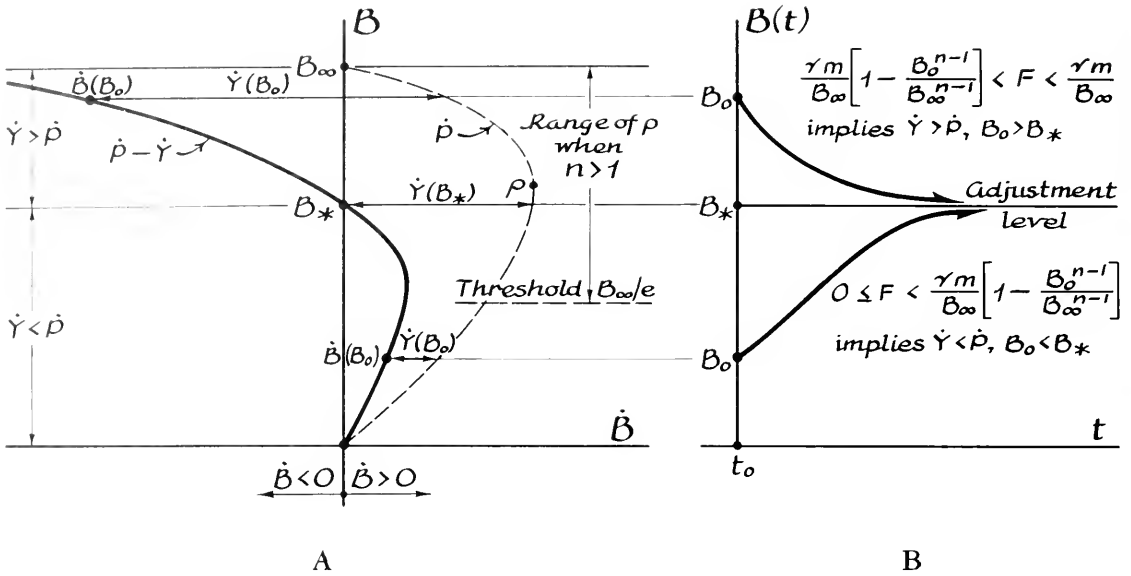


FIGURE 7.—A. Typical phase-plane graph of Equation (15) when $n>1$ and $F<\gamma m/B_\infty$, in which case root $B_*>0$. Should $\dot{Y}>\dot{P}$, the negative branch of Equation (15) applies; should $\dot{Y}<\dot{P}$, the positive branch applies. B. Typical solution trajectories, Equation (16), when $n>1$ and $F<\gamma m/B_\infty$. Should $\dot{Y}>\dot{P}$, biomass trajectory $B(t)$ declines from initial value B_0 toward adjustment level B_*. Should $\dot{Y}<\dot{P}$, $B(t)$ increases from B_0 toward B_*.

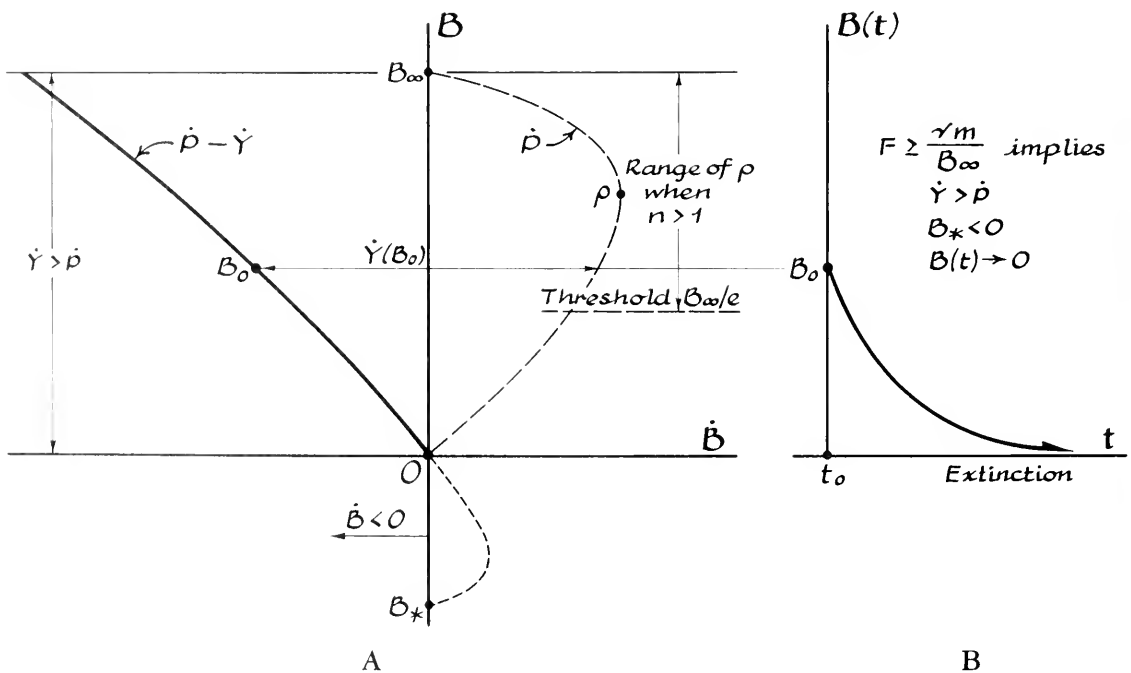


FIGURE 8.—A. Phase-plane graph of net productivity Equation (15) when $n>1$ and $F\geq\gamma m/B_\infty$. For any such combination of n and F, $B_*<0$ and the zero root of Equation (15) applies. B. Typical solution trajectory, Equation (16), when $n>1$ and $F\geq\gamma m/B_\infty$, in which case the stock declines from initial value B_0 towards extinction.

$$\dot{Y}(t) = F B_* \left[1 - \left(1 - (B_0/B_*)^{1-n}\right) \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right]^{1/(1-n)} \quad (19)$$

which is valid for all values of n save $n = 1$. Owing to the range of definition on exponent $1/1-n$, I have not found a closed form for the general time integral of Equation (19) (although existence is fairly easy to show for n positive and either less or greater than unity). But the usefulness of the analysis does not suffer too greatly for that omission, since one may accommodate Equation (19) to a numerical equation solver for finite measures of yield δY on associated intervals δt.

When F changes abruptly (as we have assumed throughout), yield rate $\dot{Y}$ changes abruptly, but the ensuing trends of adjustment are governed, in the Pella-Tomlinson system, by the following relationships:

$0 < n < 1$:
$0 < F < \infty$; stock size $B(t) \rightarrow B_*$ (Figure 6), which implies that $\dot{Y} \rightarrow FB_*$.
$n > 1$:
$F < \gamma m/B_\infty$; stock size $B(t) \rightarrow B_*$ (Figure 7), which implies that $\dot{Y} \rightarrow FB_*$.
$F \geq \gamma m/B_\infty$; stock size $B(t) \rightarrow 0$ (Figure 8), which implies that $\dot{Y} \rightarrow 0$.
$n > 0$ (both ranges):
$F = (1 - 1/n)\gamma m/B_\infty$; stock size $B(t) \rightarrow p$, which implies that $\dot{Y} \rightarrow m$ (and we may identify maximum latent productivity m with maximum yield rate in any of the time-dependent formulations of the analysis).

The quantity $\gamma m/B_\infty$, which plays such a prominent role in the analysis, can be identified as the "intrinsic growth rate" of the stock whenever exponent $n > 1$, in direct analogy to quantity k of the Graham system (and, in fact, with $n = 2$, then $\gamma = 4$ and $4m/B_\infty \equiv k$). But as a consequence of the indeterminate power form of the Pella-Tomlinson system and the switching of coefficient signs in the governing equations, the intrinsic growth rate turns out to be density-dependent when n takes on values between zero and unity. That is, by Equation (12), the intrinsic rate (if we may call it so) has the form

$$-\frac{\gamma m}{B_\infty} B^{n-1}$$

when n falls on the interval $0 < n < 1$ (in which case, $\gamma < 0$).

DISCUSSION

Any nonlinear stock-production system may be restructured along the lines of the critical-point analysis described in the foregoing sections; such a treatment will generate parametric variables most likely to be those essential to management analysis. A synopsis of the parameters that appear in the restructured Graham and Pella-Tomlinson systems is given by Table 1.

TABLE 1.—Parameters of the restructured Graham and Pella-Tomlinson systems as they apply to management components.

Management components	Control parameters	
	Graham system	Pella-Tomlinson system
Maximum stock size	B_∞	B_∞
Maximum productivity (corresponds to MSY)	m	m
Stock size for maximum productivity (the "optimum" stock size)	$B_\infty/2$ (fixed)	p
Ratio p/B_∞	½(fixed)	$n^{1/(1-n)}$
Fishing mortality	F	F
General adjustment level (consult text for mortality conditions)	B_* or 0	B_* or 0
Fishing mortality for adjustment level p (the "optimum" F)	$2m/B_\infty$	$(1 - 1/n)\gamma m/B_\infty$
Graph curvature	fixed	n

For optimization procedures on the Graham system, the essential parameters are $\{F, m, B_\infty\}$ augmented by the auxiliary parameters B_0 and B_*. For the Pella-Tomlinson system we may choose the combination $\{F, m, p, B_\infty\}$ or the combination $\{F, m, n, B_\infty\}$, either of which constitutes an essential set of mutually independent parameters. In the first set, p and B_∞ determine n; in the second, n and B_∞ determine p. The relationships in either case are governed by Equation (14).

Although the parametric influence of n is wholly prescribed by the ratio p/B_∞, exponent n also determines the curvature of all graphs of the Pella-Tomlinson system. Therefore, when the particularization of the system depends primarily on general curve fitting, the likelihood always exists that ill-determination of parameters will follow,

owing to stochastic displacement of datum points at biomass levels remote from locations p and B_∞. As revealed by Equation (14), exponent n is quite unstable to small perturbations in the ratio p/B_∞. The variational response in n exceeds the perturbation in p B_∞ by an order of magnitude near $n = 1$, and the instability increases as $p/B_\infty \rightarrow 1$. But the location of p with respect to B_∞ is far more critical to management analysis than graph curvature and its associated "good fit," since, to the left of p, the stock produces biomass at a positively accelerated rate, while to the right of p productivity decelerates.

The trait of degeneracy in the system has been noted by Pella and Tomlinson (1969) and by Fox (1971, 1975), but the exact relationships between exponent n and the quantities m, p, and B_∞ have been obscured heretofore by the conventional castings of the system. With the restructured governing equations and the explicit formulations of critical parameters, much of the statistical degeneracy associated with previous routines can be constrained. And since the management parameters appear directly in the equations of the system, their variances can be calculated directly in the estimation procedure and appeals to indirect methods are avoided.

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TROPHIC RELATIONSHIPS IN JUVENILES OF THREE SPECIES OF SPARID FISHES IN THE SOUTH AFRICAN MARINE LITTORAL

M. S. CHRISTENSEN[1]

ABSTRACT

The feeding habits of three sparids, *Diplodus sargus*, *D. cervinus*, and *Sarpa salpa*, were studied. Juveniles of these fishes occur commonly in the intertidal and immediately subtidal regions of southeast Africa, while adults were only observed in these zones at high tide. Small juvenile *D. sargus* feed largely on harpacticoid copepods, amphipods, and, in spring and early summer, cirripede nauplii, chironomid larvae, and an unidentified trochophore larva. Larger individuals mainly take amphipods and green algae. Successive size classes of *D. cervinus* feed mainly on harpacticoid copepods and chironomid larvae, the shrimp *Palaemon pacificus*, amphipods, and then polychaetes. *Sarpa salpa* ingest harpacticoids when small, diatoms and red algae as a large juvenile, and red and green algae as an adult. Corresponding changes in gut length and dentition are reported for *S. salpa*.

Marked ecological separation of the three species was observed. Small juveniles appear at different times of the year and feed on different foods (dietary and temporal separation). Larger juveniles and subadults have different diets or feed in separate parts of the littoral zone (behavioral, dietary, and spatial separation).

A brief review of methods of analyzing stomach contents is included and it is suggested that a combination of points and ranking indices would be the most valuable. The method, here termed the comparative feeding index, is described.

The food and feeding relationships of fishes in the intertidal zone of South Africa are poorly documented and the results are largely qualitative. The most important of these studies deal with one or two species of the families Gobiidae (Pitt-Kennedy[2]), Sparidae (Hutchings[3]), Cheilodactylidae (Butler[4]), and Gobiesocidae (Stobbs[5]).

Three species of sparids were investigated in the present survey, *Sarpa salpa* (Linnaeus 1758), *Diplodus sargus* (Linnaeus 1758), and *D. cervinus* (Lowe 1838). Barnard (1927), Smith (1965), and Hutchings (see footnote 3) described *S. salpa* (strepie) as being primarily a herbivore, whereas Talbot (1954) found the fish to be omnivorous. The latter study was made in an estuary, however, where algae are generally less abundant than in the intertidal region. *Diplodus sargus* (blacktail) is described as being an omnivore (Biden 1954; Talbot 1954; Smith 1965), as is *D. cervinus* (zebra). Little, however, has been published on the food and feeding habits of the juveniles of these three species, although they are abundant in the intertidal and immediately subtidal regions of this coast.

The objectives of this study have, therefore, been to determine: 1) the diet of juveniles of these three species; 2) how feeding changes with age and season; 3) the degree of overlap between species, possibly resulting in competition; 4) recruitment times and approximate growth rates of the fish; and 5) the relationship between dentition, gross gut morphology, and diet.

During the course of this study, existing methods of fish feeding analysis were found to be inadequate and a new technique is described which overcomes some of the problems.

MATERIALS AND METHODS

Fish were collected from February to December 1975 at 2-wk intervals during spring tide, in spite of the possibility of introducing biases, as diving

[1]J. L. B. Smith Institute of Ichthyology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa.

[2]Pitt-Kennedy, S. 1968. A preliminary investigation of feeding in two gobies *Coryphopterous caffer* (Günther) and *C. nudiceps* (C. and V.) with notes on their sexual maturity. Unpubl. honors proj., 39 p. Zool. Dep., Univ. Cape Town, S. Afr.

[3]Hutchings, L. 1968. A preliminary investigation into the diets of two littoral teleosts, *Sarpa salpa* (Linnaeus) and *Pachymetopon blochii* (Valenciennes), with notes on their biology. Unpubl. honors proj., 25 p. Zool. Dep., Univ. Cape Town, S. Afr.

[4]Butler, G. S. 1975. An investigation into the biology of two inter and infratidal species of Cheilodactylidae (Pisces: Teleostei). Unpubl. honors proj., 29 p. Zool. Dep., Rhodes Univ., Grahamstown, S. Afr.

[5]Stobbs, R. E. In preparation. Preliminary investigations into the feeding behaviour and food preferences of *Chorisochismus dentex* (Pisces: Gobiesocidae).

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FISHERY BULLETIN: VOL. 76, NO. 2, 1978.

conditions were most suitable at this time. Hand nets were used in the intertidal pools and multiprong spear guns in the subtidal area. Hook and line, poison, traps, and gill nets were not used as further biases may be induced to the feeding data (Randall 1967). Fish collected with hand nets were immediately placed in a 10% Formalin[6] solution, whereas this procedure was delayed for up to 1½ h in the case of those taken by spear. It was concluded that death stops or greatly slows digestion, as the stomach contents were found to be in an equally digested state in both groups on later analysis. This has also been observed by Hobson (1974).

The fish were left in Formalin for 10 to 14 days. This time period was maintained throughout to standardize any length and weight changes induced by the fixative (up to 5%, Royce 1972). About 10 scales were removed from under the pectoral fin and cleaned with a camel hair brush after having been soaked overnight in water with a trace of carbolic acid (Pinkas 1966). They were mounted dry and examined over a white background using a low-power binocular microscope. Standard lengths to the nearest millimeter were taken and the stomach removed and placed in 45% n-propyl alcohol.

The stomach is here defined as that part of the gut between the last gill arch and the gut caecae. The intestines were not examined as some food items are more resistant to digestion than others, with resultant biases as one moves along the gut (Randall 1967; Kionka and Windell 1972; Gannon 1976). Food items were identified to species where possible.

Numerous methods have been employed in analyzing the food habits of fishes and volumetric and gravimetric techniques are being more widely used today with the current trend towards greater accuracy (Windell 1971). Both suffer from the same limitation in that digestion of the food both reduces its volume and weight. This has resulted in the use of reconstructed weights and volumes where the live weight and/or volume is back-calculated from a measureable parameter, e.g., carapace length (M. Bruton, pers. commun.). In this particular study some of the fish had fed on diatoms and it is not feasible to determine the volume of such small items (Windell 1971). Similarly, the reconstructed weight could not be determined as a sample of monospecific, uncontaminated diatoms is impracticable to obtain and contains an indeterminate number of dead frustules which varies from sample to sample (Round 1971).

In such cases, the points (Swynnerton and Worthington 1940) and ranking index methods (Hobson and Chess 1973) would appear to be more satisfactory and were initially used in the present study. The points system was modified by Frost (1943) and subsequently by Hynes (1950) to take into account gut fullness, 30 points being allotted when the stomach was distended, 20 when full, 10 when half full, and so on. One, two, four, eight, or sixteen points were assigned to each food item rather than fractions of the total allotted to each stomach in proportion to their volumes. This is an artificial situation and the method was revised as described below.

After removal, the stomach is allotted between 0 and 30 points in proportion to its fullness. This is very subjective but overcome to some extent when large numbers of guts are handled. The contents are then sorted, identified, and the percentage volume estimated for each food item with the aid of Data Sheet No. 6 of Geotimes.[7] All estimations are made with the organisms spread out to an even depth throughout the microscope field or equivalent surface. The total number of points allocated to that stomach is then subdivided amongst the food items in proportion to their percentage volumes. The points gained by each food item are summed for the total sample of fish and the mean calculated. The values are then scaled down to a percentage to give the dietary composition of the fish examined. In the case of the ranking index (RI), the volume is estimated as above and the mean calculated for each food item per fish. The mean volume is then multiplied by the ratio of the number of fish containing that item to the total sampled.

The points method, however, places too much weight on single food items that have been fed on to distension by a few fish, whereas the RI method fails to consider stomach fullness. It is therefore suggested that an alternative, here termed the comparative feeding index (CFI), would be more suitable as it takes into account all three factors, i.e., the volume, fullness, and frequency of occurrence of each food item. The method involves the

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

[7]Available from the American Geological Institute, 2101 Constitution Avenue, N.W., Washington, D.C.

allotment of points to each food organism as described above and the mean value per fish is then multiplied by the percentage of the total sample of fish that contain that item. As can be seen, the CFI combines the properties of both points and RI methods and thus reduces to some extent the effect of the problems discussed.

The diet of these fish was also determined by the occurrence method (Hynes 1950) as this indicates the feeding preferences rather than the food's volumetric value. This is determined as the percentage of fish in the sample analysed which contain that particular food item.

The dietary composition of *D. sargus* was analysed for the winter (February-July) and summer (August-December) periods, as it was found to be seasonal. This was not done for the other two species, as feeding seasonality is synonymous in these fish with the change in diet with age, as they exhibit discontinuous recruitment.

All skeletal material was cleared and stained using the trypsin maceration, alizarin stain method of Taylor (1967). The gut was dissected out in the same specimens, drawn and measured, and the gut length to standard length ratio (G/S) was calculated as in Weatherly (1972).

STUDY AREA

The study area is situated about 3.2 km north of Kleinemonde in the eastern Cape and is known locally as Clayton's Rocks (Figure 1). The shoreline consists of a gently shelving, sandy beach with broken rocky areas of varying extent.

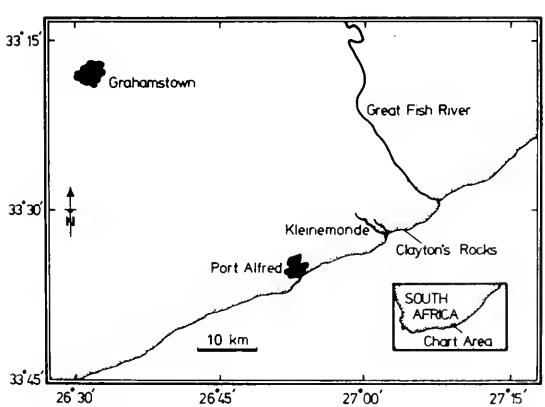

FIGURE 1.—The study area in the Eastern Cape Province, South Africa. Adapted from Topographical Chart 3326, Grahamstown.

The smaller rocky outcrops are continually covered and uncovered by sand, as the beach is unstable and backed by large, shifting sand dunes which move at right angles along the coast. The rocky area under study is made up of sandstone which strikes east-west and dips steeply southwards. This has resulted in the development of gullies and pools partially sheltered from wave action by ridges of resistant rock (Figure 2). The maximum collection depth at the seaward edge of the gullies was 3 m at low tide.

Environmental conditions vary greatly and salinities may fall to 25‰ at low tide, which is caused by freshwater seepage into the pools from springs in the beach. During the day, at low tide, surface water temperatures have been recorded ranging from 26° (summer) to 15°C (winter) in the intertidal and from 22° (summer) to 14°C (winter) in the open sea.

The other major fish species coexisting in the study area are listed below with their general biological characteristics, where known.

ARIIDAE

Tachysurus feliceps: occurs singly, as a juvenile, in crevices.

SPARIDAE

Lithognathus lithognathus: occurs in small groups of juveniles.

Rhabdosargus holubi: juveniles, in small groups.

Sparodon durbanensis: juveniles, observed from October to March, either singly or in small groups.

CHEILODACTYLIDAE

Chirodactylus brachydactylus: as juveniles and subadults, singly, mainly from June to November.

MUGILIDAE

Unidentified species: occur all year round as juveniles.

CLINIDAE

Clinus cottoides: a purely intertidal species, lives in weed, juveniles appeared about June/July.

Clinus superciliosus: lives in weed, juveniles only observed in November/December.

GOBIIDAE

Caffrogobius caffer: intertidal species, juveniles seen from June to November.

TETRAODONTIDAE

Amblyrhyncotes honckenii: singly or in small groups.

FIGURE 2.—The study site at Clayton's Rocks.

RECRUITMENT AND GROWTH

Diplodus sargus

The monthly and total length-frequency distribution is given in Figure 3. The lumped sample shows a mode in the 10- to 20-mm size class, indicating that larger fish tend to emigrate to deeper water. The juveniles appear in the littoral zone when between 9 and 10 mm standard length (SL), and leave when about 90 mm long. It appears that large fish utilize the intertidal area at high tide as two fish of 107 and 108 mm SL were collected in the intertidal area some 2 h after low tide and another 164 mm long was collected 3 h after low tide.

Visibility was <15 cm in the pools of the research area during September, October, and December due to flooding of the Fish River. No dives could be made during this period in the subtidal area with the result that fish >40 mm were not collected.

Recruitment of the juveniles into the littoral appeared to be relatively constant as no monthly peaks of abundance were found during the survey. This tends to confirm Biden's (1954) suggestion that females of this species spawn throughout the year, though mainly in summer.

No monthly modes could be followed over the period of study as it is a continuously recruiting

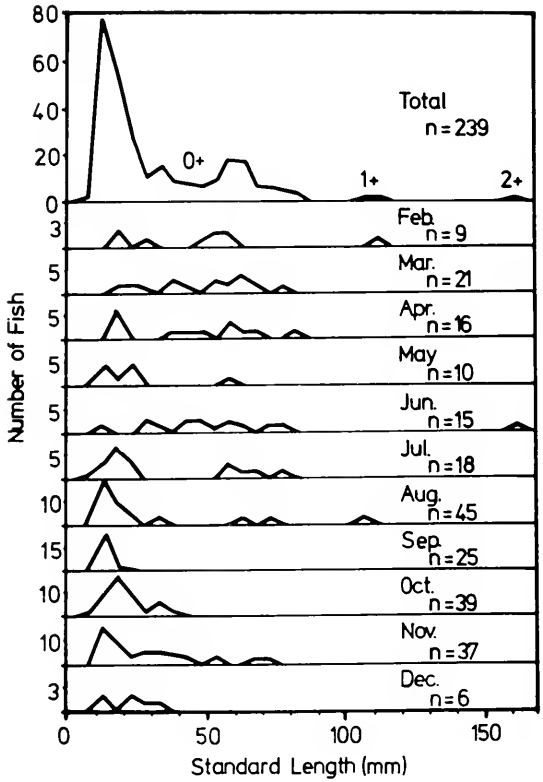

FIGURE 3.—Monthly and total length-frequency distribution of *Diplodus sargus*, showing three age-classes (0+, 1+, and 2+).

population and so growth rates were not estimated. The age of three immature specimens was determined as being 1+ years old (107 and 108 mm SL) and 2+ years old (164 mm SL).

Diplodus cervinus

The length-frequency distribution is given in Figure 4. The total pooled sample shows that this species first appears in the littoral zone when about 8 mm long and leaves again when about 140 mm long. Large fish were observed to move into the intertidal area after low tide, as was the case with *D. Sargus*, but no specimens were obtained.

Monthly modes were observed, which are age-classes 0+, 1+, and 2+ (Figure 4). Recruitment of juveniles into the tide pools is discontinuous, occurring between August and November, with a peak in October. Two fish sampled in August (132 and 129 mm SL) had just formed the second ring, giving the approximate time of scale-ring formation. The estimated average growth rate as determined for mode 1+ is 45 mm from February to December, which is about 54 mm/yr.

Sarpa salpa

The length-frequency distribution shows that the majority of the population is from 9 to 45 mm SL (Figure 5). The juveniles appear in the intertidal when ≥9 mm, and fish >100 mm were never observed in the littoral at low tide; two specimens of age-class 2+ were collected 4 h after low tide.

Three age-classes were observed, labelled as 0+, 1+, and 2+. Recruitment of juveniles into the tide pools is discontinuous, occurring between June and September. Age-classes 1+ and 2+ were approximately ¾ and 1½ yr old, respectively, when sampled. The time of scale-ring formation is then likely to have been about June. The average growth rate is estimated to be 45 mm in 5 mo, or 108 mm/yr for the age-class 0+. Two fish were obtained in April 1976 with lengths of 68 and 76 mm, which indicates that the estimate may be slightly high, the predicted length being 81 mm.

DIETARY COMPOSITION

The composition of the diet is illustrated by occurrence and CFI values scaled down to percentages.

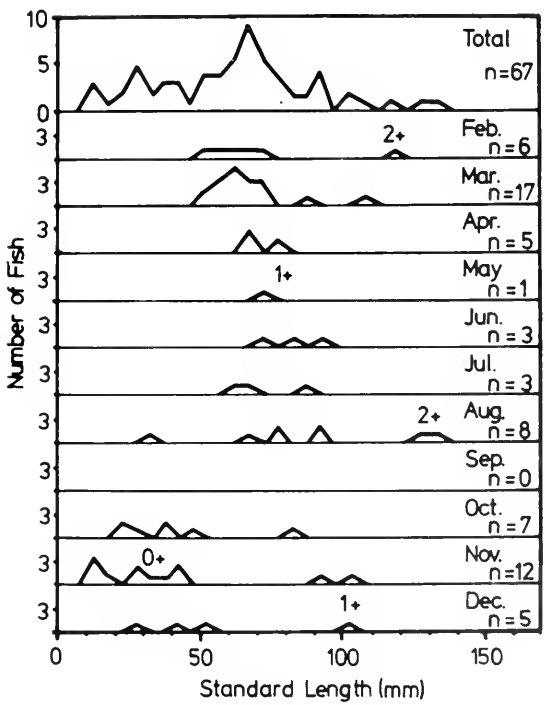

FIGURE 4.—Monthly and total length-frequency distribution of *Diplodus cervinus*, showing three age-classes (0+, 1+, and 2+).

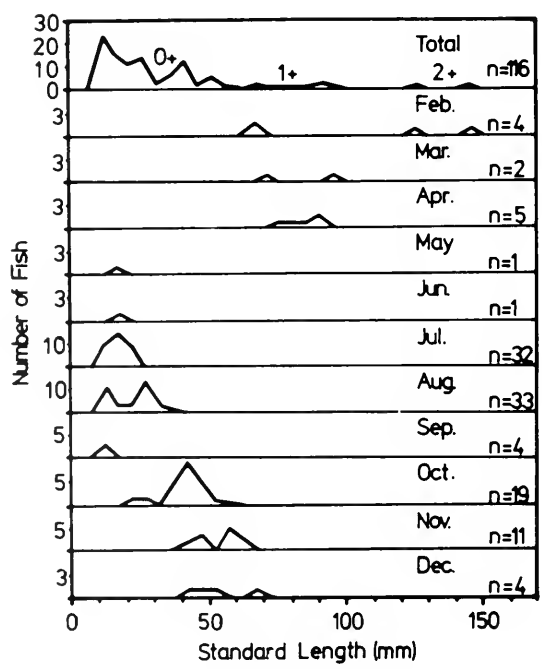

FIGURE 5.—Monthly and total length-frequency distribution of *Sarpa salpa*, showing three age-classes (0+, 1+, and 2+).

Diplodus sargus

Winter Feeding

The diet is composed mainly of harpacticoid copepods, amphipods, algae, isopods, polychaetes, and ostracods (Figure 6; Table 1, $n = 88$).

The diet of the smallest size class (5-15 mm) is composed almost equally of harpacticoid copepods and amphipods, but the percentage consumed of the former increases in the next size class whereas that of the latter decreases. The diet remained similar in the following two size classes. In the 35- to 50-mm size class, the fish fed little on harpacticoid copepods, the diet being largely composed of amphipods. The situation was similar in the largest size class, although algae and polychaetes were increasingly taken.

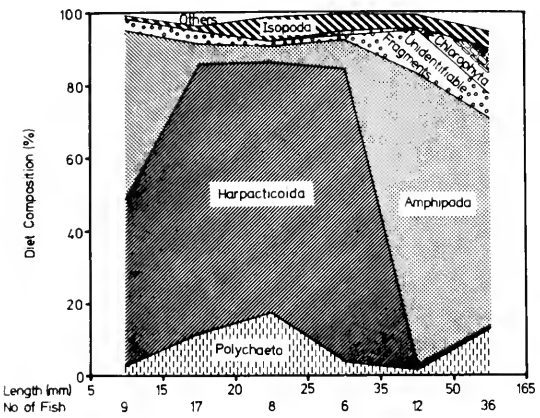

FIGURE 6.—Changes in diet with length of *Diplodus sargus*, collected between February and July 1975, as shown by the comparative feeding index. Food items included in Others are: brachyurans, crab zoaea, diatoms, echinoderms, hydrozoans, leptostracans, molluscs, mysidaceans, *Palaemon pacificus*, rhydophytan algae, sand, and unidentifiable animal fragments.

Summer Feeding

Although similar to the winter diet, chironomid larvae, diatoms, crab zoaea, and leptostracans are more significant. Cirripede nauplii and an unidentified trochophore larva were also commonly taken, and these were not found in winter specimens (Figure 7; Table 2, $n = 149$).

The diet of the smallest size class (5-15 mm SL) is composed mainly of harpacticoid copepods. The next size class (15-20 mm SL) fed on a similar diet, although the percentage of harpacticoids taken decreased and that of polychaetes and cirripede nauplii increased. These changes were further magnified in the 20- to 25-mm size class. In the next size classes (25-50 mm), there was a change and the green alga, *Ulva* sp., contributed significantly to the diet.

Poor diving conditions in September, October, and December reduced the sample size and only nine fish in the 50- to 165-mm size range were analysed. In general, these fish showed an increasing tendency to take more amphipods, and less

TABLE 1.—Changes in the percentage composition of the food of *Diplodus sargus* with length during the period February to July 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	—	—	1.3	33.3	1.0	25.0	12.8	41.7
Rhodophyta	—	—	—	—	—	—	—	—	0.2	8.3	1.6	16.7
Chrysophyta	—	—	0.2	11.8	—	—	—	—	—	—	0.3	2.8
Polychaeta	2.4	33.3	11.8	76.5	16.7	75.0	3.6	50.0	1.4	33.3	12.8	47.2
Crustacea												
Amphipoda	*47.4*	77.8	5.8	29.4	5.0	25.0	7.8	66.7	*80.1*	66.6	*58.1*	72.2
Ostracoda	0.5	22.2	4.2	58.8	1.2	75.0	0.2	16.7	0.1	8.3	—	—
Harpacticoid copepoda	*45.9*	88.9	*74.2*	82.4	*69.3*	100.0	*80.9*	66.7	1.3	25.0	0.4	11.1
Isopoda	1.2	33.3	1.0	35.3	7.4	75.0	5.0	50.0	3.3	50.0	4.2	33.3
Brachyura (zoaea)	—	—	—	—	0.1	12.5	—	—	—	—	—	—
Tanaidacea	—	—	—	—	—	—	0.1	16.7	0.1	8.3	—	—
Macrura	—	—	—	—	—	—	0.1	16.7	0.2	16.7	—	—
Mysidacea	—	—	—	—	—	—	0.2	16.7	—	—	0.1	2.8
Insecta	—	—	—	—	0.2	12.5	—	—	—	—	0.1	2.8
Mollusca	—	—	—	—	—	—	—	—	0.1	8.3	4.1	22.2
Echinodermata	—	—	—	—	—	—	—	—	—	—	0.1	2.8
Unidentifiable fragments	2.6	44.4	3.0	52.9	0.1	12.5	0.8	50.0	12.2	66.7	5.4	52.8
No. of fish examined	9		17		8		6		12		36	
Average no. of points allotted per stomach	18.8		13.4		7.3		20.3		17.2		13.2	

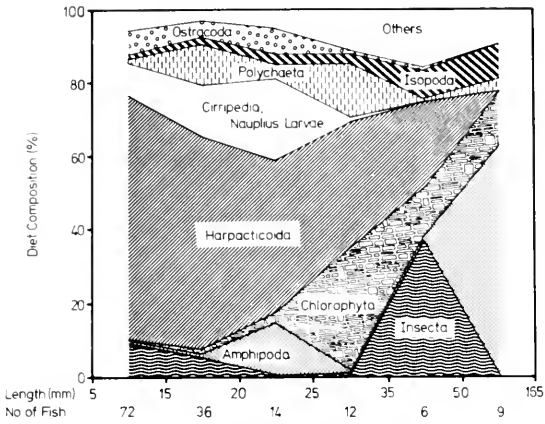

FIGURE 7.—Changes in diet with length of *Diplodus sargus*, collected between August and December 1975, as shown by the comparative feeding index. Food items included in Others are the same as for Figure 8, in addition to the unidentified trochophore larva.

algae, diatoms, chironomid larvae, and hydrozoa as they grow larger.

Identity of Food

Diatoms: two species of the genus *Licmophora*, predominantly *L. pfannkucheae*, as well as *L. ehrenbergii*.

Other algae: the chlorophytan algae of the genus *Ulva* most frequent, although some of the larger size classes also fed on *Caulerpa filiformis* (50-165 mm: 7.5% in summer and 2.9% in winter), *Bryopsis* sp., *Enteromorpha* sp., and *Valonia* sp. Some rhodophytans taken, including *Ceramium* sp., *Hypnea spicivera*, *Polysiphonia* sp., and *Tayloriella* spp.

Harpacticoid copepods: 12 species, only 4 common, identification was not possible.

Amphipods: 28 species—7 caprellid species including *Caprella danilevskii*, *C. penantis*, *C. scaura*, and *Caprellina longicollis*; *Cerapus tubularis*; *Corophium? acherusicum*, and *C.? triaenonyx*; *Cymadusa* sp.; two *Gammaropsis* species including *G. holmesi*; *Jassa* spp.; *Lysianassa ceratina*; and *L. variegata*; two *Maera* species; *Paramoera capensis*; *Parelasmopus suluensis*; two *Photis* species; *Temnophlias* sp.; *Urothoe* sp.; and three unidentified species.

Isopods: nine species—*Cymodocella pustulata*, *C. sublevis*, *Dynamenella huttoni*, *D. macrocephala*, *Exosphaeroma antikraussi*, *Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and a *Stenetrium* species.

Polychaetes: *Dodecaceria pulchra*, *Eulalia trilineata*, two *Nereis* species, an *Onuphis* sp., and terebellid tentacles most commonly found in the gut contents, as well as *Pista* sp., *Pomatoleois kraussi*, and *Serpula vermicularis*.

Ostracods were not identified.

TABLE 2.—Changes in percentage composition of the food of *Diplodus sargus* with length during the period August to December 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values greater than 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.2	4.2	0.6	8.3	2.9	28.6	*33.4*	50.0	13.5	33.3	14.3	55.6
Rhodophyta	—	—	—	—	—	—	0.9	33.3	0.8	33.3	—	—
Chrysophyta	—	—	—	—	—	—	0.7	25.0	8.7	33.3	7.4	11.1
Hydrozoa	—	—	—	—	—	—	—	—	—	—	1.1	11.1
Polychaeta	1.1	20.8	10.4	47.2	4.0	35.7	14.7	33.3	0.9	16.7	4.0	22.2
Crustacea												
Amphipoda	0.3	6.9	1.7	27.8	14.1	57.1	2.4	25.0	6.5	50.0	*62.5*	100.0
Ostracoda	6.0	37.5	5.5	55.6	6.4	64.3	0.8	16.7	0.4	16.7	0.1	11.1
Harpacticoid copepoda	*67.8*	86.1	*58.1*	94.4	*41.6*	100.0	29.6	83.3	17.6	100.0	—	—
Isopoda	1.0	16.7	2.1	25.0	3.4	42.9	3.0	25.0	6.9	50.0	9.8	44.4
Brachyura	0.1	5.6	—	—	0.2	14.3	0.2	8.3	—	—	0.2	11.1
Cirripedia	8.8	36.1	13.9	66.7	21.5	42.9	1.3	8.3	—	—	—	—
Leptostraca	—	—	0.3	5.6	—	—	—	—	—	—	—	—
Tanaidacea	—	—	—	—	0.2	14.3	—	—	—	—	—	—
Macrura	—	—	—	—	0.7	7.1	—	—	—	—	—	—
Insecta	8.8	36.1	4.8	27.8	0.5	21.4	3.8	33.3	*37.2*	50.0	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.3	11.1
Trochophore larvae	4.6	30.6	0.3	5.6	1.6	14.3	1.2	8.3	—	—	—	—
Unidentifiable fragments	1.3	20.8	2.3	30.6	2.9	28.6	8.1	41.7	7.5	50.0	0.2	11.1
No. of fish examined	72		36		14		12		6		9	
Average no. of points allotted per stomach	13.7		17.5		20.4		12.0		14.8		18.2	

Insects: only the larva of the chironomid *Telmatogeton minor*.

Brachyurans: *Rhyncoplax bovis* and the gut of an unidentified crab (in a single case).

Molluscs: *Gibbula rosea*, *Helcion pruinosus*, *Philine aperta*, and a rhaciglossid (no shell, so not possible to identify further).

Hydrozoans: *Symplectoscyphus* sp. and *Thecocarpus formosus* were ingested by one fish in the 50- to 70-mm size class.

Echinoderms: *Parechinus* sp.

Tanaidaceans: *Leptochelia barnardi* most commonly found, also an *Apseudes* sp.

Mysidaceans: only one species, *Mysidops similis*, could be identified with any certainty.

Diplodus cervinus

The diet of *Diplodus cervinus* is illustrated in Figure 8 and Table 3 ($n = 67$). The juveniles (10-20 mm) fed mainly on harpacticoid copepods and chironomid larvae. In the next size class (20-35 mm), juveniles of the sand shrimp, *Palaemon pacificus*, were taken instead of chironomid larvae. This trend continues in the 35- to 50-mm size class, the diet being composed largely of *P. pacificus* as well as harpacticoid copepods. Polychaetes are more important in this size group, a trend which is maintained in all larger size classes. In the larger fish, there was again a changeover, the percentage of amphipods taken being 65.7% (50-75 mm) and 27.6% (75-100 mm). Unidentifiable crustacean fragments in these size classes composed 12.6% and 47.9%, respectively, which is partly explained by the fact that 6 of the 40 fish were taken at night and their stomach contents were largely digested and thus indistinguishable. The diet of the largest size class (100-135 mm) was made up mainly of polychaetes.

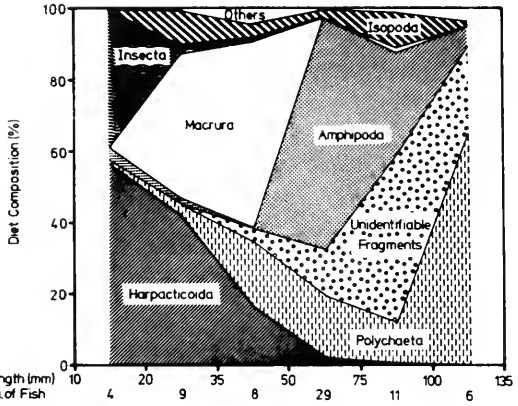

FIGURE 8.—Changes in diet with length in *Diplodus cervinus*, as shown by the comparative feeding index. Food items included in Others are: chlorophytan algae, cirripede nauplii, coralline algae, molluscs, mysidaceans, ostracods, tanaidaceans, and the unidentified trochophore larva.

Identity of Food

The diet was composed of almost all the food species listed for *D. sargus*, although in differing proportions, as well as the following: *Cymodocella eutylos* (isopod), *Littorina knysnaensis* (mollusc),

TABLE 3.—Changes in the percentage composition of the food of *Diplodus cervinus* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	10-20		20-35		35-50		50-75		75-100		100-135	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	4.6	12.5	—	—	—	—	—	—
Rhodophyta	—	—	—	—	—	—	—	—	—	—	1.9	16.7
Polychaeta	0.2	25.0	3.8	33.3	17.6	50.0	17.2	72.4	11.4	18.0	*65.4*	82.3
Crustacea												
Amphipoda	4.1	25.0	1.0	33.3	0.4	25.0	*65.7*	74.9	27.6	45.0	5.8	33.3
Ostracoda	—	—	0.2	22.2	—	—	—	—	0.6	9.0	—	—
Harpacticoid copepoda	56.5	100.0	*41.6*	77.8	16.5	87.5	2.2	51.7	0.1	9.0	—	—
Isopoda	—	—	10.0	44.4	4.2	25.0	1.5	20.7	11.0	27.0	1.7	16.7
Cirripedia (nauplii)	—	—	—	—	—	—	0.5	6.9	—	—	—	—
Macrura	—	—	*41.2*	44.4	53.2	50.0	—	—	1.0	9.0	—	—
Tanaidacea	—	—	—	—	—	—	0.2	6.8	—	—	—	—
Mysidacea	—	—	—	—	—	—	0.1	3.4	—	—	—	—
Insecta	*39.0*	50.0	2.2	55.6	0.4	12.5	—	—	—	—	—	—
Mollusca	—	—	—	—	—	—	—	—	0.4	9.0	1.9	16.7
Trochophore larvae	0.2	25.0	—	—	—	—	—	—	—	—	—	—
Unidentifiable fragments	—	—	—	—	3.1	50.0	12.6	79.3	*47.9*	36.0	23.3	33.3
No. of fish examined	4		9		8		29		11		6	
Average no. of points allotted per stomach	8.3		19.3		8.0		10.0		6.4		11.1	

Phoxostoma sp. (amphipod), and *Corallina* sp. (rhodophytan alga).

Sarpa salpa

The percentage composition of the diet of *Sarpa salpa* is illustrated in Figure 9 and Table 4. The food habits of this species changed from being primarily a carnivore as a juvenile to a herbivore as a subadult.

Juveniles in the 10- to 25-mm size classes fed mainly on harpacticoid copepods. In the next size class (25-35 mm), however, the total animal contribution is only 15.1%, diatoms and rhodophytan algae being most important. Diatoms are taken in decreasing amounts from then on and those fish >75 mm SL fed predominantly on chlorophytan and rhodophytan algae.

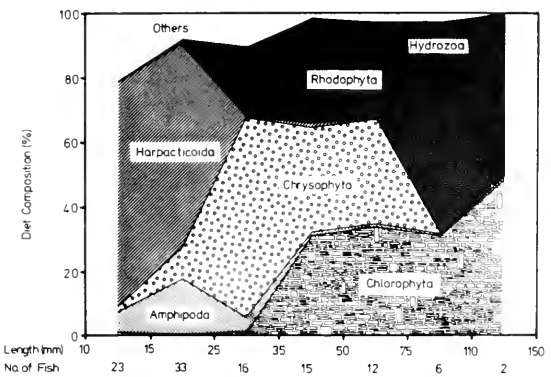

FIGURE 9.—Changes in diet with length of *Sarpa salpa*, as shown by the comparative feeding index. Food items included in Others are: bryozoans, cirripede nauplii, crab zoaea, fish muscle, insects, isopods, leptostracans, mysidaceans, ostracods, polychaetes, rhaciglossid molluscs, and tanaidaceans.

Identity of Food

Chlorophytan algae: eight species—*Bryopsis* sp., *Caulerpa filiformis*, *Chaemaedoris delphini*, *Cladophora* spp., *Enteromorpha* sp., *Rhizoclonium* sp., and *Ulva* sp.

Rhodophytan algae: *Ceramium* sp., *Champia compressa*, *Hypnea spicifera*, *Polysiphonia* sp., and *Tayloriella* sp. commonly taken as well as *Acrosorium* sp., *Arthrocardia* sp., *Centroceras* sp., *Corallina* spp., *Polyzonia elegans*, and *Pterosiphonia cloiophylla*.

Chrysophytan algae: three species of diatoms—*Isthmia enervis*, *Licmophora ehrenbergii*, and *L. pfannkucheae*.

Hydrozoans: *Gattya humilis* commonly ingested by the 75- to 100-mm size class, whereas *Sertularella* sp. and *Thecocarpus formosus* were uncommon.

Polychaetes: only two species of *Nereis*.

Isopods: uncommon, but six species were found—*Dynamenella huttoni*, *D. macrocephala*, *Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and *Stenetrium* sp.

TABLE 4.—Changes in the percentage composition of the food of *Sarpa salpa* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)													
	10-15		15-25		25-35		35-50		50-75		75-100		125-150	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.3	8.7	—	—	0.9	31.3	*31.2*	92.0	*34.0*	91.7	*30.6*	100.0	*48.3*	100.0
Rhodophyta	—	—	0.4	9.1	21.3	62.5	32.3	76.0	28.6	66.7	*45.9*	83.3	*50.1*	100.0
Chrysophyta	0.2	8.7	9.3	24.2	*62.7*	100.0	*32.4*	68.0	*33.4*	66.7	—	—	—	—
Hydrozoa	—	—	—	—	—	—	—	—	0.1	16.7	20.5	50.0	0.8	50.0
Polychaeta	5.1	17.4	2.6	30.3	—	—	—	—	0.4	8.3	0.1	16.7	—	—
Crustacea														
Isopoda	1.7	17.4	0.9	30.3	0.1	6.3	—	—	—	—	—	—	—	—
Amphipoda	7.3	30.4	17.8	63.6	4.2	50.0	0.9	16.0	0.1	16.7	0.3	33.3	0.8	50.0
Ostracoda	6.7	26.1	1.4	36.4	0.1	6.3	0.1	12.0	—	—	—	—	—	—
Harpacticoid copepoda	*71.0*	87.0	*64.5*	72.7	0.5	18.8	1.4	24.0	—	—	—	—	—	—
Cirripedia (nauplii)	5.5	22.0	2.1	18.2	—	—	—	—	—	—	—	—	—	—
Brachyura (zoaea)	—	—	0.1	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Leptostraca	0.1	4.4	—	—	—	—	—	—	—	—	—	—	—	—
Insecta	0.1	4.4	0.2	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Bryozoa	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Pisces	—	—	—	—	0.2	6.3	—	—	—	—	—	—	—	—
Unidentified fragments and sand	2.0	26.1	0.7	24.2	9.8	31.3	1.7	32.0	3.4	41.7	2.4	50.0	—	—
No. of fish examined	23		33		16		25		12		6		2	
Average no. of points allotted per stomach	7.8		9.5		13.8		15.7		16.5		15.5		28.0	

Amphipods: also uncommon except in juveniles which took the following 15 species: *Caprella eicur* and two other species of *Caprella*, *Cerapus* sp., *Corophium* sp., *Gammaropsis* sp., *Lysianassa ceratina*, *L. variegata*, *Jassa* sp., *Maera* sp., *Paramoera capensis*, *Parelasmopus suluensis*, *Photis* sp., and two unidentified species.

Harpacticoid copepods: eight species.

Insects: larvae of the chironomid *Telmatogeton minor*.

Tanaidaceans: *Leptochelia barnardi*, uncommon.

Molluscs: rhaciglossid.

DENTITION AND GUT MORPHOLOGY

Diplodus cervinus—there are six upper and four lower incisors which are narrower than those of *D. sargus*, and there are fewer molars, the number increasing with age (Figure 10A). This would indicate that adult *D. cervinus* feed on softer foods than *D. sargus*, which is borne out as the diet of the former consists primarily of polychaetes, whereas the latter took amphipods and molluscs as well. The gut of *D. cervinus* is short with a G/S ratio of 0.7 in a 16.5-mm fish and 0.95 in one 74 mm long.

Diplodus sargus—there are four stout incisors and three to four rows of fairly large molars in each jaw (Figure 10B), the latter increasing in size and number with age. The teeth are those of a typical omnivore (Weatherly 1972). The G/S ratio was 0.76 in a 16.5-mm fish and this is within the range of omnivores as defined by Nikolsky (1963).

Sarpa salpa—this species shows a change in dentition correlated with age and diet. The young fish are carnivorous and have short, pointed coni-

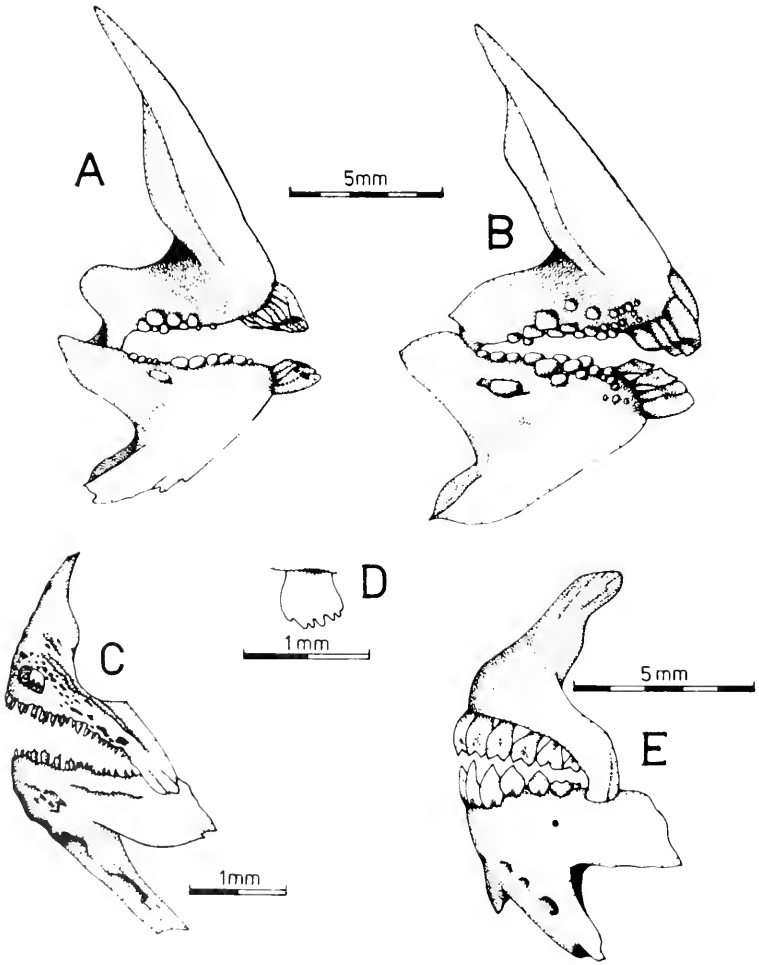

FIGURE 10.—Dentition. A. Medial view of the left upper and lower jaws of *Diplodus cervinus* (MSC 75-36, 94 mm SL). B. Medial view of the left upper and lower jaws of *D. sargus* (MSC 75-34, 107 mm SL). C. Lateral view of the upper and lower jaws of a juvenile *Sarpa salpa* (MSC 75-39, 20 mm SL). D. Lateral view of a single tooth of a subadult *S. salpa* (MSC 75-37, 39 mm SL). E. Lateral view of the upper and lower jaws of an adult *S. salpa* (RUSI 74-323, 99 mm SL).

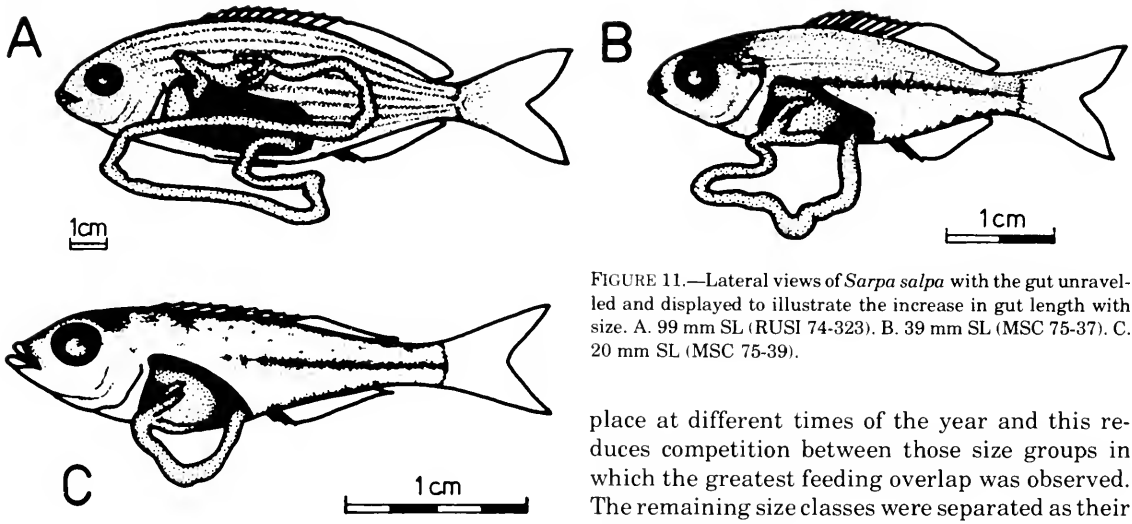

FIGURE 11.—Lateral views of *Sarpa salpa* with the gut unravelled and displayed to illustrate the increase in gut length with size. A. 99 mm SL (RUSI 74-323). B. 39 mm SL (MSC 75-37). C. 20 mm SL (MSC 75-39).

cal teeth to grasp prey (Figure 10C). Multicusped, incisiform teeth begin to break through when the fish are about 20 mm long (Figure 10D). The pointed teeth are completely replaced by the time the fish are 35 mm long, after which they feed predominantly on algae (approximately 60% CFI). The multiple cusps wear away and the teeth are bicuspid incisiform by the time the fish are 65 to 75 mm long (Figure 10E). These can nip at algae and the diet is composed of 65 to 77% plant matter at this stage.

The gut shows a corresponding change in length with diet, a long gut being characteristic of a herbivore. The G/S ratio increases from 0.86 in a 20-mm fish (Figure 11C, typically omnivorous) to 1.36 in a 39-mm fish (Figure 11B), and 2.66 in a 99-mm individual (Figure 11A). This latter value is typical of a herbivore (Nikolsky 1963), although not as pronounced as in some other herbivorous fish species.

DISCUSSION

A number of fish species occur as juveniles or spend their entire life cycle in the eastern Cape intertidal (see description under Study Area). The family Sparidae includes the largest number and the present investigation of the trophic relationships of three of these was initiated as competitive interaction is often most vigorous in closely related fish (Fryer and Iles 1972). There is an intense dietary overlap in some cases and the available resources are subdivided in two main ways. Recruitment of juveniles of the three species takes place at different times of the year and this reduces competition between those size groups in which the greatest feeding overlap was observed. The remaining size classes were separated as their diets were different.

Small juveniles of the three species have the most similar diets of all size classes studied. The resulting competition is reduced by two mechanisms. Firstly, juveniles of *Sarpa salpa* occur in the tide pools primarily from July to September (Figure 5) whereas those of *Diplodus cervinus* were found during October and November (Figure 4) and *D. sargus* was present throughout the year (Figure 3). Secondly, at the time of maximal competition (July-November), the diet of small *D. sargus* includes food items not taken at other times of the year, e.g., chironomid larvae and cirripede nauplii (Figure 7). This may be due to either the presence of these prey items only at that time of the year and/or to the effects of competition forcing *D. sargus* to include them in its diet. A combination of both factors would appear to be operative in the case of the chironomids as the larvae were obtained in bottom samples taken in October-November and not in March. No data are available for cirripede nauplii, crab zoaea, and the unidentified trochophore larva as plankton samples were not taken.

Competition for food is greatly reduced by the time the three sparids are about 25 to 30 mm long. At this stage, *S. salpa* feeds mainly on diatoms and red algae (Figure 9); *D. cervinus* ingests *Palaemon pacificus*, harpacticoid copepods, and isopods (Figure 8); and *D. sargus* takes green algae, harpacticoids, chironomid larvae, and cirripede nauplii (Figures 6, 7). The separation is equally distinct in subadult fish as *S. salpa* is then a herbivore, *D. cervinus* takes polychaetes, some amphipods, and isopods, while *D. sargus* feeds on amphipods and

green algae. The overlap on amphipods by the latter two species may be partially compensated for by behavioral separation. *Diplodus cervinus* is a secretive substrate feeder whereas *D. sargus* is a more open water fish tending to feed on vertical rock surfaces away from the bottom. The fact that neither species was very common intertidally in these size classes may also contribute towards a reduction in competition.

The diet of large juvenile *S. salpa* is unusual in that it consists mainly of diatoms and epiphytic rhodophytan algae which occur commonly on corallines, *Hypnea spicifera* and *Tayloriella* spp. (M. H. Giffen, pers. commun.). The fish must, therefore, selectively separate these food items as few fragments of the algae on which they grow were found in the stomach contents. This is in contrast to *Rhabdosargus holubi*, also a sparid, which ingests algae for their epiphytic diatoms rather than separating them, even though the algae are not digested (Blaber 1974). The situation may be similar to this in larger *S. salpa* as the rectal contents appeared to be relatively undigested and fewer diatoms were observed on the algae (Figure 12).

Temporal separation of juveniles to reduce competition has not been reported previously for tide pool fish species as far as I am aware, although it has been observed in two pelagic plankton feeders from the Adriatic, the anchovy and sardine (Vučetič 1975). Large dietary overlaps have been noted in several intertidal fish, including blennies, clinids, gobies, and labrids (Gibson 1968, 1972). These fed predominantly on crustaceans and it is possible that similar mechanisms reduce competitive pressure amongst them, although this was not determined as samples were only taken for 2 mo.

The data presented indicates that *D. cervinus* is a carnivore, *D. sargus* is an omnivore, and *S. salpa* an omnivore when juvenile and a herbivore when adult. Similar feeding habits were found for adults of the same three species in the Klein River estuary (Talbot 1954). The dentition and gross gut morphology changed with size and this was most marked in *S. salpa*, corresponding with the observed diet. Comparable transformations have been reported for other fish species (Nikolsky 1963).

Two other sparids, *Sparodon durbanensis* and *R. holubi*, cohabit with those studied in the littoral zone. The few specimens examined had fed mainly on harpacticoid copepods as small juveniles, with a resultant overlap with *D. sargus* as all three occurred in the research area in November-December. Large specimens were not examined, but *R. holubi* appears to be an omnivore as a juvenile in estuaries and a carnivore feeding on molluscs as an adult (Talbot 1954; Blaber 1974). Adult *S. durbanensis* are carnivores feeding on small fish, molluscs, and crustaceans (Biden

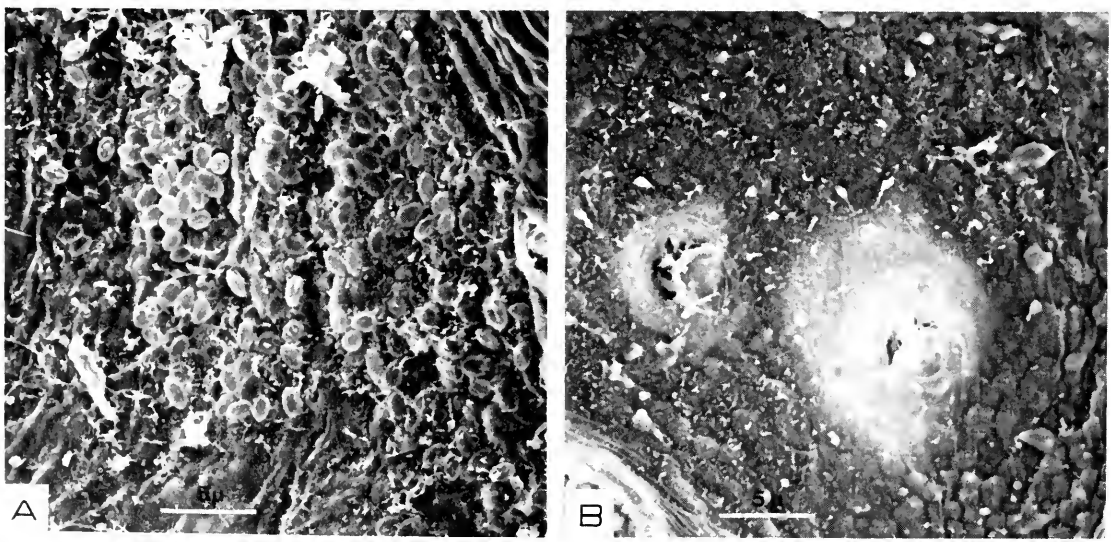

FIGURE 12.—Scanning electron micrograph of the surface of a chlorophytan alga, *Ulva* sp., removed from the gut of *Sarpa salpa* (147 mm SL) to show the disappearance of diatoms. A. Oesophageal sample. B. Rectal sample.

1954). Competitive pressure is, therefore, minimized between the five sparid fish species commonly occurring in the littoral zone.

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EFFECT OF STARVATION ON THE HISTOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, LARVAE

GAIL H. THEILACKER[1]

ABSTRACT

Histological and morphological criteria were developed to assess the nutritional condition of laboratory-reared jack mackerel, *Trachurus symmetricus*, larvae. A comparison of the histological features of fed and starved larvae revealed that the digestive tract and its associated glands were the first tissues to be affected by starvation. The extent of cellular deterioration increased with time of starvation. To classify larval condition, histological characteristics of the pancreas and gut were given numerical grades. The histological technique correctly classified 83% of the feeding and starving larvae.

The morphometric analysis relied upon a stepwise discriminant analysis that used a combination of five measurements (standard length, head length, eye diameter, body depth at the pectoral, and body depth at the anus) to estimate individual larval condition. The morphometric method was as sensitive as the histological examination in determining whether or not a larva was fed or starved. Ultimately, these histological and morphological criteria may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

Fishery scientists generally agree that observed fluctuations in recruitment of young fish to a fish stock may be the consequence of mortality during the larval stage. Because starvation is probably one of the principal causes of mortality (Hunter 1976a), a need exists to develop criteria for detecting the incidence of starvation in sea-caught specimens. Several scientists have suggested that the differences in body form between feeding and starving larvae could be used to identify the nutritional status of larvae caught in sea surveys. For example, Shelbourne (1957) based his assessment of the condition of ocean-caught plaice, *Pleuronectes platessa*, larvae on their external appearance. Certain morphometric measurements also can be indicative of starvation. A decrease in thickness of the larval fish body has been correlated with starvation for several marine and freshwater fish larvae [herring, *Clupea harengus*, and plaice (Ehrlich et al. 1976); northern anchovy, *Engraulis mordax* (Arthur 1976); anchovy, *E. japonica* (Honjo et al. 1959; Nakai et al. 1969); pike, *Esox lucius*, and carp, *Cyprinus carpio* (Kostomarova 1962)]. Other morphological features (Ehrlich et al. 1976) considered to be indicative of starvation in herring and plaice were a decrease in the angle of the pectoral girdle, a change in the ratio of the head to eye height (herring only), and a decrease in the relative condition factor. Coincident with morphometric differences caused by starvation, Ehrlich et al. (1976) described histological changes in the gut and liver. The histological approach was used to classify yellowtail, *Seriola quinqueradiata*, larvae into "feeding," "semi-feeding," and "starving" groups by Umeda and Ochiai (1975). This technique was also effective for diagnosing starvation in northern anchovy larvae (O'Connell 1976). In both species, degeneration of cells of digestive organs was the best indicator for identification of starvation. Several other studies also have correlated starvation in fish larvae with degeneration of the digestive organs, mainly the gut. Kostomarova (1962) described a retardation in development of the gut in larvae of starved carp and pike and a reduction in the depth of the epithelial cells lining the gut. Reduced gut cell height was also reported for the larvae of starved yellowtail (Umeda and Ochiai 1975), herring, and plaice (Ehrlich et al. 1976).

Morphological criteria are preferable to histological ones because they take much less time to determine and require no special preservation techniques. However, histological criteria may be more accurate for classifying individual larva.

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The purpose of this study was to develop morphological and histological criteria for assessing the nutritional condition of jack mackerel larvae and to evaluate these criteria by comparing their success in identifying fed and starved larvae reared in the laboratory. Ultimately, criteria based on these results may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

MATERIALS AND METHODS

Jack mackerel eggs were collected by towing a 1-m (mouth diameter, 0.505-mm mesh) plankton net just below the sea surface at various locations between 20 and 200 mi (32 and 320 km) off the coast of southern California in June and July 1975 and in May 1976. The eggs were separated from most of the plankton at sea and then sorted by developmental stage at the Southwest Fisheries Center, La Jolla, Calif. Temperature was maintained at 15°C during sorting and in the larval rearing containers. The light cycle was 12 h light and 12 h dark. Five hundred normally developing eggs from a single day's spawning were transferred into 100 l black Kydex[2] circular rearing tanks containing filtered seawater (5μm, Cuno filtered). There were three experiments and two treatments in each experiment; larvae in one tank were offered food while those in the other were not. The fed larvae were given a diet of a naked dinoflagellate, *Gymnodinium splendens* (50/ml), a rotifer, *Brachionus plicatilis* (30-40/ml), and a copepod, *Tisbe* sp. (1 or 2/ml). This feeding method has been described (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976b).

Histological criteria were developed in the first two experiments. The sampling procedure and the number of larvae sampled differed depending on the requirements of the analysis. Collectively, a total of 152 larvae were examined. In the third experiment, usually 15 larvae were sampled daily for 5 days from the "fed" tank (n = 69) and 3 days in the "starved" tank (n = 48). All larvae were examined both histologically and morphologically. No dead larvae were sampled because the postmortem change which takes place in tissues of fish larvae, due to digestion by their own enzymes (autolysis), resembled antemortem destruction caused by starvation. Standard length of each larva was measured on a slide; then seawater was removed and replaced by Bouin's fixative. Preserving individual larvae in this manner assured that each would be straight and flat, facilitating subsequent morphometric measurements. Five measurements were taken after preservation to monitor daily changes in larval body form and determine effects of starvation: standard length (SL, tip of upper jaw to tip of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ed), body depth at the pectoral (bd-1), and body depth at the anus (bd-2). Standard length shrinkage in Bouin's fixative was 11.5%. Next, measured larvae were prepared for histological examination using standard techniques. Larvae were transferred from Bouin's to 70% ethyl alcohol after 24 h, dehydrated with an ethyl n-butyl alcohol series in a Fisher Tissuemation, and embedded in Paraplast-plus. The Paraplast paraffin blocks were frozen with fluorocarbon spray (Cryokwick) just before the larvae were serially sectioned at 5 μm in a sagittal plane. The mounted sections were stained with Harris' hematoxylin and eosin and mounted in synthetic resin.

Histological Grading System

Recently O'Connell (1976) developed a numerical, histological grading system to characterize the nutritional condition of individual northern anchovy larvae. He examined tissues of the larvae microscopically to determine the features of tissue microstructure that were affected by starvation. A grade was assigned to each feature based on the degree of similarity or dissimilarity of the histological microstructure between the starved larvae and fed larvae. I followed this method and modified it as necessary for the tissues of jack mackerel.

Each of the histological characteristics used to assess starvation in jack mackerel larvae was evaluated and assigned a grade. A grade of "3" was given to a characteristic which resembled that in "normal or healthy" larvae, a grade of "2" was given to an intermediate condition, a grade of "1" to the starved condition. Since these criteria were established by comparing actively feeding, seemingly healthy larvae with moribund larvae, it was assumed that an average of the 12 graded features examined for each larva classified the larva into the correct nutritional group: "healthy group," average grade = 2.34 to 3.00; "intermediate group" = 1.67 to 2.33; and "starved" = 1.00 to

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

1.66 (the break points establish three equal groups).

Data Analysis

In the main, conclusions are based on the results of a stepwise discriminant analysis (SWDA). A discriminant analysis allows one to distinguish between two or more groups, given a set of variables that describe the characteristics in which the individuals in each group are expected to differ. In the stepwise discriminant analysis, all the variables are introduced into a SWDA computer program and the best set of variables, based on the generalized Mahalanobis distance (Rao 1952), is selected. The first variable chosen will usually be the one which gives the best score when classifying the individuals into their predetermined groups. The score is equal to the number correctly classified. The selection of each succeeding variable improves the score until a subset is chosen which is as good as the full set of variables for discriminating the groups. All variables not included in the final subset are considered superfluous, or not necessary for classification.

RESULTS

Histological

The histological condition of yolk-sac and actively feeding larvae ("normal") was compared with that of 3-day starved larvae and many differences were noted in the cells, tissues, and organs. The degree of apparent histological deterioration of 1- and 2-day starved larvae was intermediate between the "normal" and moribund status. This condition was termed "semi-starved" by Umeda and Ochiai (1975) and "intermediate" by O'Connell (1976).

The following section describes the normal histology of actively feeding jack mackerel larvae and that of starving larvae. Twelve histological criteria, which appeared to be indicators of starvation, were identified; they are numbered in the test below and are referenced in the photomicrographs (Figures 1-12).

Brain (Figures 3, 4)

The primitive brain cells exhibited a high incidence of mitotic activity (1) in normal larvae and there was relatively little intercellular space (2) between the round cells. In starved larvae, mitotic activity was arrested and many of the cells were shrunken, which caused large clear areas to appear between densely stained, atrophied cells.

Liver (Figures 5-8)

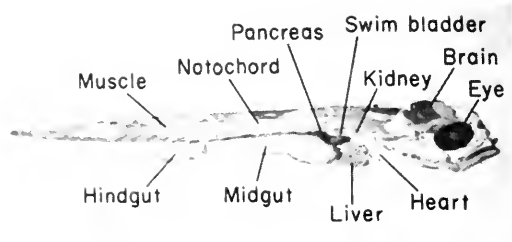
In the normal larval jack mackerel liver the hepatic cords were two cells thick. Within each hepatocyte, the nucleus (3) was regular in shape and distinct. The cytoplasm (4) was well dispersed with intracellular spaces, probably an area where glycogen and lipid are stored. Sinusoid areas, where metabolic exchanges take place between the hepatic cords, contained blood cells. After starvation for a few days, the liver atrophied, the cytoplasm condensed, stained darkly, and intracellular spaces had disappeared. There were focal degenerative or necrotic areas and accumulations of eosinophilic granules and masses. Nuclei were often irregular in shape and granules appeared around their periphery; these darkened areas are presumed to be condensed, inactive chromatin (Stein et al. 1975). The gallbladder (5) in starved larvae was always enlarged; normally it discharges its contents under the stimulus of food (Love 1970).

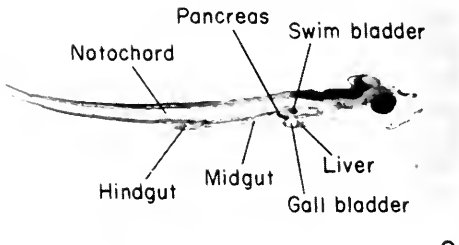
Pancreas (Figures 5-8)

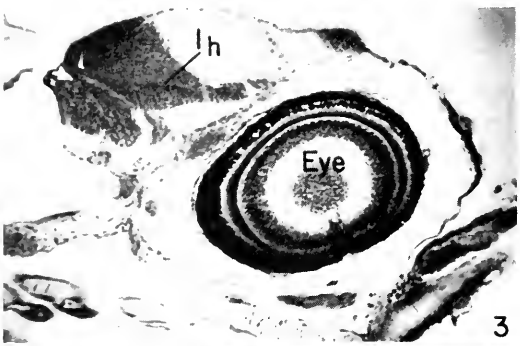
Cells of the exocrine pancreas were arranged in series, in a circular fashion, as a secretory unit called an acinus. The nucleus (6), clear and distinct, was located in the basal portion of the pyramidal cells. The acinar arrangement of the pancreatic cells (7) was found to be very sensitive to deprivation of food. A breakdown in the symmetry in the acinus was slight but usually detectable after 1 day of starvation. Tissue degeneration after 3 days of starvation was extreme. The nucleus was irregular and uniformly stained and there was no detectable acinar arrangement. The presence of zymogen, digestive proenzyme secreted by the acinus and stored as granules at its central apex, was usually associated with starvation.

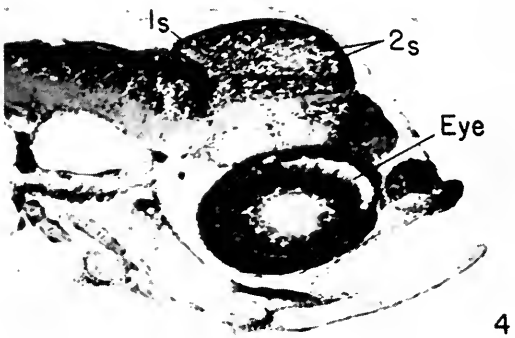
Digestive Tract (Figures 7-12)

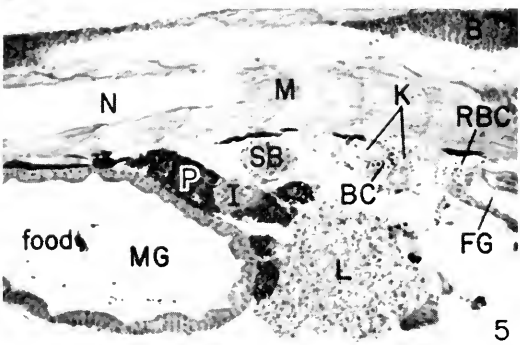
The columnar epithelial cells of the midgut were closely united (8) in a single layer. Microvilli were visible along the border of the lumen giving a brush effect. In starved larvae, the midgut cells











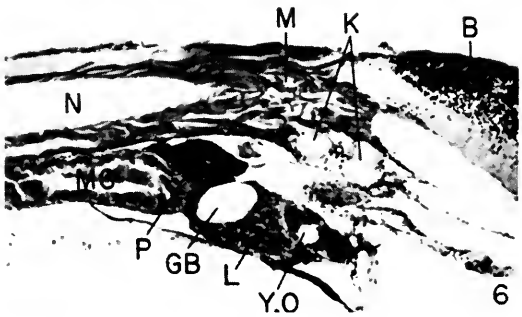


FIGURE 1.—*Trachurus symmetricus* larva, day 8, fed for 3 days. All 12 histological criteria graded as "healthy." 32 ×.

FIGURE 2.—*Trachurus symmetricus* larva, day 8, starved for 3 days. All 12 histological criteria graded as "starved." 32 ×.

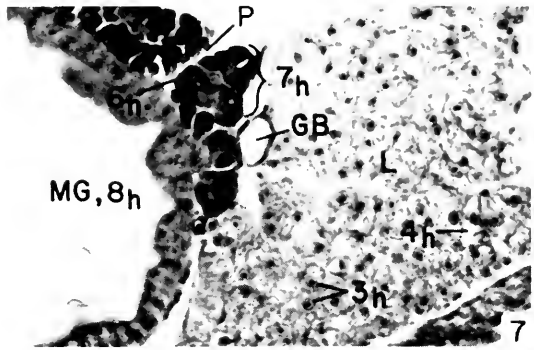
FIGURE 3.—Head of fed larva, graded "healthy." Mitotic activity (1 h) is indicated. Note close proximity of primitive brain cells to each other. 200 ×. h = histological grade = healthy.

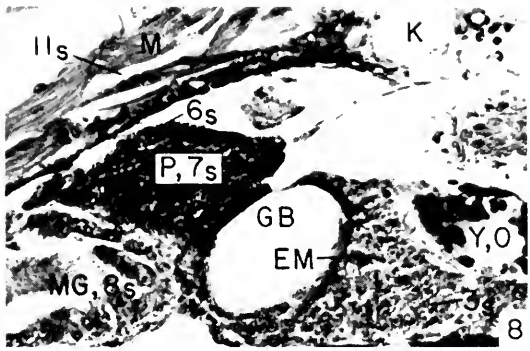
FIGURE 4.—Head of starved larva, graded "starved." Atrophied and darkly stained primitive brain cells (1 s); large intercellular spaces (2 s). 200 ×. s = histological grade = starved.

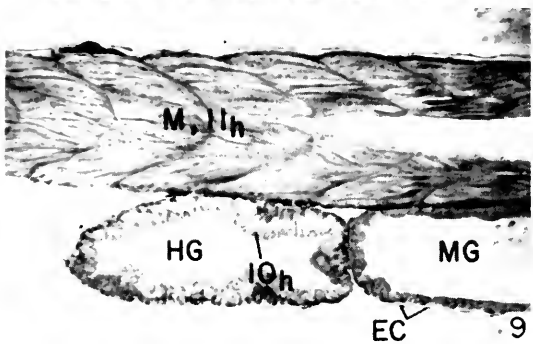
FIGURE 5.—Day 8 fed larva. Histological features graded "healthy." 200 ×. See enlargement, Figure 7. B = brain, BC = blood cells (white or immature red), FG = foregut, I = Islet of Langerhans (endocrine pancreas), K = kidney, L = liver, MG = midgut, M = muscle, N = notochord, P = exocrine pancreas, RBC = red blood cells, SB = swim bladder.

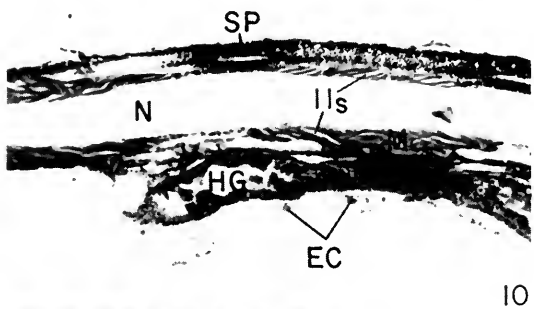
FIGURE 6.—Day 8, starved larva. Histological features graded "starved." 200 ×. See enlarge, Figure 8. GB = gallbladder, O = oil, Y = yolk, see Figure legend 5 for rest of symbols.

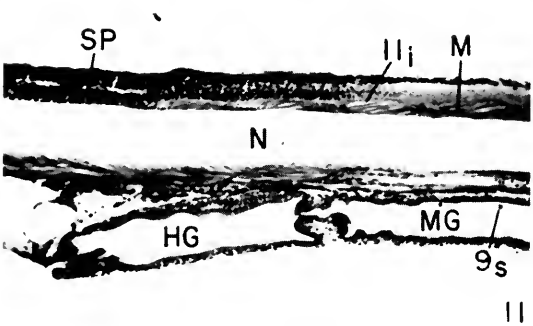
FIGURE 7.—Day 8 fed *Trachurus symmetricus* larva. Enlargement of Figure 5. Midgut cells in close union (8 h); prominent nuclei (3 h) and large intracellular spaces (4 h) in the liver; pancreatic nuclei distinct (6 h) and cells arranged in a circular unit (acinus) (7 h); gallbladder (GB) "normal." 480 ×. h = histological grade = "healthy," L = liver, MG = midgut, P = exocrine pancreas.











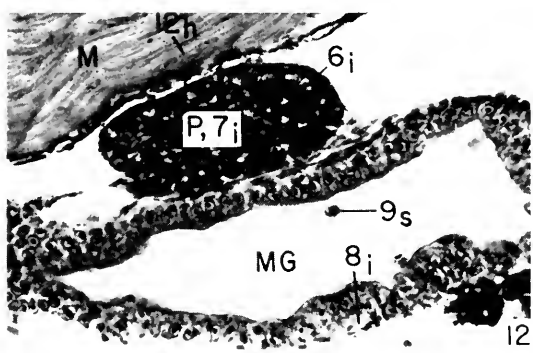


FIGURE 8.—Day 8, starved *Trachurus symmetricus* larva. Enlargement of Figure 6. Loss of integrity of midgut cells (8 s); atrophied liver with dark staining and irregular nuclei (3 s); no acinar cellular arrangement in pancreas (7 s); separated muscle fibers (11 s); swollen kidney (K); distended gallbladder (GB); note presence of yolk and oil (Y, O), and eosinophilic mass (EM) in liver. 480 ×. s = histological grade = "starved," M = muscle, MG = midgut, P = exocrine pancreas.

FIGURE 9.—Day 8 fed larva. Large eosinophilic inclusions in hindgut (10 h); muscle fibers closely packed (11 h); thin, epithelial integumental cells (EC) are prominent below gut and above trunk musculature. 200 ×. h = histological grade ="healthy," HG = hindgut, M = muscle, MG = midgut.

FIGURE 10.—Day 8, starved larva.Loss of cellular structure in hindgut; enlarged epithelial integument cells (EC); separated muscle fibers (11 s). 200 ×. s = histological grade = "starved," HG = hindgut, M = muscle, N = notochord, SP = spinal cord.

FIGURE 11.—Day 7 larva, starved 2 days and histologically graded "intermediate." No inclusions in hindgut; cellular separation in midgut (MG) and hindgut (HG); midgut cells sloughing (9 s); muscle fibers beginning to separate (11 i). 200 ×. i = histological grade = intermediate, s = histological grade = "starved," M = muscle, N = notochord, SP = spinal cord.

FIGURE 12.—Day 7 larva, starved 2 days, graded "intermediate." Abundant intermuscular tissue (12 h); no muscle (M) fiber separation; pancreatic nuclei (6 i) not distinct and cellular acinar arrangement lacking (7 i); midgut cells separating (8 i) and sloughing (9 s). 480 ×. i = histological grade = intermediate, s = histological grade = "starved," MG = midgut, P = exocrine pancreas.

began to separate from each other. It appeared that the midgut was extremely vulnerable to a deficiency of food and usually after 1 day of starvation, single mucosal cells could be seen sloughed (9) into the lumen. The margin of the lumen continued to lose its integrity as starvation advanced. Cells of the hindgut of feeding larvae exhibited an accumulation of eosin staining inclusions. The inclusion bodies, which may be the sites of intracellular digestion, have been observed in other marine and freshwater fish (Kostomarova 1962; Iwai and Tanaka 1968a, b; Iwai 1968; Umeda and Ochiai 1975; O'Connell 1976). The amount, size, and intensity of the staining (10) of these inclusions varied in feeding larvae. They were not present in starving larvae.

Musculature (Figures 9, 10, 12)

In feeding jack mackerel larvae, individual muscle fibers were close together (11); they were composed of closely packed, striated, and parallel myofibrils. After a period of starvation, the fibers separated, the fibrils were not distinct, and occasionally they lost their parallel structure. Between some fibers there was a granular, basophilic, nucleated substance called "intermuscular tissue" (12) by O'Connell (1976). In starved larvae, this tissue was usually absent.

General Histological Characteristics

After jack mackerel larvae had starved for 3 days, signs of depletion were widespread. In addition to changes in major tissues and organs there was a general atrophy and disintegration of all cells and tissues including those of cartilage, kidney, endocrine pancreas, and swim bladder. The number of pyknotic nuclei (i.e., darkening and shrinking nuclei, which give the first indication that a cell is dying) increased in all tissues (see eye and brain, Figure 4). Epithelial cells of the integument were hypertrophic, twice as large as normal in 3-day starved larvae (Figure 10), and kidney tubules were swollen (Figure 6). There was always a larger yolk reserve retained by starving larvae (Figure 6). A decrease in yolk absorption in starving larvae was also reported by Kostomarova (1962) for pike and carp and by Umeda and Ochiai (1975) for yellowtail.

Histological Grading

To determine whether the classification of a jack mackerel larva required the grading of all histological features or a lesser number, a group of 27 larvae, 14 feeding and 13 starving, was examined and the resulting grades for each criterion were submitted to a SWDA. The experimental treatment (fed or starved) was unknown until after all larvae were microscopically examined. The larvae were 7 days old and had been feeding or starving for 2 days. The grading system classified all fed larvae (n = 14) into the healthy group (individual average grade of the 12 histological features ranged between 2.42 and 2.92). The average grades for the 2-day starved larvae were more variable. The larvae were classified, about equally, into each of the three nutritional groups: four had a grade range between 2.35 and 2.54, ranking in the healthy group; four were classified as intermediate, grade range 2.08 to 2.31; and five larvae were ranked as starved with the average grades ranging between 1.15 and 1.54.

Results of the SWDA on the above data disclosed that grading only two histological characteristics, the arrangement of the cells in the pancreas (variable 7) and the sloughing of mucosal cells from the midgut (variable 9), gave the same conclusions as using all 12 features. Therefore, in all subsequent histological assessments, the average grade of these two criteria, variables 7 and 9, was used as the index of larval condition.

Morphological

The jack mackerel larvae were 2.45 mm SL (preserved) at hatching and initiated feeding at 3.35 mm, 5 or 6 days after hatching (hatching = day 0, Figure 13A). At the time of first feeding, some yolk and oil were present but the yolk sac was not discernible. The relationship between the five morphological characteristics, measured to determine the effects of starvation, and days of starvation is illustrated in Figure 13B-F. Since no data have been published on the daily growth rate of field-caught jack mackerel larvae, I used length as an estimate of age. When the morphometric measurements were plotted against length, no single measurement was a reliable index of starvation, as illustrated by pectoral body depth plotted for fed and starved larvae (Figure 14). However, some limits can be set from this graph: 1) all larvae <3.30 mm SL that do not have a yolk sac probably are starving (feeding is initiated at 3.35 mm); and 2) larvae with a body depth >0.47 mm are feeding. This leaves the size class between 3.30 and 3.55 mm where the cases cannot be separated. Most individuals in this class (29 fed and 24

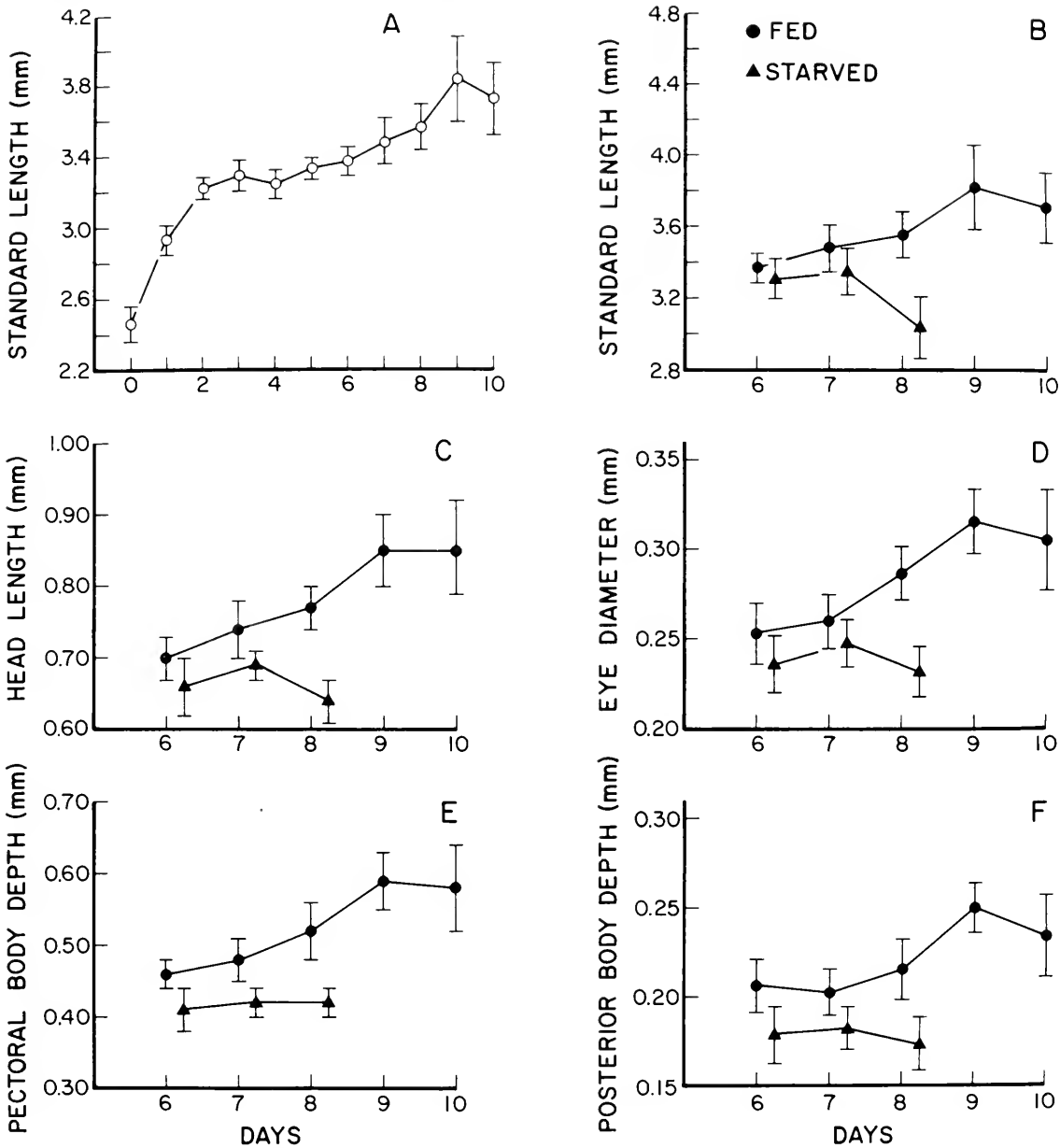


FIGURE 13.—A. Growth of *Trachurus symmetricus* larvae, with means and standard deviations. Sample size on any day was usually 15. B-F. Relationship between five morphological characteristics of *T. symmetricus* larvae and days of starvation, with means and standard deviations. Sample size was usually 15.

starved) have been feeding or starving for 1 or 2 days.

To determine whether a set of several morphometric variables could predict the condition of larvae in the 3.30 to 3.55 mm size class, a SWDA was run. Eleven morphometric variables, in which the two predetermined groups (fed and starved) were expected to differ, were entered into the SWDA: 1) HL, 2) ed, 3) bd-1, 4) bd-2, 5) HL/SL, 6) ed/SL, 7) bd-1/SL, 8) bd-2/SL, 9) ed/HL, 10) bd-1/

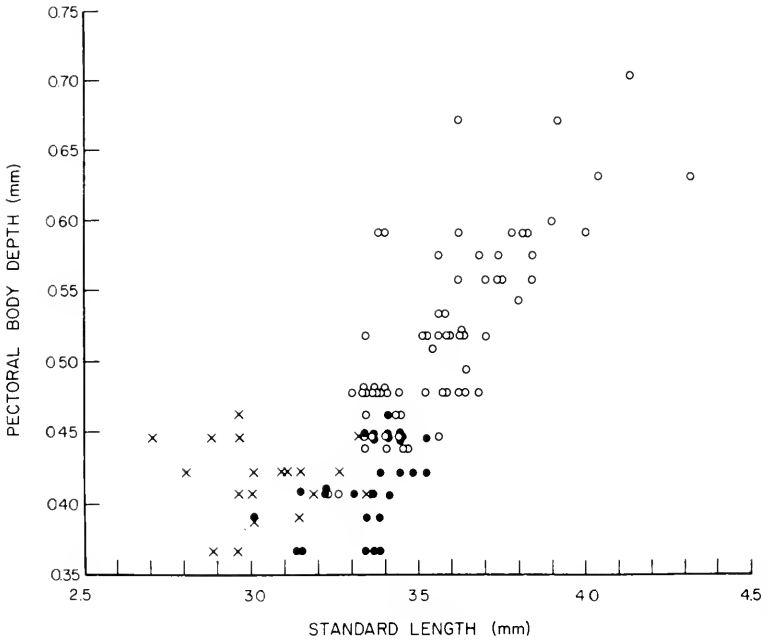


FIGURE 14.—Relationship between pectoral body depth and standard length of *Trachurus symmetricus* larvae which were fed (open circles), starved 1 and 2 days (dots), and starved 3 days (x's).

HL, and 11) bd-2/HL. Standard length was used in ratios and not as a unit to allow discrimination between fed and starved larvae of the same length. To discriminate between the two groups, the analysis selected a set of five variables, listed in the order of selection: 1) bd-2/SL, 2) bd-2/HL, 3) bd-1/HL, 4) ed/SL, and 5) bd-1. With these five variables, 83% of the fed and 86% of the starved larvae in the select size class were correctly classified. When all the larvae, 69 fed and 48 starved (Figure 14), were included in the analysis and the discriminant functions derived from the above five variables were used, 87% of the fed and 94% of the starved were correctly classified.

Comparison of Histological and Morphological Techniques

All larvae classified using morphometric characters were also analysed histologically (Table 1). The histological grading system classified 83% of the larvae which were fed into the healthy group and 83% of the larvae deprived of food for 3 days into the starved group. The histological grades of 1- and 2-day starved larvae were not as well defined; 19% of the cases were graded as healthy, 44% were graded intermediate, and 37% were graded starved. This outcome was similar to results of the initial histological study of 2-day starved larvae reported under Histological Results.

In the morphometric SWDA (Morphological Results), all the starved larvae (1-, 2-, and 3-day starved) were entered into the analysis as one group (n = 48). However, from the above histological grades of the starved larvae, the class should be divided into two groups, early starvation (including 1- and 2-day starved larvae which received all three histological grades) and prolonged starvation (including 3-day starved larvae which were mostly graded as starved). Preliminary laboratory experiments supported this decision. Food was offered to 1-, 2-, and 3-day starved larvae and some 1- and 2-day starved larvae did initiate feeding. No 3-day starved larvae ate food. The

TABLE 1.—Histological classification of *Trachurus symmetricus* larvae.

Item	n	Average histological grade: Healthy 2.34-3.00	Intermediate 1.67-2.33	Starved 1.00-1.66
Days fed				
1	14	12	1	1
2	15	13	2	—
3	15	11	4	—
4	6	6	—	—
5	14	11	3	—
Days starved:				
1	13	3	5	5
2	14	2	7	5
3	18	2	1	15

feeding capability reported for other pelagic fish larvae, after an initial period of starvation, was similar to jack mackerel (Blaxter 1965; Lasker et al. 1970; May 1971). Because of these variables, the morphometric analysis was refined further to differentiate three groups.

Two methods of analyzing the morphometric data for three predetermined groups (fed, early starvation, and prolonged starvation) were examined using 1) all 11 variables previously described, and 2) the set of 5 variables chosen to discriminate between fed and starved larvae morphometrically. In the first test, the SWDA selects the best set of variables to discriminate between the three groups and in the second test, the analysis separates groups with a given set of variables.

The variables selected by the first test (in order of selection) were: 1) bd-2, 2) bd-2/SL, and 3) HL. The set of three variables correctly classified 84% of the fed larvae, 93% of the early starved larvae, and 79% of the prolonged-starved larvae (Test 1, Table 2). The inclusion of two more variables, bd-2/HL and bd-1/HL, did not improve the classification scores. The second test, using the previously chosen set of five variables, correctly classified 84% of the fed larvae, 90% of the early starved, and 74% of the prolonged-starved larvae (Test 2, Table 2). The first test had a better score for both the early and prolonged starvation groups, but either set of variables is a reliable predictor of larval condition.

TABLE 2.—Morphological classification of *Trachurus symmetricus* larvae. The number of larvae in the predicted groups (experimental conditions) is compared with the actual group membership determined by a stepwise discriminant morphometric analysis. Test 1 uses a set of three variables: posterior body depth, posterior body depth divided by standard length, and head length, and Test 2 uses a set of five variables: posterior body depth divided by standard length and head length, pectoral body depth divided by head length, eye diameter divided by standard length, and pectoral body depth.

Experimental conditions	*n*	Fed	Starved	
			1 and 2 days	3 days
		Group membership test 1		
Fed	69	58	10	1
Starved.				
1 and 2 days	29	1	27	1
3 days	19	0	4	15
		Group membership test 2		
Fed	69	58	10	1
Starved.				
1 and 2 days	29	2	26	1
3 days	19	1	4	14

Either the morphological or the histological technique can be used to identify fed larvae and 3-day starved larvae (Table 3). Fifty-three of the 64 (83%) larvae which were offered food were classified as fed (column 2) by the morphometric SWDA and as healthy (column 3a) by the histological method; but, only 44 of these larvae had the score in common (Table 3). Within the 3-day starved group, 14 of the 18 (78%) larvae were correctly classified (column 2) with the morphometric analysis and 15 (83%) were labelled correctly with the histological technique; 13 larvae had the starved score in common. It is difficult to compare the morphological and histological scoring of the early starvation (1- and 2-day starved) group. The morphometric analysis was extremely sensitive for selecting this group, 96% were correctly classified; however, the histological analysis may be more accurate for indicating which larvae in this group can still feed. Five of the 27 (19%) early starved larvae were histologically graded as healthy and may be capable of feeding. It is also possible that intermediate grade larvae (44%) would eat if exposed to food. Eleven of the 12 fish in this intermediate group had a score in common with the morphometric analysis. Intermediate larvae exhibit some tissue degeneration which may be reversible. Additional laboratory experiments are required to determine survi-

TABLE 3.—*Trachurus symmetricus* larvae were fed or starved for 1, 2, or 3 days (column 1). Each larva was classified with the morphometric method (column 2) and the histologic method (column 3). The percent of the larvae correctly classified with each method and the number of larvae correctly classified by both methods is also indicated.

Experimental conditions[1] (1)	Morphometric analysis (2)		Histological analysis (3)		
			Healthy	Intermediate	Starved
		n	53/83%	10	1
Fed *n* = 64	Fed	53/83%	44	8	1
	Starved 1 and 2 days	10	8	2	0
	Starved 3 days	1	1	0	0
		n	5	12/44%	10
Starved 1 and 2 days *n* = 27	Fed	1	0	1	0
	Starved 1 and 2 days	26/96%	5	11	10
	Starved 3 days	0	0	0	0
		n	2	1	15/83%
Starved 3 days *n* = 18	Fed	0	0	0	0
	Starved 1 and 2 days	4	1	1	2
	Starved 3 days	14/78%	1	0	13

[1]The total number of larvae within each experimental group agrees with Table 1 but differs from Table 2 because several larvae were lost during the microtechnique procedure

val when feeding is only delayed for 1 or 2 days and to ascertain whether tissue degeneration noted during the period of early starvation is reversible.

DISCUSSION AND CONCLUSION

The effects of starvation could be seen throughout the body of larval jack mackerel. There was atrophy of all tissues, with the digestive tract and its associated glands the first tissues affected by starvation. The extent of cellular deterioration increased with time of starvation. Many histological changes, which were associated with starvation in jack mackerel, were similar to changes described in other starving fish larvae: 1) atrophy and cellular and nuclear degeneration of the liver (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976; plaice, Karl Ehrlich pers. commun.), 2) separation of muscle fibers (northern anchovy, O'Connell 1976; herring and plaice, Ehrlich pers. commun.), 3) cellular and nuclear degeneration in the pancreas (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976), and 4) decrease in the size of the epithelial cells in the digestive tract (pike and carp, Kostomarova 1962; yellowtail, Umeda and Ochiai 1975; herring and plaice, Ehrlich et al. 1976; northern anchovy, O'Connell 1976). Some histological changes present in starved jack mackerel larvae, enlargement of the gallbladder and deterioration of the primitive brain cells, have not been reported for other starved fish larvae.

The onset of starvation in jack mackerel larvae was manifested as 1) a change in acinar arrangement of the pancreatic cells and 2) a sloughing of mucosal cells from the midgut into the lumen. These two criteria were shown to be critical variables and were histologically graded to assess the nutritional condition of jack mackerel larvae. O'Connell (1976) reported that the condition of the pancreas was of primary importance for classifying starving northern anchovy larvae. His criteria for good pancreatic condition depended on the abundance of zymogen as well as continuity of cellular structure. The presence of zymogen was not used as a criterion to classify jack mackerel larvae; absence of zymogen was usually associated with feeding, however, the correlation was not consistent. O'Connell also noted mucosal cells in the midgut of larval anchovy but he did not grade this feature. Love (1970) suggested that sloughed midgut cells may be used as an energy source.

During starvation, growth was retarded, larvae shrank, and the soft tissues collapsed causing larvae to look abnormal; the body became bent and thin and the head disproportionately large. An array of larval fish morphometric characteristics have been associated with nutritional condition. A decrease in depth of the larval body has been considered to be an important indicator of starvation although Blaxter (1971) did not find it to be a sensitive character for elongate clupeoid larvae. However, body depth divided by standard length appears to reflect the condition of postlarval anchovy (Nakai et al. 1969) and older, larval northern anchovy (Arthur 1976), but the ratio did not identify feeding and starving post yolk-sac northern anchovy (O'Connell 1976). Nakai et al. (1969) also related the diameter of the posterior digestive tract to condition in postlarval anchovy. The height of the body in the posterior part of the trunk was measured by Honjo et al. (1959) and was found to differ between postlarval anchovy collected from two fishing grounds. Honjo et al. (1959) suggested that the anatomical difference was indicative of a higher availability of food organisms in one area than in the other. Another predictive parameter for the condition of post yolk-sac larvae was the relative condition factor reported by Ehrlich et al. (1976) for herring and plaice. Its estimation involves weighing each larva. All of the above mentioned morphological criteria reflect larval nutritional condition and may be considered reference parameters, but no one criterion accurately identifies larval condition on an individual basis. The lack of sensitivity of a single morphometric indicator may be due to natural variability alone or more probably to the rapid morphological changes which occur in larval fish. For example, Zweifel[3] using the data of Hunter (1976b) has shown that for feeding northern anchovy larvae the condition factor weight/length^3 was neither constant nor monotonic even when food densities were carefully controlled. For variation in food levels (including no food) it would be expected that there should be even more complex relationships.

Even though the histological and morphological techniques have proven to be effective for predicting condition of laboratory-reared animals, both techniques must be field tested with wild-caught

[3]Zweifel, J. 1977. A non-linear model for allometry in larval fish. Unpubl. manuscr., 25 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

larvae. Evidence of morphological differences between laboratory-reared and sea-caught larvae indicates that it may be difficult to transfer laboratory results to the sea. Blaxter (1968, 1971), for example, found laboratory-reared herring larvae exhibited a greater size variation and a higher condition factor than sea-caught larvae. Balbontin et al. (1973) reported differences in body depth, head depth, and head length between laboratory and wild herring juveniles of the same length. The laboratory-reared animals had a deeper body and a deeper or longer head.

The usefulness of the morphometric discriminant technique will depend upon the consistency of changes in morphological pattern in individuals when feeding and starving. However, even if the changes are not constant, useful indicators of larval survival will not require the exact allocation of all individuals into feeding and starving groups but rather only reasonable estimates of the relative proportions will be needed. My results indicate that a multivariate statistical approach, combining several morphometric measurements in a SWDA, may provide this information. Species that do not yield to a morphological analysis should yield to the histological approach.

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IDENTIFICATION OF STOCKS OF BRISTOL BAY SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, BY EVALUATING SCALE PATTERNS WITH A POLYNOMIAL DISCRIMINANT METHOD[1]

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ABSTRACT

A polynomial discriminant method is developed for the racial classification of stocks of sockeye salmon. The method is based upon the nonparametric estimation of the multivariate probability densities of the scale characteristics for each stock considered. Errors in classification are examined and a correction procedure is extended to the n-class case. As an example, sockeye salmon of age 2.2 sampled on the high seas are classified to river of origin based on freshwater scale growth patterns. Also, freshwater and marine scale characters are evaluated for stock identification purposes involving certain Bristol Bay runs.

Racial analysis of high-seas salmon has important applications both in life history studies of various stocks and in management considerations of these stocks. As a result, many have examined the characteristics of scale structure to differentiate salmon subpopulations. Konovalov (1971) notes that some investigators were ignoring many characteristics in scale structure which arise under the effects of ecological factors in specific bodies of water. When the ecological conditions affecting scale characters are seriously considered, statistically significant differences between subpopulations can often be found. The ability to recognize salmon subpopulations depends upon the differences between the stocks in terms of examined characteristics and the accuracy of the analytic technique. Various discriminant function analyses have been traditionally used.

Fukuhara et al. (1962), Amos et al. (1963), and Dark and Landrum (1964) used linear discriminant functions based upon morphological characteristics to identify the continent of origin of Pacific salmon. Scale characteristics and linear discriminant functions were used by Anas (1964) and Mason (1966). Anas and Murai (1969) used linear and quadratic discriminant functions. Recent investigations by Major et al. (1975) and Bilton and Messinger (1975) used unspecified discriminant function techniques, probably similar to those of Anas and Murai (1969). These and other studies show the utility of discriminant function methodology for identifying races of Pacific salmon.

Salmon managers need a flexible and easily implemented stock identification technique. This paper applies a generalized discriminant function technique to measurements of sockeye salmon scales to attempt to fulfill this need.

DISCRIMINANT FUNCTION ANALYSES OR PATTERN RECOGNITION[4]

Discriminant function analysis depends on the recognition of underlying patterns differing among classes of objects. In this case, scale patterns characterize a sockeye salmon of a particular origin. A set of p-scale characters (a p-tuple or vector in p-space) measured on an individual salmon provides a description of that salmon. A sample of p-tuples for a number of salmon from one origin (the learning sample) establishes a region in p-space characteristic of that class of sockeye. Samples from salmon of different and known origins establish regions in p-space which may be separated by decision surfaces. A sockeye salmon of unknown origin may be classified according to which region its p-tuple occupies. The accuracy of classification depends upon the precision with

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[4]A good text on pattern recognition is given by Patrick (1972). A review of the literature is given by Das Gupta (1973).

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which the regions are described and the inherent separation between them.

These regions are described mathematically by multivariate probability density functions. Fisher's (1936) linear discriminant function defines a linear decision surface (hyperplane) derived by describing these regions as multivariate normal density distributions with common variance-covariance matrices (Welch 1939). Quadratic discriminant functions have been developed (Smith 1947). The resulting decision surfaces are nonlinear. The quadratic discriminant function does not require common variance-covariance matrices. Anas and Murai (1969) compared the classificatory abilities of the linear and quadratic discriminant functions. They found (in agreement with Isaacson 1954) that even if the assumption that the distributions have common variance-covariance matrices is violated, the linear discriminant function would still give good results for large sample sizes. But the quadratic function gave slightly better results.

All investigators utilizing discriminant analyses to separate races of Pacific salmon have assumed that the density distributions of measurements from a particular class of salmon were multivariate normal. The frequency distributions of scale characters in Major et al. (1975) show that multimodal and skewed distributions occur for chinook salmon scale characters even in the univariate case. In many other cases, the underlying distribution functions may be non-Gaussian. Discriminant functions based upon non-Gaussian distributions or obtained by distribution-free methods are preferable to those based upon an unrealized assumption of normality.

Nearly all of the discriminant function analyses used in the investigations of Pacific salmon have been two-class analyses designed to determine the continent of origin of salmon taken on the high seas. For the two-class situation only one discriminant function need be calculated. These two-class problems are a special case of the many-class problems in which a separate discriminant function is calculated for each class. Bilton and Messinger (1975) calculated discriminant functions for each of several runs in a classification study on sockeye salmon. If several stocks of salmon intermingle and are to be classified, analyses of this type are needed.

Specht's (1966) polynomial discriminant method does not require that the underlying density distributions be multivariate normal nor that they have common variance-covariance matrices. Since this method is nonparametric, various scale characteristics may be used for discrimination with no particular regard to the underlying distributions. Thus, the method is flexible and practical.

Specht (1966) uses an estimated probability density function of the form described by Parzen (1962) and extended by Murthy (1966) to the multivariate case. The underlying multivariate density for each class is modeled by a sum of functions that are multivariate Gaussian in form, one such function for each fish in the learning sample for that class. This set of functions is complete. Therefore, for each class the underlying continuous probability density, Gaussian or not, may be approximated arbitrarily closely by such a sum. A power series expansion of this estimated denisty then results in a polynomial term in the density function, the coefficients of which are functions of the observations (fish) in the learning sample. One such set of coefficients is computed for each class to be considered. These polynomials determine the nonlinear decision surfaces and are the basis for discrimination.

The individual multivariate Gaussian functions (which when summed model the underlying multivariate distribution for that class) contain a "smoothing parameter," σ, which appears in the place of a standard error. This parameter is then incorporated in the estimates of the polynomial coefficients. The reader is referred to Specht (1966) for a discussion of the effect of this smoothing parameter and for the algorithm for the calculation of the sets of polynomial coefficients $\{D_{k_i \ldots k_j \ldots k_h}\}$. The polynomial discriminant function is:

$$
\begin{aligned}
P(X) = {} & D_0 - D_1X_1 + D_2X_2 + \ldots + D_pX_p \\
& - D_{11}X_1^2 + \ldots + D_{k_1k_2}X_{k_1}X_{k_2} \\
& - \ldots - D_{pp}X^2_p + D_{111}X_1^3 \\
& + \ldots + D_{k_1k_2k_3}X_{k_1}X_{k_2}X_{k_3} + \ldots \\
& - D_{ppp}X^3_p + \ldots \\
& - D_{k_1 \ldots k_j \ldots k_h}X_{k_1} \ldots X_{k_h} \\
& - \ldots .
\end{aligned}
$$

where p = dimension of the vector X (set of scale characters)

$1 \leq k_j \leq p$

$j = 1, 2, \ldots, h$

h = the degree of the variable portion of the term.

The decision on an unknown X (set of scale measurements from a salmon of unknown origin) is thus:

$$\text{Choose } d(X) = \theta_r \text{ so that } h_r P^r(X) \geq h_s P^s(X) \text{ for all } s \neq r$$

where $d(X)$ = the decision on an unknown X

θ_i's = the classes (origins)

$p^i(X)$ = the polynomial value for X calculated using the discriminant function for class θ_i

h_i = the a priori probability, the uses of which will be described later.

APPLICATION OF THE METHOD

Three scale sample sets are required to implement the polynomial discriminant method: learning samples, test samples, and unknown samples. The learning and testing samples are collected from each subpopulation when they are segregated (i.e., in the rivers of origin). Scale characters to be measured in the unknown sample for the required discrimination are determined by evaluating characters measured in the learning samples. The learning samples and the characters selected are used to calculate the coefficients in the polynomial discriminant functions. To calculate these coefficients, the value for the smoothing parameter and the point at which the discriminant function should be truncated must be determined. Various circumstances will dictate different choices. When a smoothing parameter of 1.5 was chosen, all terms in the discriminant function greater than the fourth order contributed negligibly to polynomial values and so were truncated in our applications. Often, polynomial discriminant functions of lower order yield adequate results.[5]

[5]A polynomial discriminant function with six variables and of the fourth order will contain 210 terms. Since our calculations were performed by computer, we chose not to delete the third or fourth degree terms. However, if more than six variables are used, it would be wise to truncate further in order to keep the number of terms down.

The fish comprising the test samples are classified to test the effectiveness of the polynomial discriminant method and to determine the a priori probabilities. (Each test sample consists of fish from one class.) Finally, fish collected from the zone of intermingling are classified to determine the degree of intermingling in the area of interest.

Appraisal of the method using scale samples of sockeye salmon collected from the 1967 escapement in five Bristol Bay rivers showed large percentages of fish comprising the test samples were correctly classified. However, misclassified fish in the test group (set of test samples from all rivers being considered) were not assigned to the rivers in proportion to the known relative test sample sizes. To balance these misclassifications, wherever a greater number of fish comprising the test group was assigned to a particular river than should have been (according to the relative test sample sizes), the a priori probability for that river was lowered. Corresponding increases were made for those classes with insufficient assignment. By alternatively using the decision procedure of the polynomial discriminant method and adjusting the a priori probabilities, we obtained solutions so that the number of fish belonging to a certain river that were misassigned to all other rivers approximately equaled the number of fish misassigned to that certain river from all other rivers. Thus the a priori probabilities were not used in the manner their name suggests, but a priori knowledge may dictate test sample sizes. The relative test sample sizes in the test group may be in the relative proportions to be expected in the unknown sample (i.e., historical relative run sizes). The adjustment procedure, then, shifts the nonlinear decision surfaces between the probability densities so that the incorrectly identified samples are assigned to the various rivers in the proportions dictated by the test sample sizes in the test group. However, the primary purpose of the adjustment procedure is not to balance the misclassifications but to maximize the number of correct classifications. As the misclassifications are balanced, the number of correct classifications generally increases. At this point the result is a classification method that maximizes the total number of correct classifications and balances misclassification rates for a test group in which the test sample sizes are in particular proportions.

However, it is obvious that the proportions of fish from the various classes in the test group would rarely be identical to those proportions in

the unknown sample. Thus, imbalance among the misclassified fish will recur, unless the expected accuracy of classification is very good (near 100%). We have devised a method to correct for this.

Based upon the results of classification of the known test group, the classification matrix, C, is estimated:

$$\hat{C} = \begin{bmatrix} \hat{c}_{11} & \hat{c}_{12} & \cdots & \hat{c}_{1n} \\ \hat{c}_{21} & \hat{c}_{22} & \cdots & \hat{c}_{2n} \\ \vdots & \vdots & & \vdots \\ \hat{c}_{n1} & \hat{c}_{n2} & \cdots & \hat{c}_{nn} \end{bmatrix},$$

where $\hat{c}_{ij}$ is an estimate of the fraction of fish allocated to class i belonging to class j, such that $\sum_{i=1}^{n} \hat{c}_{ij} = 1.0, \ \forall j$. (Note that for each j the $\hat{c}_{ij}$'s are a set of estimated multinomial probabilities and that each test sample size should be adequate.) If the discrimination is error-free, C would be an identity matrix. The adjustment of a priori probabilities causes the initially estimated classification matrix to evolve to the point where

$$\hat{C}T = R_t \text{ such that } T \approx R_t.$$

The ith component of the vector T is the fraction of fish in the test group from test sample i (class i), and the ith component of the vector R_t is the fraction of fish in the test group allocated to class i by the adjusted polynomial discriminant method.

The test samples comprising T are not independent of the classification scheme since they are used to determine the a priori probabilities used in the decision rule. Hence, the estimated probabilities in the classification matrix may not be unbiased. However, we did chi-square tests that show elements of the classification matrix are not significantly different when estimated with either the test samples used to determine the a priori probabilities or a second independent test group. Thus, we prefer to use only one test group to determine the a priori probabilities and to estimate the elements of the classification matrix because the test sample sizes will be larger (and the variance of the $\hat{c}_{ij}$'s smaller) if we do not subdivide the fish available.

Now, let u_i be the fraction of fish in a sampled group that belong to the ith class. The vector U is then unknown except for the obvious side condition $\sum_{i=1}^{n} u_i = 1$. The classification matrix now operates on U to give:

$$CU = R_u{}^{6}$$

where the ith component of R_u is the fraction of fish in the unknown sample allocated to the ith class. Since C is estimated, R_u is known and since C is usually nonsingular, we can estimate U by

$$\hat{U} = \hat{C}^{-1} R_u.$$

Each point estimate ($\hat{u}_i$) obtained will have some variance. This variability will depend upon the accuracy with which fish from class i are classified, the accuracy with which the elements of C are estimated, and variance due to sampling error encountered when obtaining the unknown sample. Thus, if any u_i is small, then its estimate ($\hat{u}_i$) may be negative. Such solutions are meaningless. In such cases the classes with negative solutions should be dropped (assume such $u_i \approx 0$) and the analyses repeated.

We did simulation work to evaluate the classification matrix correction procedure for the two- and three-class situations. Five hundred simulated experiments were done for each situation. For the two-class case the average error of the classification results was 0.100 while that of the corrected estimates was 0.055. In 84% of the experiments the corrected estimate was closer to the true value than classification result. For the three-class case the average error of the classification results was 0.127 while that of the corrected estimates was 0.054. In 89% of the experiments the corrected estimate was closest to the true value. The results of these simulations show that the classification correction procedure improves estimates of the true proportion of a class present.

This classification matrix correction procedure will reduce to the correction procedure developed for the two-class case by Worlund[7] in the following manner:

[6] A similar relationship and a least squares solution technique is given by Worlund and Fredin (1962).

[7] Worlund, D. D. 1960. A method for computing the variance of an estimate of the rate of intermingling of two salmon populations. Unpubl. manuscr., 13 p. Bur. Commer. Fish., Biol. Lab., Seattle, Wash.

$$U = C^{-1} R_u$$

or

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \dfrac{c_{22}r_1 - c_{12}r_2}{c_{11}c_{22} - c_{21}c_{12}} \\ \dfrac{c_{11}r_2 - c_{21}r_1}{c_{11}c_{22} - c_{21}c_{12}} \end{bmatrix}$$

Generally $$u_i = \frac{r_i c_{jj} - c_{ij} r_j}{c_{ii}c_{jj} - c_{ji}c_{ij}}.$$

Since $$r_j = 1 - r_i,$$
$$c_{ji} = 1 - c_{ii},$$
$$c_{jj} = 1 - c_{ij},$$

substitution yields $$u_i = \frac{r_i - c_{ij}}{c_{ii} - c_{ij}},$$

which is the correction formula of Worlund and Fredin (1962) (except for differences in notation and terminology) that has been used in many two-class Pacific salmon stock identification studies.

Application to Sockeye Salmon Samples Taken in High Seas Sampling

A problem of interest to the nations bordering the North Pacific Ocean is the origin of sockeye salmon taken on the high seas. The rivers of origin of sockeye salmon south of the central Aleutian Islands in summer are of particular interest to the United States since an index of their overall relative abundance is used to forecast the numbers of mature fish returning to Bristol Bay in the following year (Rogers 1975). These fish are primarily of Bristol Bay origin (Hartt 1962, 1966; Hartt et al. 1975). Knowledge of the relative abundance of the various runs of the Bristol Bay stock south of the central Aleutians would be useful for forecast purposes and might provide insight into the high seas life history of the various runs.

In order to recognize age 2.2 immature sockeye salmon on the high seas in 1976, the freshwater growth patterns of scales from three of the major rivers in Bristol Bay were examined.[8] Scales from the smolt outmigrations of 1974 for the Kvichak and Naknek Rivers were used as learning and testing samples. For the Egegik River scales from age 2.2 adult fish returning to spawn in 1976 were used as learning and testing samples because smolt scales were unavailable. The freshwater scale patterns of fish from these runs were used to classify the sockeye salmon captured south of Adak Island during summer 1976 after having spent two winters in the ocean.

The scale patterns were examined under a microprojector of the type described by Dahlberg and Phinney (1968). The widths of the summer, winter, and plus growth zones were measured in terms of circuli counts and distance. The width of the widest circulus was also measured. Each scale character was then ranked over all classes (rivers) and the Kruskal-Wallis statistic (Kruskal and Wallis 1952) calculated. The difference between the average sum of ranks for each pairwise class combination was also calculated. On the basis of these statistics the scale characters providing the best univariate separation were selected for use in the polynomial discriminant method. Highly dependent scale characters were not used.

By examining the learning samples, six scale characteristics were chosen for use in the polynomial discriminant method: 1) The number of the circuli in the first winter growth zone, 2) the number of circuli in the second summer growth zone, 3) the number of circuli in the plus growth zone, 4) the width of the first summer growth zone, 5) the width of the second winter growth zone, and 6) the width of the widest circulus.[9] Learning sample sizes of 25, 25, and 24 for the Egegik, Kvichak, and Naknek River classes, respectively, were used to calculate the coefficients in the polynomial function for each class. The classificatory ability of these functions was then tested.

The relative test sample sizes for each class were determined by examining run size data. According to the average run sizes of age 2.3 salmon for the last 8 yr approximately equal numbers of fish from each class were expected to occur in the unknown sample. However, since the Kvichak River test sample size was twice that of the Egegik or Naknek River sample size, the fish in the latter test samples were given a weight of 2 when the a priori

[8]Age designation indicates fish which migrated to sea after two winters in freshwater and have spent two winters at sea. They are expected to return from the ocean primarily at age 2.3, or after spending three winters at sea.

[9]It should be mentioned that all data points were "normalized." That is, the mean and standard deviation for each scale character were calculated from the learning samples (all categories combined). All data points were then transformed by subtracting off the mean and dividing by the standard deviation for the appropriate scale character. This is done for numerical purposes.

probabilities were adjusted. After adjusting the a priori probabilities, we obtained the results given in Table 1. The classification matrix was then estimated:

$$\hat{C} = \begin{bmatrix} 0.800 & 0.040 & 0.167 \\ 0.080 & 0.740 & 0.208 \\ 0.120 & 0.220 & 0.625 \end{bmatrix}$$

where the subscripts of the matrix elements ($\hat{c}_{ij}$'s) were 1, 2, and 3 for the Egegik, Kvichak, and Naknek River classes, respectively. Seventy-two percent of the fish in the test group were correctly classified. The fish in the high seas sample were then classified with the adjusted polynomial discriminant method.

Of the 101 sockeye salmon, 25 were classified as Egegik River fish, 22 as Kvichak River fish, and 54 as Naknek River fish. The resultant vector was:

$$R_u = \begin{bmatrix} 0.267 \\ 0.222 \\ 0.511 \end{bmatrix}.$$

The estimated unknown vector was thus:

$$\hat{C}^{-1} R_u = \begin{bmatrix} 1.300 & 0.037 & -0.360 \\ -0.078 & 1.498 & -0.478 \\ -0.222 & -0.534 & 1.837 \end{bmatrix} \begin{bmatrix} 0.267 \\ 0.222 \\ 0.511 \end{bmatrix}$$

$$= \begin{bmatrix} 0.171 \\ 0.067 \\ 0.761 \end{bmatrix} = \hat{U}.$$

Based upon preliminary data for the 1977 Bristol Bay sockeye salmon run from the Alaska Department of Fish and Game, the actual unknown vector was:

$$U = \begin{bmatrix} 0.325 \\ 0.061 \\ 0.614 \end{bmatrix}.$$

The classification matrix correction procedure gave a slightly better estimate than the direct results of the polynomial discriminant method. The differences between the u_i's and the $\hat{u}_i$'s were due to bias and variability. (We are presently examining methods to reduce the variability of our $\hat{u}_i$'s.)

A problem with the high seas sample is that some of these sockeye salmon originate in rivers other than those considered. Although the three classes considered will account for nearly all of the age 2.2 sockeye salmon bound for Bristol Bay, some may be non-Bristol Bay fish. When the Bristol Bay runs are at a low point in their cycle, up to 20% of the high seas sockeye salmon at Adak Island may be non-Bristol Bay fish (Hartt et al. 1975). The possible bias from classifying the non-Bristol Bay fish into the classes established should be considered since 1977 is a low year in the sockeye salmon run cycle.

TABLE 1.—Results of the polynomial discriminant method on a known test group of Bristol Bay sockeye salmon. The a priori probabilities were 0.340, 0.332, and 0.328 for the Egegik, Kvichak, and Naknek River classes, respectively.

Calculated decisions	Correct decisions			Total (all calculated decisions)
	Egegik	Kvichak	Naknek	
Egegik	40	2	8	50
Kvichak	4	37	10	51
Naknek	6	11	30	47
Total (all correct decisions)	50	50	48	148

In conclusion, the polynomial discriminant method can be used to identify certain runs of sockeye salmon on the high seas by differences in freshwater scale growth patterns. Possibly the relative proportions of sockeye salmon that will be returning to inshore areas can be predicted. Eventually the method will be used to predict one year in advance the relative run sizes to the major Bristol Bay rivers by sampling these sockeye on the high seas.

Application to Inshore Fishery Stock Separation

A problem of interest to the Alaska Department of Fish and Game is the separation of stocks in commercial catches in inshore areas, particularly the separation of Kvichak, Naknek, and Egegik River sockeye salmon. The Division of Commercial Fisheries is collecting data on scale measurements for growth studies. They are interested in how well these data and the polynomial discriminant method can separate Bristol Bay sockeye salmon stocks.

Scale data from samples of the 1973 spawning escapement were examined. Each of two age-classes was examined separately. Distance and circuli counts to both the freshwater and saltwater annuli were examined for use in the polynomial discriminant method with the Kruskal-Wallis and multiple comparison procedures. The accuracy of classification for age 1.2 and age 2.2 sockeye salm-

on was examined for each age-group with known test groups.

The degree of separation for age 1.2 sockeye salmon is shown in Table 2. (Egegik River fish are historically insignificant in this age-class.) The scale characters providing this separation were: 1) the circuli count to the first annulus, 2) the distance to the first annulus, 3) the distance from the first to the second annulus, 4) the distance from the second to the third annulus, 5) the circuli count from the third annulus to the edge of the scale, and 6) the distance from the third annulus to the edge of the scale. Ninety-five percent of the fish in the test group were correctly classified.

The degree of separation for age 2.2 sockeye salmon is shown in Table 3. The scale characters providing this separation were: 1) the circuli count to the first annulus, 2) the distance to the first annulus, 3) the circuli count from the first to the second annulus, 4) the distance from the second to the third annulus, 5) the distance from the third to the fourth annulus, and 6) the circuli count from the fourth annulus to the edge of the scale. Seventy-seven percent of the fish in the test group were correctly classified.

Thus, the polynomial discriminant method can provide adequate separation with a given data base. The data collected for growth studies provide good separation in some cases. Sockeye salmon from the Egegik, Kvichak, and Naknek Rivers are distinguishable in terms of these scale measurements and it should be possible to estimate their relative proportions in catch samples.

TABLE 2.—Results of the polynomial discriminant method on 1.2 age Bristol Bay sockeye salmon from 1973. The a priori probabilities were 0.52 and 0.48 for the Kvichak and Naknek River classes, respectively.

Calculated decisions	Correct decisions		Total (all calculated decisions)
	Kvichak	Naknek	
Kvichak	18	0	18
Naknek	2	19	21
Total (all correct decisions)	20	19	39

TABLE 3.—Results of the polynomial discriminant method on 2.2 age Bristol Bay sockeye salmon from 1973. The a priori probabilities were 0.342, 0.330, and 0.328 for the Egegik, Kvichak, and Naknek River classes, respectively.

Calculated decisions	Correct decisions			Total (all calculated decisions)
	Egegik	Kvichak	Naknek	
Egegik	20	3	3	26
Kvichak	1	22	4	27
Naknek	5	1	14	20
Total (all correct decisions)	26	26	21	73

COMMENTS AND CONCLUSIONS

The key to successful implementation of the polynomial discriminant method is the choice of scale characters that reflect differences between the subpopulations of concern. The scale characters that are most likely different are those that are formed when the populations are geographically separated. Genetic and environmental influences on scale formation probably interact to create these differences. Although it is likely that no single characteristic will provide the required separation, a group of characteristics analyzed with multivariate techniques (e.g., the polynomial discriminant method) will often provide this required separation. The polynomial discriminant function technique requires no consideration of the underlying probability density functions for these scale characters because these density functions are estimated nonparametrically. Once the characters that provide the best separation are determined (by rank order comparison procedures in this paper) the discriminant function analysis may be implemented.

A learning sample is needed to calculate the discriminant function for each subpopulation. These fish comprising these samples must be collected before or after the populations intermingle (either as smolts or returning adults in the respective rivers). Learning samples must be taken from the same year class and freshwater age-group as the unknown (mixed) population if the scale characters are known or thought to vary from year to year. Using Specht's (1966) algorithm and the data from these learning samples, the coefficients in the discriminant functions are calculated. The next step is to appraise the effectiveness of these polynomial discriminant functions.

By classifying a group of test samples the proportion of correctly identified fish and the classification error rates can be determined. The proportion of correctly identified fish will likely be low until a good set of a priori probabilities is determined. As the a priori probabilities are adjusted to balance the classification error rates, the proportion of correctly identified fish will generally increase. The proportion of correctly identified fish, when the classification error rates are satisfactorily balanced, gives an indicator of the effectiveness of the polynomial discriminant method. The classification error rates specific to these final a priori probabilities are now estimated so that they may be corrected for when the polynomial discriminant

method is applied to the unknown mixed sample. This is done with the classification matrix correction procedure.

First, the fish in the unknown mixed sample are classified with the polynomial discriminant method (using the adjusted a priori probabilities). The proportions resulting for each subpopulation and the decision matrix allow simple algebraic solution for the estimated true proportions of the various subpopulations in the zones of intermingling.

Estimates of this type are often needed in particular management situations involving Pacific salmon. By using scale samples and the polynomial discriminant method, the proportions of the major classes present in areas where the subpopulations mix can be estimated. We have considered only two possible applications in this paper: high seas monitoring for predictive purposes and the analysis of catch samples. Many other possibilities exist for other situations and other salmon species: the timing of inshore runs could be examined in estuarine areas or in river systems, the continent of origin of salmon on the high seas could be examined (for those species or areas not already analyzed), or the intermingling of hatchery and native populations could be analyzed for certain fisheries. Since scale samples are relatively easy to collect and exchange and since computers are readily available to do the necessary calculations, the polynomial discriminant method is a flexible and practical tool for the racial analysis of Pacific salmon, particularly sockeye salmon.

ACKNOWLEDGMENTS

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EFFECTIVENESS OF ESCAPE VENT SHAPE IN TRAPS FOR CATCHING LEGAL-SIZED LOBSTER, *HOMARUS AMERICANUS*, AND HARVESTABLE-SIZED CRABS, *CANCER BOREALIS* AND *CANCER IRRORATUS*[1]

JAY S. KROUSE[2]

ABSTRACT

During 1976 a study was conducted to find an escape vent that would select similar sized lobsters as the rectangular vent, yet retain *Cancer* crabs ≥90 mm carapace width. Analysis of the size composition of research and commercial catches from experimental traps revealed that circular (58 mm in diameter) and rectangular (44.5 × 152.4 mm) vents release shorts and retain legal lobsters (≥81 mm carapace length) equally well, and decidedly more marketable-sized crabs were captured in traps with circular vents. Length-width relationship shows that crabs ≥90 mm carapace width have lengths ≥58 mm, thus precluding the possibility of marketable-sized crabs exiting through an opening 58 mm in diameter. Escapement studies for lobsters confirm that with the present minimum legal size of $3^3/_{16}$ in, a 58-mm diameter vent will select legals and allow most of the sublegals to escape.

Accordingly, the Maine Department of Marine Resources recommends that either circular (≥58 mm in diameter) or oblong (≥44.5 × 152.4 mm) escape vents be incorporated in all crab and lobster traps along the Maine coast.

Although rectangular escape vents are a very beneficial type of savings gear for the lobster fishery (Templeman 1939; Wilder 1945, 1948, 1954; Krouse and Thomas 1975; Krouse 1976), this vent does not retain marketable-sized rock crab, *Cancer irroratus*, and Jonah crab, *C. borealis*. Since these commercially important crab species are often caught incidental to lobsters, I undertook the present study to find an escape opening that would retain harvestable-sized crabs and have similar fishing selectivities for the lobster, *Homarus americanus*, as the rectangular vent.

In designing a trap to catch crabs and exclude lobsters, Stasko (1975) observed in laboratory tests that circular holes retained commercial-sized crabs yet allowed small lobsters to escape; however, the effectiveness of escape holes was not tested in the field. Jow (1961) demonstrated the advantages of circular escape openings in the trap fishery for Dungeness crab, *C. magister*.

In this paper I evaluate the relative efficiency of circular and rectangular vents by examining data from: 1) commercial and research catches compiled from vented and nonvented traps; 2) studies of escapement from traps; and 3) certain morphometric relationships of crabs and lobsters.

METHODS

From November 1976 through March 1977 a commercial fisherman recorded and provided me with catch data from traps with circular vents (58-mm diameter) fished alongside traps without vents. This experimental gear was arranged into two groups with four trawls [series of six traps spaced about 6 fathoms (11.0 m) apart with a surface buoy at either end] per group. In each group half the traps in a trawl had no vents, while the remainder had either single (end of trap) or paired (side of trap) vents depending upon the group (Figure 1B, D). Every time the fisherman hauled these traps he recorded the following information: 1) number of days traps were set between hauls; and 2) number of lobsters ≥81 mm carapace length, CL (keepers), and <81 mm CL (shorts) caught in the vented and nonvented traps for each trawl string.

From July through November 1976, project personnel fished commercial lobster traps near

[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 3-153-R.

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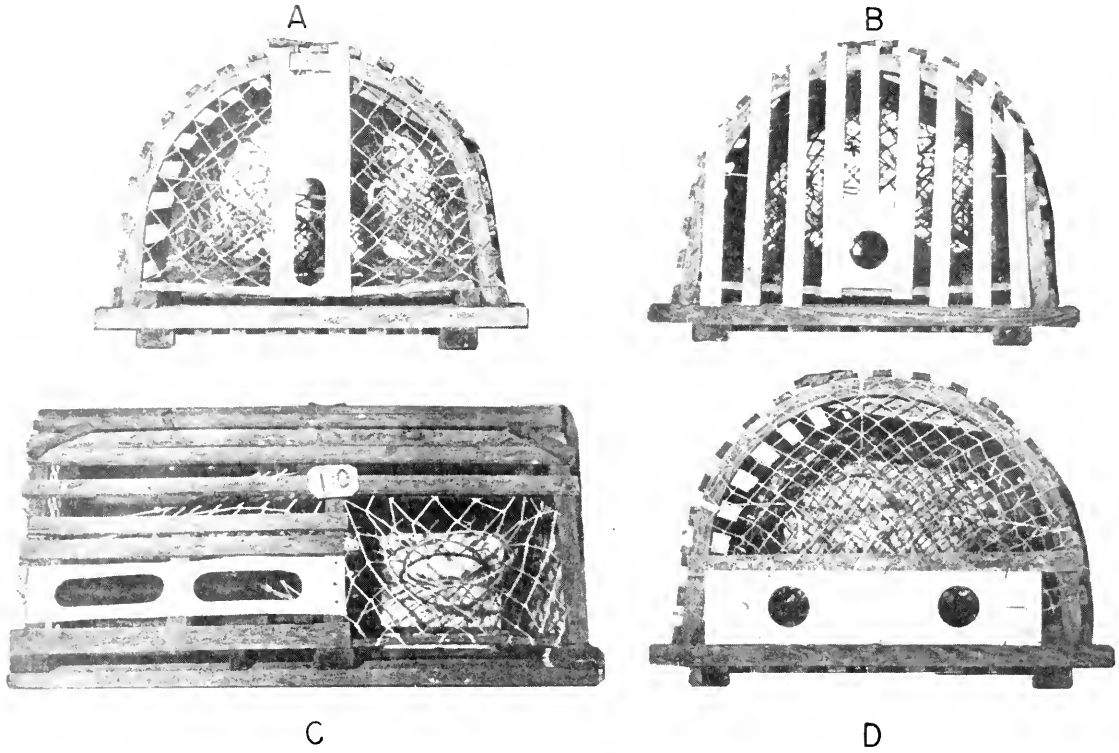

FIGURE 1.—Lobster traps having a rectangular vent positioned vertically (A) and horizontally (C) and single (B) and paired (D) circular vents.

Boothbay Harbor, Maine, with: 1) circular [58-mm (2.3 in) and 61-mm (2.4 in) diameter] vents; 2) vertical and horizontal rectangular [44.5 mm (1.8 in) × 152.4 mm (6.0 in)] vents; and 3) traps without vents. Carapace length of lobsters was measured from posterodorsal edge of eye socket to posterior margin of carapace and carapace width (CW) of crabs, distance between the two most posterior notches on the anterolateral border of the carapace, to the nearest millimeter.

Trap escapement was studied by placing lobsters of known sizes in traps with circular openings of 58, 60, and 61 mm in diameter. Side entrances of each trap were closed so escapement had to be via the vents. Traps were secured to the laboratory dock and usually checked daily for escapement for about a week.

To determine whether or not a crab or lobster could pass through a round opening of a given size, we correlated carapace length of lobsters with carapace height (CH), and the carapace width of crabs with carapace length. For 217 lobsters (sexes combined), ranging from 70 to 98 mm CL, carapace height was determined by positioning the lobster's ventral surface on a flat board and then measuring the greatest perpendicular distance from the board to the top of the carapace. Carapace length of crabs was measured from the anterior margin of the frontal region to the posterior border of the intestinal region. Measurements for the two *Cancer* species were treated separately due to the species disparities in body shapes. We recorded carapace length for 103 male rock crabs (females were excluded due to commercial unimportance) ranging from 90 to 122 mm CW, and 96 Jonah crabs (sexes combined) ranging from 96 to 132 mm CW.

RESULTS AND DISCUSSION

Lobsters in Research Gear

There are marked differences in size composition and number of lobsters caught in nonvented

TABLE 1.—Lobsters caught with nonvented and various types of vented traps from July through November 1976.

Vent type	Catch: Total no.	Catch: Sublegals: legals	Catch: Mean carapace length (mm)	Catch: Standard error	Catch effort: Legals per trap haul	Catch effort: No. of trap hauls	Catch effort: Months fished
Nonvented	749	4.3:1	76.2	±0.28	0.53	265	July-Nov.
Honzontal	198	0.6:1	83.9	±0.62	0.54	229	July-Nov.
Vertical	107	0.5:1	84.3	±1.05	0.56	129	July-Sept.
Circular:							
58 mm	25	0.6:1	82.8	±1.35	0.30	53	Oct.-Nov.
61 mm	42	0.4:1	85.9	±1.35	0.47	66	Sept.

and vented traps (Table 1). Vented traps caught fewer sublegal lobsters per trap-haul than nonvented traps (t-test, $P<0.01$).

The ratio of sublegal to legal lobsters did not differ among the four types of vents (t-test, $P>0.1$), with the exception of 61-mm circular vents which caught fewer sublegals than horizontal vents ($P<0.01$). As will be discussed later, the 61-mm hole is slightly oversize for a minimum size of 81 mm CL, thus some smaller legal lobsters and most shorts escape. Nevertheless this information suggests that circular openings are as effective as the rectangular vent (Krouse and Thomas 1975) in permitting escapement of short lobsters.

To further assess the relative efficiencies of the various vents, catch-effort values (numbers of lobsters per trap haul set over day, CPUE) were calculated and plotted for legal-sized and all-sized lobsters combined for each vent type (Figure 2). For this figure, 58- and 61-mm circular vent data were pooled because of the small sample size and similar catch values. Figure 2 graphically shows that the CPUE for legal-sized lobsters was similar for all vent types; however, for combined catches of legals and sublegals, the CPUE for nonvented traps was several fold greater. Thus, this indicates that all traps tested were about equally efficient in capturing legal lobsters; but, as to be expected, nonvented traps caught substantial numbers of short lobsters which probably would have escaped from vented traps. Most importantly, these data support an earlier conclusion that circular vents select about the same size lobsters as do rectangular vents.

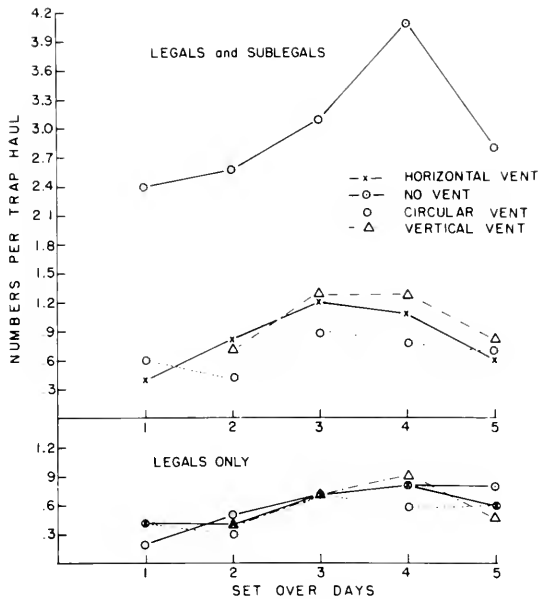

FIGURE 2.—Comparison of the number of lobsters (legals only; sublegal and legals combined) per trap haul set over day for lobster traps with rectangular (horizontal and vertical) and circular vents (58 and 61 mm combined) and traps without vents.

Lobsters in Commercial Gear

Catch data provided by a local lobsterman were compiled according to the following categories of gear: 1) end vented traps with a single circular hole of 58 mm diameter (Figure 1B); 2) side vented traps with paired round openings of 58 mm diameter (Figure 1D); and 3) two groups of nonvented traps (one for nonvented traps fished in the same trawl string with end vented traps and the second for traps paired with side vented traps). Comparisons of the CPUE and the ratios of sublegals to legals indicated that vented traps caught fewer sublegal-sized lobsters than the corresponding groups of nonvented traps (t-test, $P<0.01$) (Table 2). Higher CPUE values for vented traps show that circular vents are at least as efficient if not more effective in catching legal-sized lobsters than nonvented traps (t-test, $P<0.01$). In an earlier study Krouse and Thomas (1975) reported that traps with 44.5 × 152.4 mm rectangular vents were more successful in catching legal lobsters than traps with smaller vents or no vents.

TABLE 2.—Comparison of commercial catches of sublegal and legal-sized lobsters caught in traps with 58-mm circular vents and traps without vents.

Trap type	No. of sublegals trap haul	No. of legals trap haul	No. of trap hauls	Sublegals legals
Side vent double opening	0 98	0 56	144	1 8 1
No vent	2 33	0 49	132	4 7 1
End vent. single opening	1 80	0 72	144	2 5 1
No vent	2 76	0 57	144	4 9:1

Possible explanations for these disparities in efficiency may be that: 1) larger lobsters are less likely to enter traps containing several other lobsters, and/or 2) after legal lobsters are caught, their attempts to escape might be intensified as the density of lobsters increases within the trap.

Aside from the previously mentioned differences in the number of shorts caught per trap haul for vented and nonvented traps, end vents (single hole) captured 1.80 shorts/trap haul, whereas side vents (double hole) caught only 0.98 shorts/trap haul (t-test, $P<0.01$). Apparently, the additional vent will insure greater escapement.

Crabs in Research Gear

Since male *C. irroratus* attain larger sizes than females (Krouse 1972), commercial catches of this species are comprised almost entirely of males, so in the following analyses only catches of male crabs are considered. Variations in size composition of catches with different vents as manifested by width-frequency histograms (Figure 3) and mean carapace widths which are statistically different (Duncan's new multiple range test, $P<0.01$) indicate that: 1) fewer large crabs (≥90 mm CW) were captured in traps with horizontal vents (mean 91.2 mm CW); and 2) as many, if not more, larger crabs were collected with circular (mean 96.5 mm CW) than nonvented traps (mean 93.8 mm CW). According to this data, the 58-mm circular vent is at least as efficient in retaining marketable-sized crabs as the nonvented trap and certainly much more efficient than the horizontal vent. Escapement of subcommercial-sized crabs through circular openings has long been recognized by west coast States with Dungeness crab fisheries (Miller 1976). These states require crab traps to have one or two escape rings with diameters ≥4 in.

This situation was further evaluated by comparing the numbers (crabs ≥90 mm CW) per trap haul

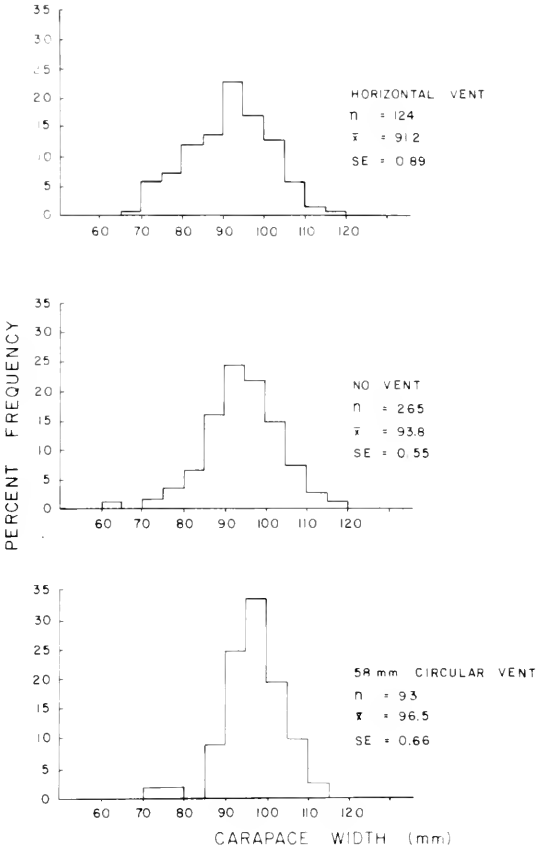

FIGURE 3.—Width-frequency distributions for male rock crabs caught with nonvented traps, traps with 58-mm circular vents, and traps with horizontal vents fished near Boothbay Harbor, Maine.

set over day for each of the different vents (Figure 4). CPUE values were highest for circular vents, lowest for horizontal vents, and intermediate for vertical and nonvented traps. Thus circular vents relative to the other vents were most effective in retaining crabs ≥90 mm CW and based on the following ratios of nonkeepers (<90 mm CW) to keepers (≥90 mm CW), selectively fished for larger crabs:

	Vent type			
	Circular	Nonvented	Horizontal	Vertical
Nonkeepers:keepers	1.5:1	2.5:1	4.1:1	5.7:1

Even though smaller crabs can egress quite readily from traps with horizontal and vertical vents, the above values at first glance appear to reflect the converse, i.e., more nonkeepers are caught in

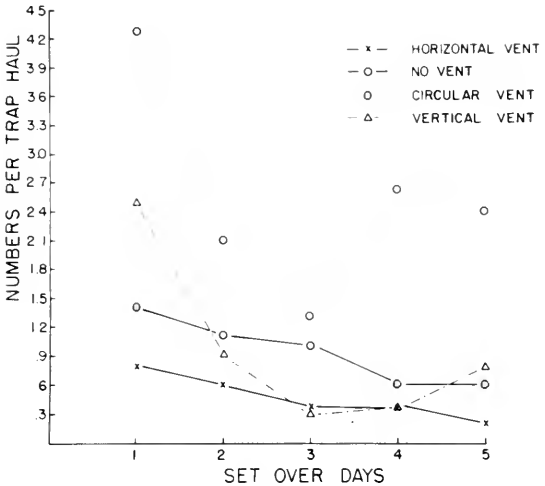

FIGURE 4.—Comparison of the number of rock crabs (≥90 mm carapace width) per trap haul set over day captured with nonvented and circular and rectangular (horizontal and vertical) vented lobster traps.

horizontal and vertical vented traps than in the circular and nonvented traps. Actually, horizontal and vertical vents, unlike circular and nonvented traps, also permit harvestable crabs to escape, resulting in reduced catches of keepers. Consequently, the proportion of nonkeepers to keepers is markedly greater for horizontal and vertical holes.

As evidenced by the aforementioned catch data, selectivity features of horizontal and vertical rectangular vents are similar; however, compared to circular vents they are unsatisfactory for catching large crabs. Prior to field testing, guided by opinions of some fishermen and our own thoughts, it seemed plausible that a vertically positioned rectangular opening (Figure 1A) might inhibit escapement of those crabs with carapace length exceeding the vent's width (smallest dimension). Of course, this was predicated on the assumption that when a crab encounters such a narrow upright opening it will only attempt to egress in a horizontal plane and will not tilt the body diagonally. However, laboratory observations and size composition of catches in traps with vertical vents indicate crabs will readily turn on end or side to exit.

Prior to this, only escapement through the vent itself has been discussed; this certainly does not preclude escapement through entrance heads. Diminishing CPUE values plotted against set over days in Figure 4, particularly for circular and nonvented traps where escapement could only result via the entrances, vividly demonstrate the crab's ability to escape as trap soak time is increased. Evidently, after the voracious crabs become satiated by eating the trap's bait, which frequently occurs in 1 or 2 days during the summer, the trap loses its attractiveness and crabs try to escape. Therefore, crab fishermen can maximize their catches by hauling their traps daily, particularly during periods of high catches. Contrasted to declining crab catches with greater soak times are lobster CPUE values which increase until 4 or 5 set over days, after which catches begin to diminish (Figure 2). Similar trends in CPUE data for commercial catches have been reported by Thomas (1973). Thus it appears that crabs are more adept at escaping from traps than lobsters.

Escapement and Morphometric Studies

Lobsters

Passage of lobsters through a round hole is related to the lobster's carapace height (greatest cross-sectional dimension) relative to hole diameter. Figure 5 shows that: 1) most legal-sized

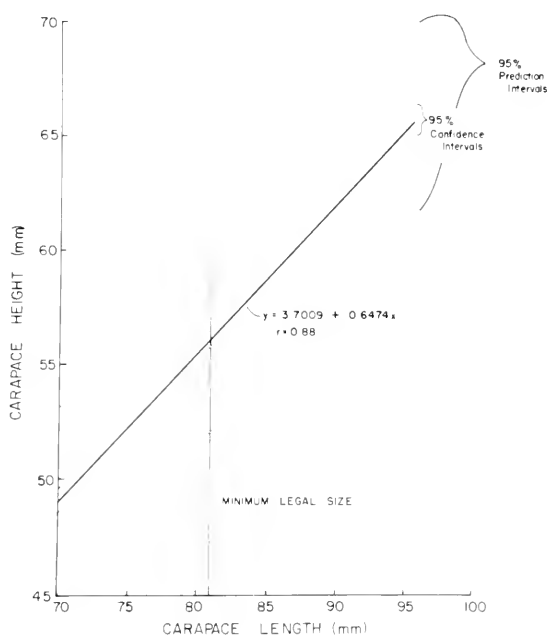

FIGURE 5.—Carapace length-carapace height relationship for lobsters with 95% confidence and prediction intervals.

lobsters with 81 mm CL had <58 mm CH; 2) about half those lobsters with 84 mm CL had <58 mm CH; and 3) lobsters ≥90 mm CL had ≥58 mm CH. Based on this relationship alone, it appears that many lobsters ranging from 81 to 89 mm CL would be able to squeeze through a 58-mm diameter hole; however, this is refuted by the previous sections on the commercial and research catches of lobsters with circular vented traps and the following discussion of escapement studies. Lobster escapement through a round opening cannot be accurately determined by carapace height alone since this measurement excludes the walking legs which contribute to the lobster's overall height or depth. Whether or not a lobster is successful in passing through a round hole will be determined not only by the lobster's greatest transverse dimension (carapace height plus protruding legs) but also by the lobster's ability to maneuver through a tight opening.

Obvious limitations with the aforementioned morphometric relationship caused me to seek an alternate approach to assess escapement. Thus, I decided to determine the largest size lobster that could be manually passed through a 58-mm diameter hole. Lobsters 81 mm CL passed through the hole rather easily following careful manipulation of the walking legs and 82-mm CL lobsters required considerable force, often causing bodily harm, while larger lobsters (>82 mm CL) could not pass through the opening.

Patterns of escapement for lobsters ranging from 78 to 84 mm CL from traps with 58-, 60-, and 61-mm diameter vents varied decidedly as depicted by retention curves in Figure 6. Only the 58-mm vent retained all legal-sized lobsters and still had reasonably high escapement of sublegals; whereas, the other vents which were merely 2 or 3 mm larger allowed legal-sized lobsters to escape. These data emphasize the importance of accurately producing the 58-mm opening, else the vent's desired effect will be lost.

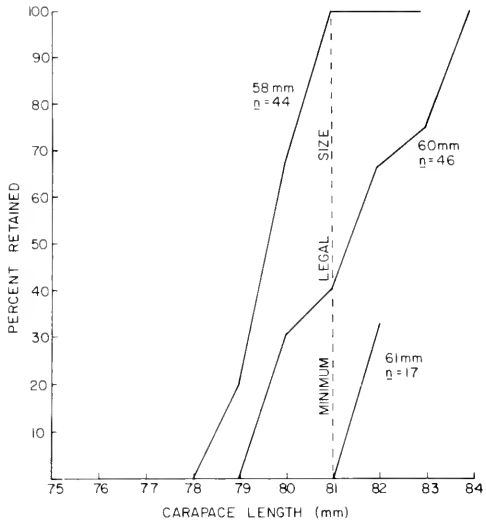

FIGURE 6.—Retention curves for lobsters placed in lobster traps with circular vents of 58, 60, and 61 mm in diameter.

Crabs

Carapace width-length relationships for *C. borealis* and *C. irroratus* graphically show that crabs ≥90 mm CW (commercially harvested size) have carapace lengths (dimension limiting escapement) which exceed 58 mm (Figures 7, 8). Accordingly, commercial-sized crabs of either species cannot egress through a circular opening 58 mm in diameter. In fact, if the vent diameter were increased to as large as 65 mm (certainly, an over estimate) to accommodate an upward shift in the lobster minimum size (Maine Department of Marine Resources recommends an increase from $3^3/_{16}$ to 3½ in CL by $^1/_{16}$-in increments annually over a 5-year period) this would have little or more likely no effect on catches of marketable crabs.

RECOMMENDATIONS

In view of the findings of this study and past investigations (Krouse and Thomas 1975; Krouse 1976), all lobster and crab traps fished in Maine waters should have a rectangular escape vent not less than 1.75 in (44.5 mm) by 6 in (152.4 mm) or at least two circular escape vents not less than 2.28 in (58 mm) in diameter. To insure maximum escapement of sublegal lobsters, vents should be installed next to the sill on the side or end of the trap's parlor section.

Although fishermen should certainly have the option to fabricate their own vents, provided that the prescribed dimensions are adhered to, the use of synthetic, prefabricated vents is highly recommended (Krouse and Thomas 1975). Recently, a plastics manufacturer assured me that vents could be produced and retailed for about 20¢ each. At this low price and with today's high price of laths (about 5¢ each), if a synthetic vent replaces two laths every 3 yr, then after 6 yr the original cost of

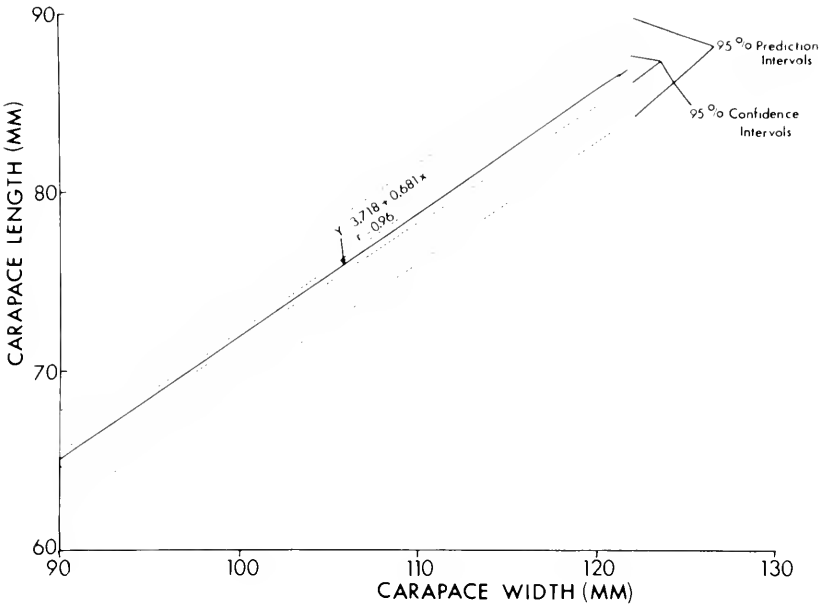

FIGURE 7.—Carapace width-carapace length relationship for male rock crabs with 95% confidence and prediction intervals.

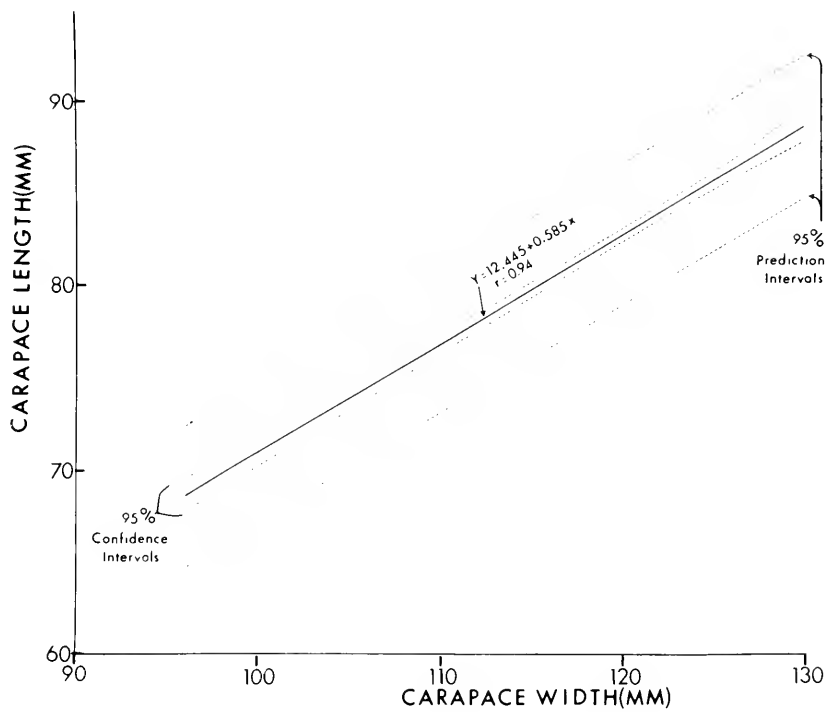

FIGURE 8.—Carapace width-carapace length relationship for Jonah crabs with 95% confidence and prediction intervals.

the vent will be defrayed by the replacement cost of the laths, resulting in a cost savings.

Therefore, those fishermen interested in capturing only lobsters and, perhaps, minimizing their crab catches, would be encouraged to use rectangular vents, while fishermen interested in both lobsters and crabs or solely the latter should employ circular vents.

ACKNOWLEDGMENTS

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SCHOOL STRUCTURE OF THE SQUID *LOLIGO OPALESCENS*

ANN C. HURLEY[1]

ABSTRACT

The squid *Loligo opalescens* forms schools which are similar in many respects to those of obligate schooling fishes. These schools are marked by parallel orientation of individuals and strong cohesiveness. Laboratory experiments indicate that the main sensory modality regulating schooling is vision. Squid on opposite sides of a clear rigid Plexiglas barrier readily schooled. The structure of schools of six squid depended on size of individuals and was modified by environmental disturbance. Parallel orientation was weaker in schools of smaller squid (ca. 7 cm dorsal mantle length) than it was in larger ones (ca. 12 cm). In the field, *L. opalescens* schools are composed of uniformly sized individuals. Laboratory experiments designed to determine whether this was due to actual size selection were inconclusive, but they did suggest mechanisms which might be important in determining squid position in the school.

Considerable effort has been spent in understanding the schooling behavior of fish in terms of physiological mechanisms and possible survival value and ecological consequences. (See reviews by Radakov 1973 and Shaw 1970, 1978.) Virtually no work has been done on schooling behavior of invertebrates which occur in the same environments as schooling fish. The most evident schooling invertebrates in the pelagic environment are the squid. Squid and fish play very similar ecological roles and the two groups of organisms possess a large number of similarities. (See Packard 1972, for a discussion of convergent evolution.)

Loligo opalescens is common off the west coast of North America with a reported range from Baja California to lat. 55°N (Fields 1965; Bernard 1970). Relatively little is known of the behavior or general ecology of *L. opalescens* in spite of the fact that there is a fishery for this species in California. The fishery is based primarily upon the tendency of squid to spawn in large aggregations in shallow water (McGowan 1954; Fields 1965). Very little is known about the distribution or location of newly hatched squid as well as squid in later stages of life. Attempts to catch the juveniles have often been unsuccessful (Okutani and McGowan 1969) and only recently have attempts been made to catch nonspawning adults. Even though field data are difficult to obtain, it is possible to keep both juvenile (Hurley 1976) and adult *L. opalescens* alive in the laboratory. Schooling in the laboratory was examined to provide insights about the function of schooling in squid.

METHODS

The squid used in the behavioral studies were obtained either by dipnetting them after they had been attracted to an underwater light or by purchasing them from a local bait dealer. In the laboratory, the squid were maintained in a 3-m diameter circular tank with rapidly circulating seawater. They were fed irregularly on small fish (either mosquitofish, *Gambusia affinus*, or goldfish, *Carassius auratus*). Mosquitofish were taken much more readily than were the goldfish. Occasionally, the squid could be trained to take dead food. This was accomplished by first getting them to accept live fish and by then throwing dead fish in along with the live ones. In this manner, the squid could also be coaxed to accept pieces of frozen northern anchovy, *Engraulis mordax*. If the squid were undamaged when they arrived at the laboratory and there was an abundant supply of small fish available, it was relatively easy to keep them for over a month.

Experiments designed to examine various aspects of schooling behavior were run in a 2 × 3 m rectangular Plexiglas[2] tank which was filled to a depth of 0.4 m. The tank was painted flat white and the primary source of lighting (in addition to general room illumination) was provided by

[1]Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

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

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fluorescent lights placed around the perimeter of the tank which shone through the walls. This provided even, diffuse light in the tank. The water in the tank was noncirculating.

Schooling behavior was recorded on Tri-X film using a 35 mm camera with motor drive and a variable setting automatic timer. A mirror was placed above the tank and pictures were taken of the squid by photographing the surface image reflected in the mirror. A black plastic barrier surrounded the experimental tank. A small hole in the barrier allowed observations to be made of the squid without disturbing them. Exact methods, timing of pictures, etc. varied with the experiment and will be described in the appropriate section.

After the films were developed, they were analyzed using a Scientific Data Products data tablet (Graf-Pen) coupled with a PDP 11-45 computer. The data tablet is a set of microphones placed at right angles which record the sound produced by an electrical spark made by a special marking pen. The x and y coordinates of a point were relayed to the computer by pressing the pen down on the tablet at that point. This device allowed the recording of large amounts of squid position data. In each frame, the tip of the tail, the tip of the outstretched arms, and a point midway between the two eyes were recorded for each squid. Other information, such as the position of barriers, was recorded in the same way. Measurements taken from the photographs were subsequently converted to real distances by multiplication by appropriate scale factors.

Students of schooling have examined school geometry both as a two-dimensional system on a horizontal plane (Breder 1959; Williams 1964; John 1964; Hunter 1966, 1968; Van Olst and Hunter 1970) and as a three-dimensional structure (Cullen et al 1965; Symons 1971a, b; Pitcher 1973). Since squid schools do have a three-dimensional structure in nature, a three-dimensional analysis will eventually be necessary to determine all of the structural details of the school. A three-dimensional analysis, however, is much more difficult than a two-dimensional analysis. It was felt that a two-dimensional analysis would suffice to examine certain aspects of squid schooling behavior. In these experiments, the squid were very nearly confined to a two-dimensional plane by the shallow water depth in the experimental tank. Observations of small schools (up to six squid) in a deeper tank (1 m depth) indicated that the two-dimensional structure observed in the experimental tank was not uncommon.

Three indices were chosen to quantify the angular orientation of individuals in a school, the overall shape of the school, and the distance between neighboring individuals in a school. These indices were proposed by Hunter (1966) and he includes a detailed discussion of their properties. The three indices are:

1. Mean separation distance: An average of the horizontal distances separating each squid from every other squid in the school. It is influenced by school shape, distance between neighboring squid, and number of squid in the school. Distances between all possible pairs of squid are measured and these values are averaged. Distance is measured between the two closest points on the midline of the bodies (including outstretched arms) of the two squid.
2. Mean distance to nearest neighbor: An average of distances from each squid in the school to its nearest neighbor. The measurement is made between the two closest points on the midline of the bodies (including outstretched arms) of the two squid. The same measurement is used twice if two squid are closer to each other than to any other squid.
3. Mean angular deviation: This is a measure of the differences in orientation among squid within a school. The heading of each squid is determined and the resultant direction of the school is computed by assigning each squid a value of one and adding the headings vectorally. The mean number of degrees individual squid deviated from this resultant direction of the school was calculated as the index of orientation.

One difference between squid and most of the schooling fish which have been studied is that squid readily swim both forward and backward. Thus, a squid with an orientation that was 180° out of phase with the rest of the school might still be swimming with the rest of the school. For this reason, one orientation measure was calculated which regarded the squid as a line segment rather than as a directed vector and measured the smallest angular deviation between line segments. Such measurements were rarely different from measurements made considering the orientation of the squid and therefore will not be considered further in this paper.

Where measurements of squid length are given, they are of dorsal mantle length from tip of the pen to the tip of the tail. The total length of the squid (including arms but excluding tentacles) is about 1.3-1.5 times the dorsal mantle length (Fields 1965).

RESULTS

Response to Disturbance

One set of factors that caused changes in schooling can be grouped under "external disturbances." These included introducing objects (such as a net) into the water near the squid or tapping on the side of the tank. The typical response was for the squid to group more tightly and, in cases where it was not already marked, to increase the degree of parallel orientation. The amount of change in schooling behavior and the temporal characteristics of this change depended upon the nature and intensity of the disturbance and upon its duration.

One attempt at quantifying the stimulus involved placing an aquarium air stone in the tank. Pressurized air delivered to this air stone in differing amounts and duration produced a stream of bubbles which could be used as a disturbance stimulus of varied intensity and duration. A small stream of bubbles produced little squid reaction, while vigorous water action due to the bubble stream produced marked changes in behavior. Figure 1 shows the changes in three of the schooling indices in response to a moderate disturbance caused by turning on the air bubble stimulus. The degree of parallel orientation, which was already pronounced, did not change appreciably. But the squid did draw noticeably closer together.

Schooling Structure as a Function of Squid Size

Six squid of nearly equal size were haphazardly taken from the holding tank and placed in the experimental tank. The squid swam in this tank for an hour before measurements were made. With the exception of one experiment, a picture was taken of the squid every minute for approximately 1 h. During this other experiment, a picture was taken every 10 s for 10 min. This set of experiments was conducted during the daylight hours of two different days. All of the squid used in this set of experiments had been captured on the same night.

There was a decrease in the mean angular deviation as the size of the squid increased (Table 1). Since small values of the mean angular deviation index are associated with increased parallel orientation, the degree of parallel orientation is greatest in schools composed of large individuals. Even in the case of the small individuals, however, the value of the index does not approach what would be expected if the squid were each orienting in a random direction. In a simulation of 1 million values for six randomly oriented fish, Hunter (1966) found that the mode of the frequency distribution was 69°.

Although the average values for mean angular deviation do give a measure of average departure from parallel orientation for a whole experiment, they do not give an indication of how variable a particular group of squid is in its orientation over time. For example, an experiment of 30 pictures and an average value of the mean angular deviation index of 20° could have had all of the 30 values close to 20°. This would indicate a consistent moderate degree of parallel orientation over time. On the other hand, such an average value could also come from a situation where the squid had strong parallel orientation part of the time and were much more loosely oriented the rest of the time (e.g., the index value could have been 10° on 15 frames and 30° on 15). This kind of difference can be detected if a measure of the variability of the mean angular deviation index for each experiment is calculated. The variability (standard deviation, SD, Table 1) increased with decreasing squid size, indicating that not only do the smaller squid not orient on the average in as parallel a manner as larger squid, but they are also more temporally variable in their orientation. This difference can also be seen if individual experiments are examined. Figure 2 shows the values for mean separation distance and mean angular deviation

TABLE 1.—Relationship between average size of *Loligo opalescens* and parallel orientation and separation of individuals in the six-squid experiments. Each index was calculated for each frame.

Group number	Mean mantle length (cm)	No. frames examined	Mean angular deviation index (degrees)		Mean separation distance index (cm)	
			$\bar{x}$	SD	$\bar{x}$	SD
1	7.5	44	32.0	18.4	32.3	26.5
2	7.6	58	29.0	15.3	25.6	8.0
3	7.7	60	18.1	10.7	16.2	4 5
4	9.7	19	18.5	5.7	14.0	4.2
5	9.7	62	16.2	6.2	18.7	5.2
6	10.2	69	17.2	6.6	20.9	5.0
7	11.9	65	11.1	5.6	18.5	4.0
8	12.0	55	9 6	2.8	15.3	2.7
9	12.0	46	9.1	4.2	13 8	3.0

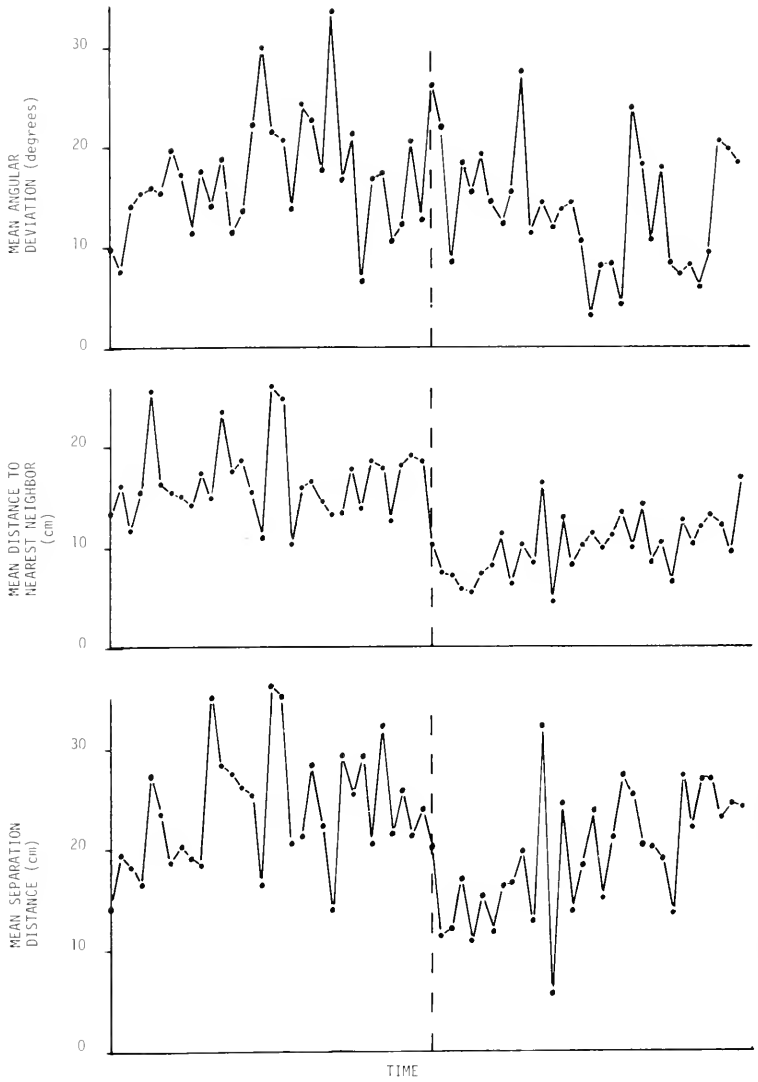

FIGURE 1.—Values of schooling indices for a school of six *Loligo opalescens* before and after disturbance (turning on bubbler). Dashed line indicates when air was turned on. Pictures were taken every minute for 64 min.

for two (Groups 3 and 7) of the experimental runs summarized in Table 1. The parallel orientation is stronger and the variability less in the larger squid (Figure 2C, D). The mean separation distance index is not as clear a function of size (Table 1; Figure 2A, B).

Schools in the Ocean

Very little is known of the natural behavior of *Loligo opalescens* when it is not in large mating schools. In many areas, there often is a large concentration of squid in the vicinity of the deep-scattering layer (C. Recksiek, Moss Landing Marine Laboratories, Moss Landing, CA 95039, pers. commun., October 1976) and large layered concentrations of *L. opalescens* have been reported by those involved in submersible exploration (A. Flechsig, Sea Grant Marine Advisory Service, University of California at San Diego, La Jolla, CA 92093, 1973). There is evidence to indicate, however, that *L. opalescens* is often found in much smaller schools and that these schools contain a narrow size range of individuals. Fields (1965) presents data on the uniformity of size of young squid taken from the same fish catch (presumably the same squid school) and speculates that the size ranges in the schools he observed represent approximately one-half or less than one-half of a year's growth.

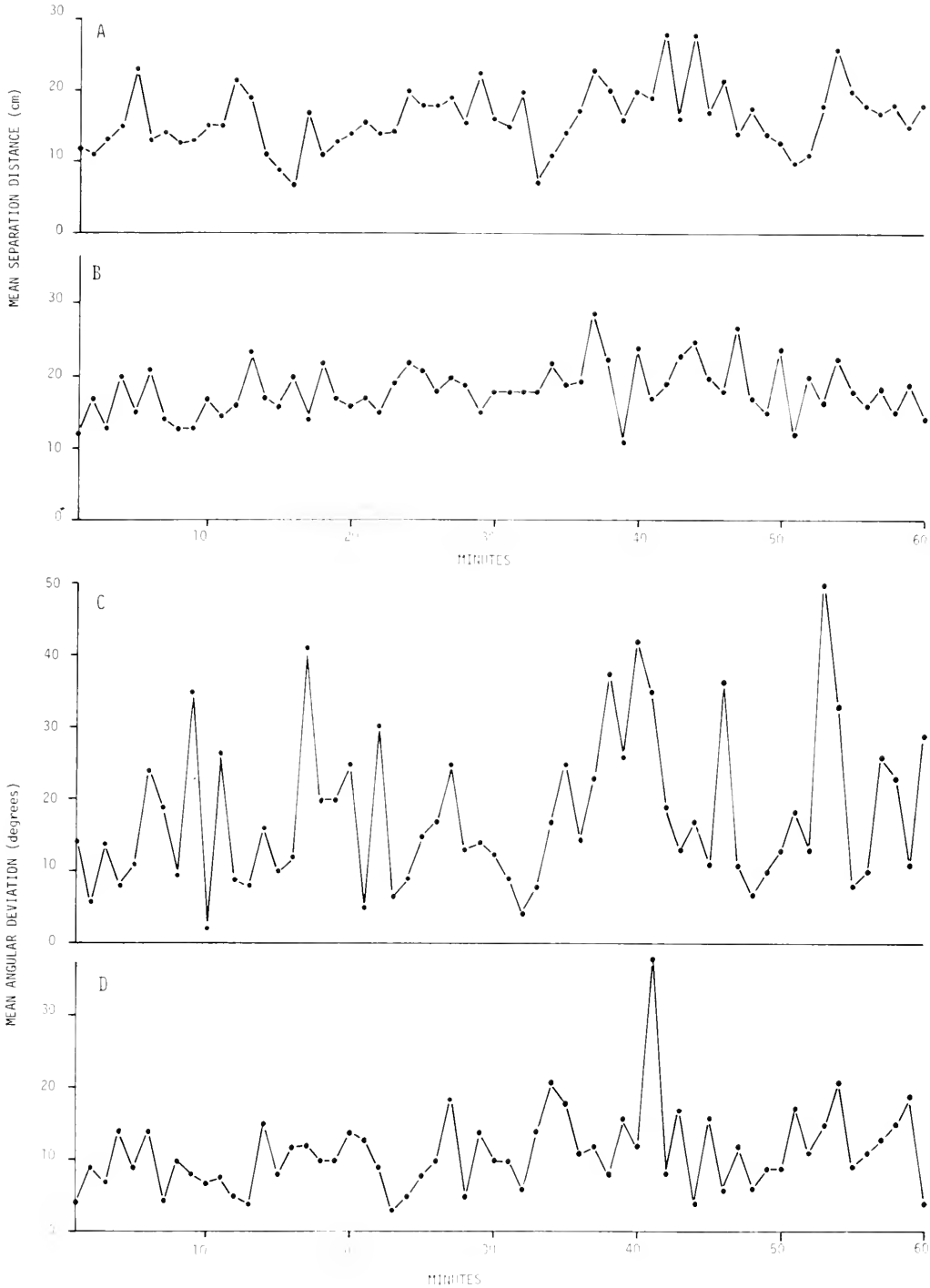

FIGURE 2.—Values of mean separation distance and mean angular deviation for two (Groups 3 and 7) of the experiments presented in Table 1. Mean size of *Loligo opalescens* in the experiment represented in A and C was 7.7 cm mantle length. Mean size of squid in the experiment represented in B and D was 11.9 cm mantle length.

I also obtained data on the uniformity of size in individuals of the same school. The squid were caught during a 1-wk period in August in locations ranging from San Diego to Santa Catalina Island, Calif. A night-light was placed off the stern of the ship in the center of an L-shaped 3-m long mesh net. Squid were attracted to the light and would rush into the net. The net was then raised and the squid could be removed with dip nets. The "schools" were all of the squid which swam into the net at the same time. Squid caught during this period ranged from 5.8 to 17.3 cm dorsal mantle length. But for a given school, they were much more uniform in length. The average size range for 29 schools of 2 to 32 individuals was 2.5 cm.

Maintenance of School Structure and Orientation

Experiments in the laboratory have indicated that vision is sufficient sensory input to mediate schooling behavior. Squid on different sides of a clear, rigid Plexiglas barrier will readily school with each other and they appear to maintain the same type of parallel orientation that is present in normal schooling behavior. Preliminary experiments using such Plexiglas barriers were run to try to elucidate the mechanisms by which spacing is maintained.

Two-Squid Experiments

Experiments were run to determine whether squid would school in the same manner with or without a clear Plexiglas barrier in place. Measurements were obtained for squid swimming together and for the same squid swimming on opposite sides of a Plexiglas barrier which divided the tank into two compartments. The order of the treatment was randomized for each pair of squid. Squid ranged in size from 7 to 13 cm mantle length. For a given experiment, the two squid were of similar length. Pictures were taken of the squid in each treatment every 10 s for 3 min after they first came together and again every 10 s for 3 min after the squid had been left undisturbed for 15 min. If the squid did not come together to within at least 0.5 m within 1 min, the experiment was terminated.

Table 2 shows the results of five such experiments. The first 3-min periods have been compared with each other, as have the later runs. This was to see if the pattern of schooling changed after the squid became more adapted to the experimental regime. This table presents results for the median nearest distance between the two squid for each run and for the median separation angle for these same runs. Separation angle for each frame is simply a measurement of the angle between the two squid and is a measure of orientation (0° separation angle indicating parallel alignment facing the same direction).

TABLE 2.—Median nearest distances and median separation angles for two-squid (*Loligo opalescens*) experiments.

Item	With barrier	Without barrier	Difference[1]
Nearest distance (cm) first 3 min	20.6	16.2	$P = 0.05$ barrier greater
	11.3	6.6	$P<0.01$ barrier greater
	38.6	11.65	$P<0.01$ barrier greater
	14.9	7.9	$P<0.01$ barrier greater
	13.8	6.4	$P<0.01$ barrier greater
Nearest distance (cm) second 3 min	24.2	15.8	$P<0.01$ barrier greater
	18.4	6.3	$P<0.01$ barrier greater
	23.9	18.35	$P<0.05$ barrier greater
	14.35	13.1	$P<0.05$ barrier greater
	12.5	8.2	$P<0.01$ barrier greater
Separation angles (degrees) first 3 min	16.4	52.7	$P<0.01$ barrier less
	24.3	11.2	$P<0.05$ barrier greater
	75.1	21.0	$P<0.01$ barrier greater
	21.2	12.2	NS[2]
	17.0	30.9	$P<0.05$ barrier less
Separation angles (degrees) second 3 min	28.2	15.4	$P<0.05$ barrier greater
	15.4	13.6	NS
	19.1	18.0	NS
	25.4	18.3	NS
	11.1	24.9	$P<0.05$ barrier less

[1]Significance of difference in medians from Mann-Whitney *U*-test.
[2]NS = no significant difference, $P > 0.05$.

The barrier has an effect upon the separation distance between the two squid. In all cases, there was a significant difference between the distance between squid with and without the barrier. When the Plexiglas barrier was present, the squid tended to space themselves farther apart. There is not a clear relationship between angular separation and the presence of the barrier. Of the six runs showing significant differences, three had greater median separation angles with the barrier in place and three had greater median separation angles when the barrier was not present.

Three-Squid Experiments

The experimental tank was divided crosswise into three equal compartments (1 × 2 m each) by clear Plexiglas partitions. A squid was chosen from the holding tank and was placed in the central compartment. Then a squid for each of the outer compartments was selected. These squid were assigned at random to each of the outer compartments. The squid were allowed to adapt to the experimental situation for 15 min and then were filmed for 5 min (one picture every 10 s). The two

outer squid were then switched from one outer compartment to the other and the squid were again allowed to adapt for 15 min. They were then filmed for 5 min (once every 10 s). Squid in these experiments ranged from 9.2 to 15.3 cm mantle length.

It was hoped that this experimental design would indicate whether the center squid, if given a choice, would choose to school with a larger or smaller squid or one closer to its own size. One way to determine whether such a choice is being made would be to determine whether the center squid spends more of its time closer to one outer squid than to the other. Each 5-min run was considered as a unit and each frame was scored according to which outer squid the center squid was nearest. For each run, the data were compared with a binomial distribution which assumed that the center squid had an equal probability of being closest to either outer squid. Of the 17 runs, 16 showed a significant deviation from the expected binomial distribution ($P \leq 0.05$ for 1; $P \leq 0.01$ for 15). These 16 runs were now grouped according to whether the center squid was closest to the larger or smaller outer squid. In 8 of the 16 cases, the center squid was nearest the larger outer squid, while in the other 8 cases, it was nearest the smaller squid. There is no evident preference for large versus small squid. The data can also be arranged to determine whether the center squid spent most of its time near the squid closer to its own size. There were 14 runs for which it was possible to say that the center squid was closer in size to one of the outer squid. Of these 14 runs, the center squid was significantly nearer to the squid closer to its own size 9 times and nearer to the squid farther from its own size 5 times.

These experiments may be viewed in another way by looking at the absolute position of the squid in the tank. The nearest distances of the squid to the Plexiglas barriers were calculated for each frame. These data are summarized in Figure 3 for the 17 runs. The side squid usually are very near the barrier which separates them from the center compartment, while the center squid varies his position within the center compartment, but approaches the Plexiglas barriers much less often.

DISCUSSION

Pelagic fish and squid represent a striking case of convergent evolution, not only morphologically (Packard 1972), but behaviorally as well. One aspect of behavior where this is particularly apparent is schooling. Since many of the same ecological pressures exist for both pelagic groups, it is not surprising that some sort of schooling behavior would have developed in both fish and squid. What is surprising, given the very different physiology and mode of locomotion, is that so many aspects of this behavior are the same.

Loligo opalescens fits Breder's (1967) definition of obligate schoolers. Single *L. opalescens* are rarely caught in the field, and they immediately come together when placed in a tank in the laboratory. As has been reported for many species of fish (Radakov 1973), *L. opalescens* schools consist of individuals of approximately the same size. It has been suggested that the reason that fish school in such groups has to do with swimming speed. Small and large individuals would not swim at the same speed and thus would not normally stay together. This is possibly also true for squid, but data on the swimming speed of large and small *L. opalescens* are not available to substantiate the argument. For several reasons, the swimming speed hypothesis seems less plausible for squid than for fish. In schools of fish which show parallel orientation, the fish continually maintain forward motion and thus swimming speed is likely to be an important factor. But field and laboratory observations have indicated that individuals in squid schools spend much of their time hovering in the same position in the water column with only

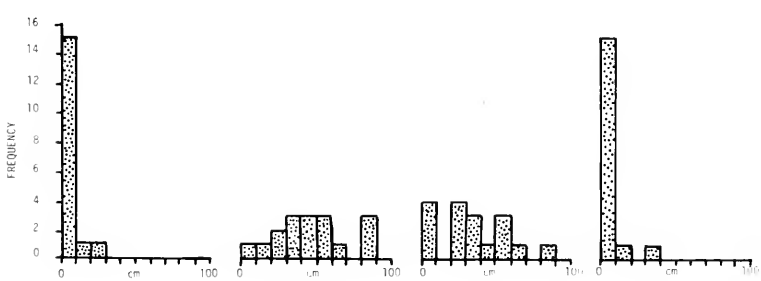

FIGURE 3.—Histograms of mean nearest distance between *Loligo opalescens* and barrier in the 17 three-squid experiments. Distances are broken up into 10-cm intervals. From left to right: left outer squid to left barrier, center squid to left barrier, center squid to right barrier, right outer squid to right barrier.

slight backward and forward motion caused by jets of water from the siphon. Even when disturbed, the squid do not make long extended swims which would tend to sort out those of differing swimming ability. In the field, the most common response of a squid school to a disturbance (the presence of a scuba diver or a shark) is to clump closer together and move off a slight distance. On one occasion when I was diving in a large spawning school (several thousand individuals), the squid executed the same type of maneuver that has been reported for fish schools. Instead of moving off, the school completely enclosed me, leaving a spherical space of approximately 3 m radius around the "predator."

One other piece of evidence suggests that it is not differences in swimming speed alone which cause the squid to school according to size. While diving in the Bahamas in the Hydrolab underwater habitat, we observed a school of squid which routinely visited the habitat. This school was composed of *Doryteuthis plei*, a species which quite closely resembles *L. opalescens* and presumably has similar swimming ability. This school consisted of seven squid and, in this case, was not composed of individuals of the same size, the largest individual being at least two times the length of the smallest individual. We chased this school several times but were never able to force them to separate. The smallest squid maintained the same swimming speed as the largest squid.

It is possible that squid maintain schools of individuals of a fairly narrow size range because of social factors. Generally, workers studying schooling have assumed that all of the fish in a school may be treated as equivalent individuals in the production of the behavior and that there is no social structure in the schools. In fact, some workers have suggested that schooling is really just a modified form of individual cover-seeking behavior (Williams 1964; Hamilton 1971). This assumption of equality of individuals may be an untenable one for squid schools. In the field, Hochberg and Couch (1971) observed signaling by some members of a school of *Sepioteuthis sepioidea* which they felt prevented other squid from joining the school. Furthermore, in the laboratory, I have observed complicated agressive interactions in *L. opalescens* which certainly demonstrate that all squid cannot be considered behaviorally equivalent individuals at all times (Hurley 1977).

One aspect of schooling in fish which has been emphasized by many workers is that the structure of schools may change as a function of the age or the physiological condition of the fish. Van Olst and Hunter (1970), for instance, found that in five species of marine fishes, schools of young fish were less compact and showed greater differences in angular headings than did schools of adult fish. In addition, Hunter (1966) showed that distances between jack mackerel tended to increase with food deprivation, while Keenleyside (1955) noticed that sticklebacks were more densely packed in a school when well fed than when starved.

I attempted to determine whether similar phenomena were observable in squid schools. Schools of small squid (7-9 cm mantle length) gave the impression of being less cohesive than schools of larger squid (13-15 cm mantle length). This was supported to some extent by the quantitative measurements, particularly those of angular orientation. The variability was also higher for all of the indices for the smaller squid. It has been suggested for fish (Van Olst and Hunter 1970) that the observed change with size could have been an adaptation to the higher food requirements of the juvenile fish. This speculation is supported by observations that a number of species school less cohesively under conditions of food deprivation. The same explanation may also hold for squid, but my existing data do not support it. I ran two experiments in which schools of six squid were filmed before and after feeding. In one experiment, there were no significant differences in the schooling indices before and after feeding, while in the other, there was significantly less school cohesion and parallel orientation after feeding. In any event, it is not possible to guess which factors are instrumental in this increased cohesiveness and consistent geometry.

As is the case for fish, vision seems to be the primary sensory system used in squid schooling. Squid will readily school across a clear, rigid Plexiglas barrier, although they tend to stay somewhat farther apart than they normally would. Investigators dealing with fish also found that the presence of a clear, rigid barrier caused abnormalities in the spacing between individuals, in some cases increasing the fish-to-fish distance (Cahn 1972) and in some cases decreasing it (Shaw 1969). These workers speculated that this change was due to lack of lateral line input and a resultant loss of information concerning the position of the adjacent fish. Squid do not have a similar extensive vibration-sensitive system, although they may be able to detect vibrations with their stato-

cysts. In the case of *L. opalescens,* the most likely explanation for this change in spacing is that the presence of the barrier physically limits the extent to which each squid can compensate for the other individual's movements. In the experimental tank, squid seemed to differ in their motivation to school. When the barrier was not present, a squid with a strong tendency to school could always maintain proximity to another squid. But if the barrier were present, that squid could only follow another squid as far as the barrier and had to remain there until the other squid returned.

I had hoped that the experiments with the three squid separated by Plexiglas barriers would give some clue as to whether the squid actively chose to school with individuals of the same size, but the results were inconclusive. The results did indicate, however, a possible mechanism for maintenance of spacing within a school. The center squid tended to stay toward the middle of the compartment, while the side squid maintained positions very near the Plexiglas barrier. It is possible that the center squid was attempting to equalize the visual angle subtended by the squid on each side, while the outer squid were attempting to get into positions with squid on each side. The measurements of visual angle which I can get from my photographs are not accurate enough to determine whether this is happening. If outer squid are continually trying to achieve a position where they have squid on either side of them, individuals in a school should be continually shifting positions. Casual observations have indicated that this does happen some of the time; but at other times, the individuals maintain the same positions relative to one another.

An area where a comparison of squid and fish schooling may be useful is in the speculation concerning the evolution of the schooling behavior and its possible advantages. Many recent papers have concentrated on the hydrodynamic advantages of fish schooling (e.g., Breder 1976) and base their explanations of many of the details of school structure on the fish mode of tail-flip locomotion and the vortices which are subsequently created. Van Olst and Hunter (1970) suggest that the typical nearest neighbor distance in fish schools is about one-half a body length and that this distance may be explained by considering the amplitude of the tail beat in swimming. It is interesting that in squid, with their very different mode of locomotion (jet propulsion as opposed to tail flips), the spacing between nearest neighbors is still maintained between one-half and one body length in undisturbed squid.

Other investigators have speculated that a primary function of schooling is as a defense against predation. (See reviews by Shaw 1970 and Radakov 1973.) Squid have many of the same reactions to disturbance that fish do. They both clump more closely together as a result of disturbance and both have been seen to surround their predators. Further evidence which suggests that predator defense may be an important function of squid schooling comes from the development of the behavior in juvenile squid. In the course of rearing *L. opalescens* (Hurley 1976), I made observations on schooling behavior. The newly hatched squid appeared to have no attraction to each other, but after 6 or 7 wk schooling was occasionally observed. This schooling was only evident in response to disturbance (tapping on the tank or putting a net into the water). When the squid were feeding undisturbed, there was no obvious schooling behavior.

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NORTHERN ANCHOVY SCHOOL SHAPES AS RELATED TO PROBLEMS IN SCHOOL SIZE ESTIMATION

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ABSTRACT

Horizontal fish school profiles of the northern anchovy, *Engraulis mordax*, taken from day aerial photographs and video tapes of school bioluminescence at night were examined to determine the percentage of school area within a circular field of view and the school length and width ratios. Schools observed during the day had an average length to width ratio of 2.09:1, at night the ratio was 2.53:1. The percent coverage of the school's area in relation to a circle drawn tangent about the school averaged 42.1% during the day and 29.2% during the night. The effect of school shape on estimation of individual school area as observed with a side-looking sonar was determined. School width measurements, similar to that obtained by the sonar, were used to determine school area and indicated a possible average overestimate of the actual school area of 1.72:1. The relation of school length and width to the error was determined, indicating the greater the length to width ratio the greater the error.

Profiles of fish schools as viewed and photographed in the horizontal plane from an airborne platform have been published by numerous authors. Radakov (1972), in his review of fish schooling, described the characteristic horizontal shapes of fish schools in nature as being very diverse and extremely changeable. He stated that a spherical shape of a school is the rarest of all and also that a school's shape, size, or density is a result of the interaction between the fish and the physical and biological environment.

School shape and behavior in nature have been studied with such techniques as aerial observation, hydroacoustic measurements, and underwater observation. Each of these methods has limitations. Underwater visual observations are subject to restrictions due to illumination and restricted visibility. Aerial observation is limited in the day by water transparency, illumination, and reflectance from the water surface resulting from wind and wave action. Visual observation of school shape at night, as outlined by bioluminescent organisms, is limited to the moon's dark cycle or to periods of no moon, and is affected by water transparency and the density of bioluminescent organisms present in the water. Both day and night observations are limited by the school's proximity to the surface in relation to the factors affecting water visibility.

Hydroacoustic observations using lower frequency sounders of the type used commonly in sonar fish surveys give imprecise images of fish schools in the form of echograms that must be interpreted. Greater resolution of fish school shapes, but with limited range, can be obtained with ultrasonic scanning equipment (Voglis and Cook 1966).

All of these observation techniques may alter the environment and in many cases may result in modification of fish school behavior. Fish school behavior is affected when in close proximity to ships, submersibles, and divers, and aircraft (noise, shadow) could possibly modify the school, though this is not documented.

Surveys and research studies using variations of these three observation techniques are currently in use for direct biomass estimation of fish populations by observation of individual schools, school groups, and the internal structure of the school.

Hydroacoustic research on schooling fish is currently being conducted by the Southwest Fisheries Center (Smith 1970; Hewitt et al. 1976). Coastal, hydroacoustic surveys are conducted by the State of California (Mais 1974) to determine a relative abundance estimate of the northern anchovy, *Engraulis mordax*. These surveys are conducted during the daylight hours, as comparative tests indicate an increased probability of detection during this period (Smith 1970).

Aerial observations by commercial fish spotters, in the form of school counts and estimates of total tonnage, are being used by the Southwest

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Fisheries Center to calculate indices of apparent abundance for several coastal species, including the northern anchovy (Squire 1972). To aid in the detection and quantification of pilchard, *Sardinops ocellata*, shoal occurrence off South Africa, Cram (1974) used an airborne, low-light-level, electron image intensifier to view the ocean's surface, detecting the bioluminescence of fish schools. During these night aerial surveys the school's horizontal surface area was interposed on the instrument's circular field of view, and running estimates of the percentage of coverage were made. These percentage estimates were then used in the computation of biomass estimates.

The intensifier used by the Sea Fisheries of South Africa has been used by the author off the southern California coast on an experimental basis. Due to the highly variable school shapes encountered, making estimates of the percentage of school coverage in the circular field of view are difficult. Experience indicated that examination of aerial color photographs and night low-level video tapes of anchovy school shapes for determination of the percentage of school coverage within a circle would be useful, particularly if in the future, surveys were to be conducted at night using this method for the development of biomass estimates for the northern anchovy and other near-surface schooling pelagic species.

In addition, an analysis of anchovy horizontal school shapes may assist hydroacoustic researchers in determining error parameters for computation of sonar biomass estimates. Hydroacoustic surveys currently conducted for the northern anchovy use both side- and vertical-looking sonar to detect and measure fish schools and school groups during the day along a predetermined survey track line. The acoustic "beam" used in these surveys varies according to the unit and is of ±5° to 10°. When detecting the school, the side-looking sonar measures the maximum dimension in one aspect of the school, either normal to or parallel to the ship's track. For the purpose of calculating horizontal area, in contrast to the aircraft's vertical view of the actual horizontal school area, the echogram school width is assumed to be elliptical (Smith 1970). Preliminary attempts at biomass estimation from sonar surveys have used the simple assumption that a series of estimates of the width of an elliptical school from random aspects will result in an unbiased estimate of school horizontal area. In a side-looking sonar the school width is measured and provides two points of reference with the orientation of these points about the school's profile being unknown. If an ellipse is fitted randomly between these two points, the resulting average area will equal a circle, a condition that was not observed in aerial photographs of anchovy schools.

METHODS

To examine the shape of northern anchovy schools as observed during day and night and to determine what percentage the school occupies of a circle tangent to two points along the school's edge and containing the school inside the circle, a circle was drawn about school profiles obtained from a series of 20 day oblique aerial color photographs (from the photographic files of the Southwest Fisheries Center) and of 20 night photographs of fish school bioluminescence. The bioluminescent anchovy school shapes were photographed from a television monitor as it projected video tapes recorded from an airborne low-light-level television camera used during anchovy resource surveys off northwestern Mexico. The night photographs were made available through the courtesy of Zapata, Inc.[2] (Zapata Fisheries), Houston, Tex. The night surveys using low-light-level television were conducted at elevations of up to 1,828 m (6,000 ft) and this survey technique is effective because the northern anchovy commonly migrates to the near-surface area during hours of darkness (Squire 1972).

The actual area of the schools observed in the photographs are unknown due to lack of data on the aircraft's altitude, camera angle, and camera geometry; however, all were taken from angles approaching vertical. However, all area calculations are expressed in percentages of a circle drawn tangent about the school's edge.

The day school profiles were further analyzed to determine what the school area would be if the width measurement were considered to be equal to the school's diameter and what the area would be if viewed systematically from six points 30° arc) about an arc of 180° around the school (based on school width or diameter as determined similar to the measurements made from a hydroacoustic sounder). These area data calculated from the six points of observation to determine school width were then compared to the actual school area.

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

School length to width ratios were determined for both day and night schools.

The school area, as expressed in terms of percentage of the circle drawn about it, was determined by tracing the school profile upon paper, cutting the school out of the circle and weighing both the school profile and the nonschool portion of the circle on a sensitive laboratory balance. School areas for the six points of school width (diameter) measurement about the 180° arc were computed statistically.

RESULTS

Night Observations

Figure 1 illustrates the profiles of schools recorded by the airborne low-light-level television system. On each figure are given the area percentage of a tangent circle that the fish school occupies and the length to width ratio.

The average percent coverage of a night anchovy school, in relation to the circle tangent to the school, is 29.2%. The average ratio of school length to width is 2.53:1.

Day Observations

Figure 2 illustrates profiles of schools observed during the day. On each figure are given the percentage of a circle tangent to the school that is occupied by the fish school, the length to width ratio, and the 30° arc points that were used to determine the school's estimated diameter and area, simulated as randomly viewed by a side-looking sonar. The ratio of the actual school area to the calculated area of the school's average, high and low estimate, as viewed every 30° of a 180° arc based on simulated sonar measurements of width, is given in Table 1.

The average percent coverage of a day anchovy school to the tangent circle about the school is 42.1%. The average length to width ratio for all day schools is 2.09:1. The ratio of estimate of the area of all day schools, as calculated from measurements from 30° arc points about the school, to the actual area of the school is 1.72:1. The ratios, length to width, and estimate of school area to actual school area were compared and Figure 3 graphs the relationship. The graph displays the variables plotted on log-log paper showing two main points: One, that the variance is changing proportionally to the mean. This is expected as there should be more variation as the school length to width increases. Two, the plotted regression line indicates that more bias (higher estimated actual school ratio) is introduced as the school length to width ratio increases. The line is significant at the 95% confidence interval as proven by the t-test ($1.98 < 2.298$). The confidence limits are from 0.0545 to 0.734.

TABLE 1.—Ratio of the actual anchovy school area to the average area based on six points of observation as viewed every 30° of a 180° area, and the high and low ratio.

School	Average	High	Low
1D	1 2.61	1 3.95	1 0.83
2D	1 1.96	1 2.91	1 0.90
3D	1 1.22	1 1.56	1 0.85
4D	1 2.12	1 3.71	1 0.63
5D	1 1.13	1 1.41	1 0.80
6D	1 2.73	1 4.53	1 1.18
7D	1 1.50	1 2.35	1 0.60
8D	1 1.32	1 2.00	1 0.54
9D	1 1.49	1 1.88	1 1.19
10D	1 1.31	1 1.60	1 1.04
11D	1 2.65	1 4.82	1 0.62
12D	1 1.33	1 2.02	1 0.85
13D	1 1.47	1 2.35	1 0.77
14D	1 1.68	1 2.54	1 0.49
15D	1 1.97	1 3.30	1 0.65
16D	1 1.60	1 2.69	1 0.44
17D	1 1.38	1 2.10	1 0.84
18D	1 1.38	1 2.00	1 0.68
19D	1 1.99	1 3.52	1 0.42
20D	1 1.77	1 2.90	1 0.66

SUMMARY AND COMMENTS

The data on day/night school length to width ratios support what is commonly known about the schooling shapes of the northern anchovy. They are more common in the near-surface area at night, generally in large elongate thin surface schools. These elongate schools tend to group together in the early morning hours and descend to depth to form more compact schools during the day (Mais 1974). Studies by Squire (1972) of aerial fish spotter data show anchovy schools to be more frequently observed, and observed in larger quantities at night, when compared with day observations.

The schools percent area coverage of the tangent circle at night is 12.9% less than its coverage during the day and the length to width ratio is greater by 0.44. In addition, analysis of school length to width ratios compared to the ratio of estimated school size to actual size (Figure 3) shows that as the length to width ratio increases a greater error in school area estimate will occur. Schools with a length to width ratio of 2:1 have an estimated to actual error of about 1.5:1 while more elongate schools of a ratio of 3:1 have an estimated error of about 1.75:1.

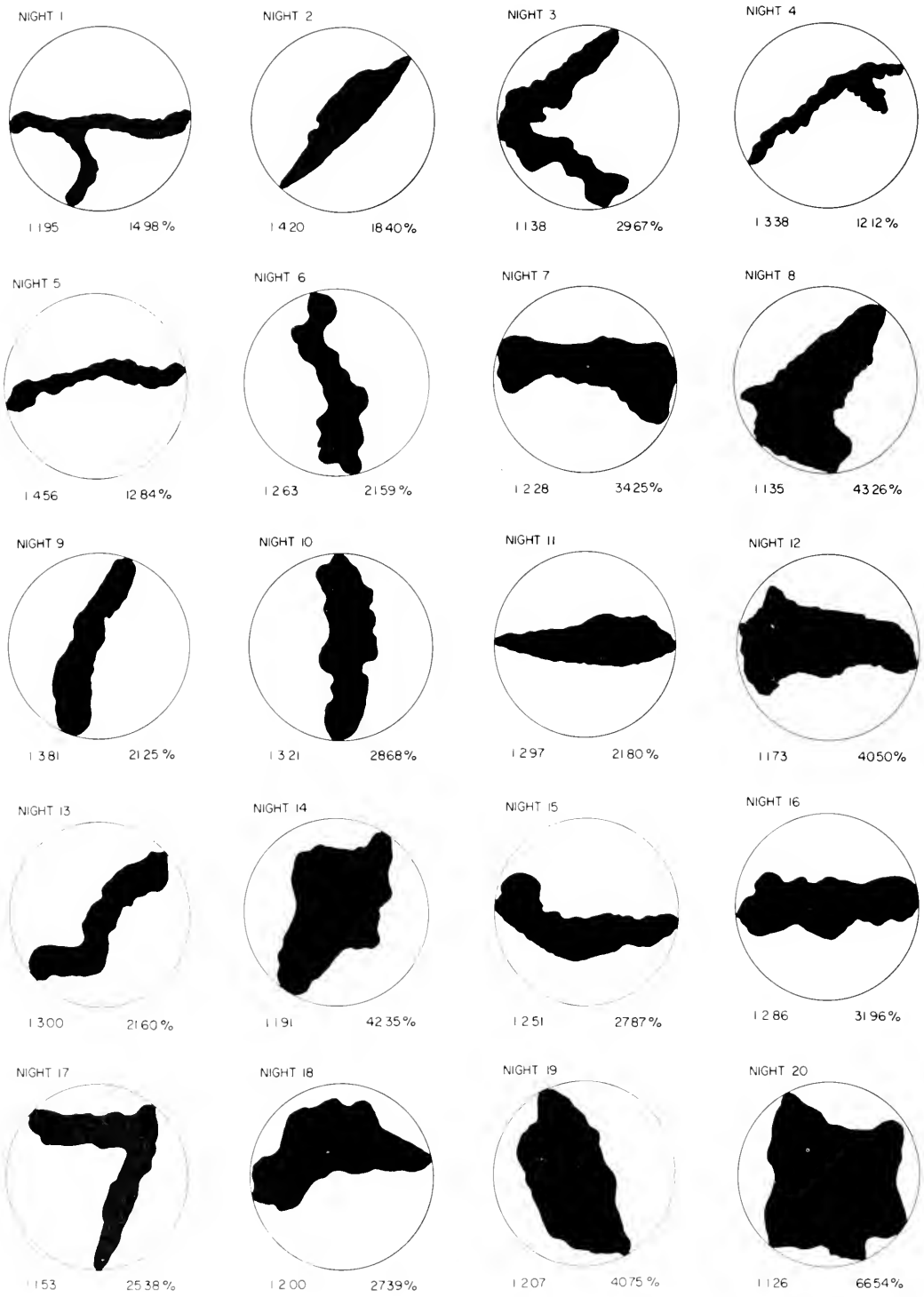

FIGURE 1.—Profiles of anchovy schools observed at night off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school.

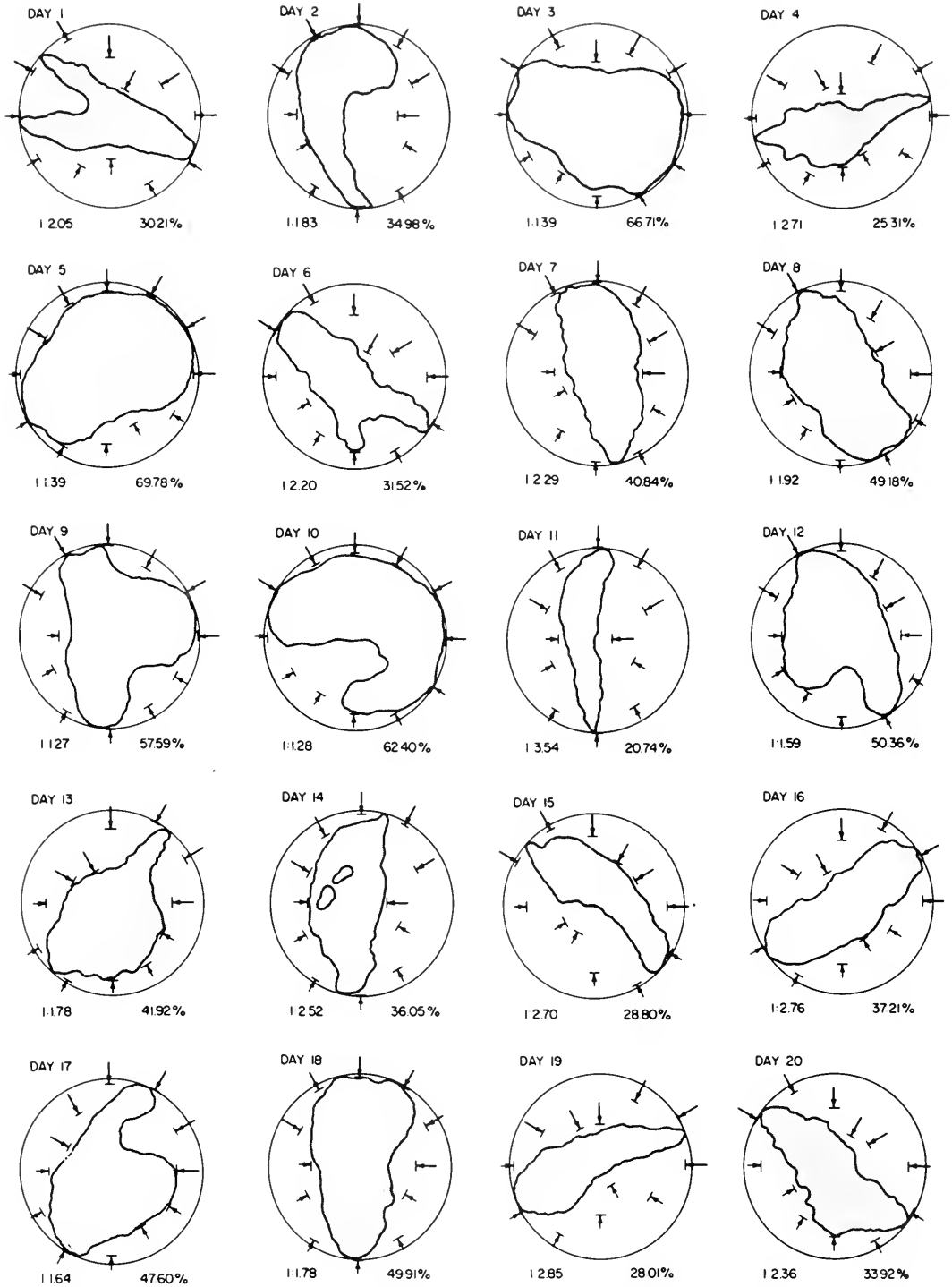

FIGURE 2.—Profiles of anchovy schools observed during the day off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school. Measurements of school width were taken at the six points (long arrow shaft) indicated about a 180° arc.

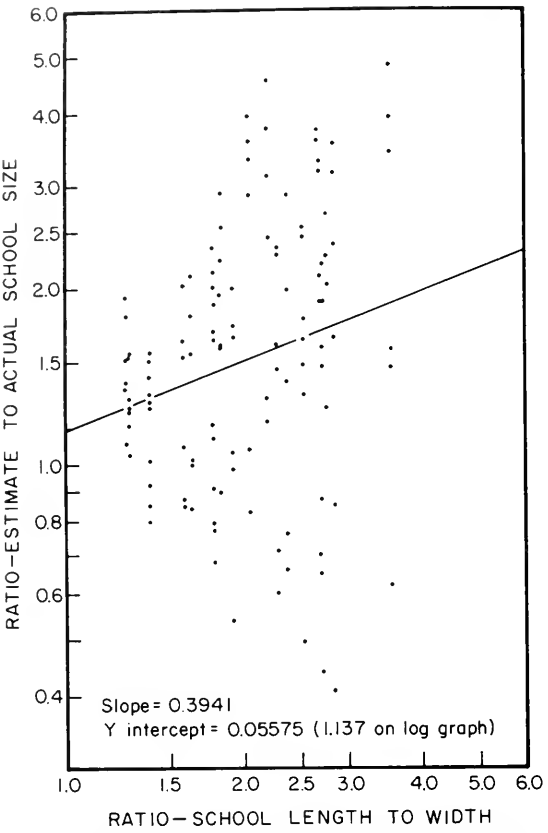

FIGURE 3.—Regression plot for the ratio estimated anchovy school size to actual size compared with the school length to width ratio.

For simulated sonar observations of school widths used in the calculation of school area, the preliminary examination of these data indicates a possible 1.72:1 average overestimate of area due to school shape deviations from a circle or ellipse.

Fish schools, being highly variable in horizontal profile, are probably equally complex in vertical structure; the relationship of horizontal complexity to vertical complexity is not known. Also unknown is the question of whether the individual school's axis is oriented in the same general direction within a group of schools, a possible factor which, if it occurs, could provide a source of substantially higher or lower school area error estimates from sonar track line surveys.

The problem of accurately estimating the percentage of school area within view of a low-light-level viewer is difficult, as the examples of school shapes within the target circle would indicate. Parameters of human viewing error could be established for this survey technique. However, the conduct of surveys using a low-light-level television system where the video signal can be recorded and later electronically analyzed with the aid of an image analyzer, should result in a higher degree of survey accuracy.

School shapes were taken from photographs randomly selected from an aerial photo file. Many of the photos were taken in the nearshore areas. There is the possibility that schools may be slightly more elliptical in shape over deep water than in the nearshore areas, but this is not documented. If this were true the error estimate would be reduced. This and other aspects of school profile and orientation should be investigated further and estimates of length to width ratios from aerial surveys, done in conjunction with each acoustic survey, may be useful for determination of a correction factor for the acoustic data.

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SYNERGISTIC EFFECTS OF ENVIRONMENTAL VARIABLES ON THE METABOLISM OF THE COPEPOD *EUTERPINA ACUTIFRONS* FROM TWO DIFFERENT AREAS OFF THE COAST OF THE STATE OF SÃO PAULO, BRAZIL[1]

G. SOARES MOREIRA[2] AND W. B. VERNBERG[3]

ABSTRACT

The combined effects of temperature and salinity on the respiratory rate of two populations of the copepod *Euterpina acutifrons* have been determined. One population was taken from a nonpolluted area, São Sebastião Channel, and the other from a polluted area, Santos Bay, both off the coast of the State of São Paulo, Brazil. Four groups of copepods were used in the experiments: 1) São Sebastião animals kept in São Sebastião water (35‰ salinity); 2) Santos animals kept in Santos water (28‰ salinity); 3) São Sebastião animals kept in Santos water; and 4) São Sebastião animals kept in diluted São Sebastião water (28‰ salinity). Results showed that São Sebastião copepods in either full strength seawater (35‰) or lower salinity seawater (28‰) could metabolically regulate over a wider range of salinities than could Santos copepods in Santos water or São Sebastião copepods maintained in Santos water. It was concluded that the water quality of the Santos Bay was responsible for changes in the metabolic regulatory capacity of the copepods exposed to Santos water.

The planktonic harpacticoid *Euterpina acutifrons* (Dana) is distributed in the warm waters of the world between lat. 66°N and 40°S (Haq 1972). It is a euryhaline species and has been reported in salinities ranging from 8‰ (Cananeia Estuary, southern Brazil, Tundisi 1972) to 39‰ (Mediterranean Sea, El-Maghraby 1965). Laboratory studies have shown that reproduction can occur over a salinity range of 15 to 45‰ (Moreira and Yamashita 1975). *Euterpina acutifrons* is an important link in the marine trophic web serving as food source for both adult and larval fishes (Pouchet and de Guerne 1887; Lebour 1918; Blin 1923; Carvalho 1945; Marques 1951; Thayer et al. 1974).

In an earlier paper, Moreira (1975) reported that salinity tolerances for Brazilian populations of *E. acutifrons* from Santos were very different from those of populations of this species from São Sebastião. This in itself is not surprising since the salinity regimes of the two areas are different. The salinity in the Santos Estuary varies widely from 17 to 30‰ depending on the tide and season of the year, while in São Sebastião Channel the salinity is approximately 35‰ throughout the year. Water temperatures in both areas are essentially the same, ranging from 19° to 30°C depending upon season. It was not determined, however, if the observed differences in salinity tolerances of the two populations were genetically or environmentally induced. Subsequently, a study was initiated to resolve this question by measuring metabolic response patterns of specimens from both populations to different thermal-salinity regimes. It soon became apparent that environmental parameters other than temperature and salinity were factors in determining the metabolic response patterns of these copepods.

A detailed chemical analysis of the water in Santos Bay is not available, but great numbers of tankers and other vessels continuously operate near shore, discharging ballast water and contaminating seawater and adjacent regions with petroleum. In addition, there are a large number of industries that discharge wastes directly into the water. One sample analysis of Santos Bay seawater was found to contain 270 ppb lead and 200 ppb nickel (unpublished data). Furthermore, to minimize the effects of human waste or degradation products, approximately 400 tons of chlorine are added monthly near shore. The data presented in this paper demonstrate that

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metabolic response patterns of *E. acutifrons* to the normal fluctuations found in estuarine systems were significantly altered by the water quality of Santos Bay water.

MATERIALS AND METHODS

The copepods were collected in two fixed locations off the coast of the State of São Paulo, one in Santos Bay (lat. 23°59'S; long. 46°19'W), the other in São Sebastião Channel (lat. 23°50'S; long. 45°25'S). Collections were made with a nylon plankton net (20 mμ) during the winter when water temperatures averaged approximately 21°C. All samples were brought immediately into the laboratory whereupon *E. acutifrons* were sorted from the plankton using a mouth pipette under a binocular microscope. The copepods were placed in 2-l crystallizing dishes, 20 cm in diameter and 15 cm high. In the first two series of experiments, the copepods were placed in the water obtained from the collection points, i.e., copepods from São Sebastião Channel were placed in São Sebastião water (35‰) and copepods from Santos were placed in Santos water (28‰). In the last two series of experiments, copepods from São Sebastião were placed either in Santos water or in São Sebastião water diluted to 28‰. The copepods were maintained under temperature and photoperiod regimes approximating field conditions: 19°-24°C and 11 L:13 D. The copepods were fed with *Phaedactylum* and *Platymonas* daily and kept in the laboratory at least 1 wk before being used in the respiration experiments.

Oxygen uptake was determined using Cartesian diver respirometers (Holter 1941), which have a total volume of 8-13 μl. Only nongravid females were used. Two or three copepods were placed in each diver, depending upon the salinity/temperature regime of the experiment. The oxygen uptake was determined during a 2-h interval. The first 30-min reading was discarded; after this initial reading, uptake rates remained constant.

Oxygen uptake rates were measured under the following environmental conditions: São Sebastião animals maintained in São Sebastião water, Santos animals in Santos water, and São Sebastião animals in Santos water, 15°, 20°, 25°, 30°, and 32°C at 15, 25, 35, 45, and 55‰ salinities. The oxygen uptake of São Sebastião animals maintained in São Sebastião water diluted to 28‰ was determined at 15°, 25°, and 30°C over the same salinity ranges used in the other experiments. Ten determinations were made under each set of environmental conditions. Distilled water or freeze-concentrated brine was added to filtered seawater to attain the desired salinities. Salinities were determined by titrating against silver nitrate (Harvey 1955).

Dry weights for the copepods were obtained using a Torbal[3] torsion balance, 0.01 mg sensitivity. The copepods were rinsed with distilled water and dried at 70°C for 24 h before they were weighed. Three replicates of 200 nongravid females from each area of collection were used. Results were expressed as microliters of oxygen per milligram per hour. Significant difference of means was calculated by the method of Simpson et al. (1960) for small samples.

The metabolic data obtained in the first three series of experiments were analyzed statistically using multiple regression techniques. The basic experimental design used in this study is usually referred as a factorial design. Specifically, the plan was a 5 × 5 factorial using five levels of temperature and five levels of salinity, making in all 25 combinations of experimental conditions. Since 10 determinations of oxygen uptake were made in each combination, a total of 250 observations were made in each series. Thus, the 250 observations may reasonably be considered as continuous responses of a function of the two factors and interactions.

Oxygen uptake data were analyzed as percentage of oxygen consumption relative to that at 25°C and 35‰ salinity for São Sebastião animals in São Sebastião water and at 25°C and 25‰ salinity for Santos animals in Santos water and São Sebastião animals in Santos water, i.e., the rate under these "standard" conditions was assumed to be 100%, and rates obtained under other regimes were calculated as the percent deviation from that rate. Since the observations are treated as percentage measurements generated by data from binomial populations, the transformation $Y = \text{arc sin } \sqrt{x}$, where x is observed percent respiration, is appropriate to stabilize variances (Mendenhall 1968). Analysis of variance for this data indicated which of the factors (temperature, salinity, or temperature-salinity interactions) had significant effects on the metabolism of the copepods. The program was run on an IBM 360 computer.

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

RESULTS

Animals From São Sebastião in São Sebastião Water (35‰)

The metabolic rate of *Euterpina acutifrons* from São Sebastião which were maintained in water from São Sebastião Channel was less influenced by changes in salinity than were the other groups of *E. acutifrons* (Figure 1). Rate did, however, increase with increasing temperature up to 30°C; at 32°C, rates either leveled off or decreased. Greatest increases in respiration rates were observed between 15° and 20°C. These increases are reflected in the relatively high metabolic rates within this thermal range obtained from this group of animals.

At 20°C metabolic rates were not significantly different over the entire salinity range of 15-55‰, and at 15°C the copepods were able to regulate their metabolism over a range of 25-55‰. At higher temperatures (25°, 30°, and 32°C) rates generally were lower at the salinity extremes (15, 45,55‰) and highest at 35‰. Rates varied from a minimum of 4.87 to a maximum of 22.36 μl/mg h^{-1} dry weight (Figure 1).

Statistical analysis indicated that 66% of the observed variability in the rates could be explained by the temperature-salinity combinations (Table 1), although the linear effect of temperature was the single significant factor (1% level). The linear effect of salinity, the quadratic effects of the temperature and salinity, and the temperature-salinity interaction did not contribute significantly to the observed changes in respiration rates. Figure 2A shows the response surface contours fitted over the experimental design.

TABLE 1.—Analysis of variance of data for *Euterpina acutifrons* (São Sebastião animals in São Sebastião water, 35‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T	0.54953	1%
T^2	0.65769	Not significant
S	0.65796	Not significant
S^2	0.65885	Not significant
T × S	0.65933	Not significant

Animals From Santos in Santos Water (28‰)

In the Santos animals maintained in Santos water, the rate of oxygen uptake also increased over the temperature range to 30°C for the entire salinity range. In most of the salinities, the largest metabolic increase occurred between 25° and 30°C. This contrasts with São Sebastião copepods which exhibited the largest increase between 15° and 20°C. The Santos animals did not show the metabolic regulation observed in the São Sebastião animals maintained in São Sebastião water, and tended to have low metabolic rates at the salinity extremes, i.e., 15, 45, and 55‰. Highest rates occurred at salinities of 25-35‰. The rates varied from a minimum of 7.97 to a maximum of 28.20 μl/mg h^{-1} dry weight (Figure 1).

Statistical analysis indicated that only 46% of the observed variability in the respiration rates of these animals could be explained by the temperature-salinity combinations (Table 2). The significant factors were the quadratic effects of temperature and salinity (0.05% level) and the linear effect of salinity (0.05% level). The temperature-salinity interaction was not a significant factor. Figure 2B shows the response surface contours fitted over the experimental design.

TABLE 2.—Analysis of variance of data for *Euterpina acutifrons* (Santos animals in Santos water 28‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T^2	0.24350	0.05%
S^2	0.28955	0.05%
S	0.46193	0.05%
T × S	0.46198	Not significant

Animals From São Sebastião in Santos Water

Transfer of São Sebastião copepods into water from Santos markedly altered their metabolic responses, especially their response to salinity. Respiration rates increased with temperature up to 25°C at the extreme salinities (15, 45, 55‰) and up to 30°C at salinities of 25 and 35‰, before leveling off or decreasing. The copepods which were transferred to Santos water did not regulate metabolically at any temperature at the salinity extremes. Lowest rates were obtained at salinities of 15 and 55‰, and the highest rates were observed at 25‰ at 15° and 25°C. At 30° and 32°C, peak metabolic rates occurred at 35‰ (Figure 1). Rates varied from a minimum of 6.80 to a maximum of 37.23 μl/mg h^{-1} dry weight (Figure 1).

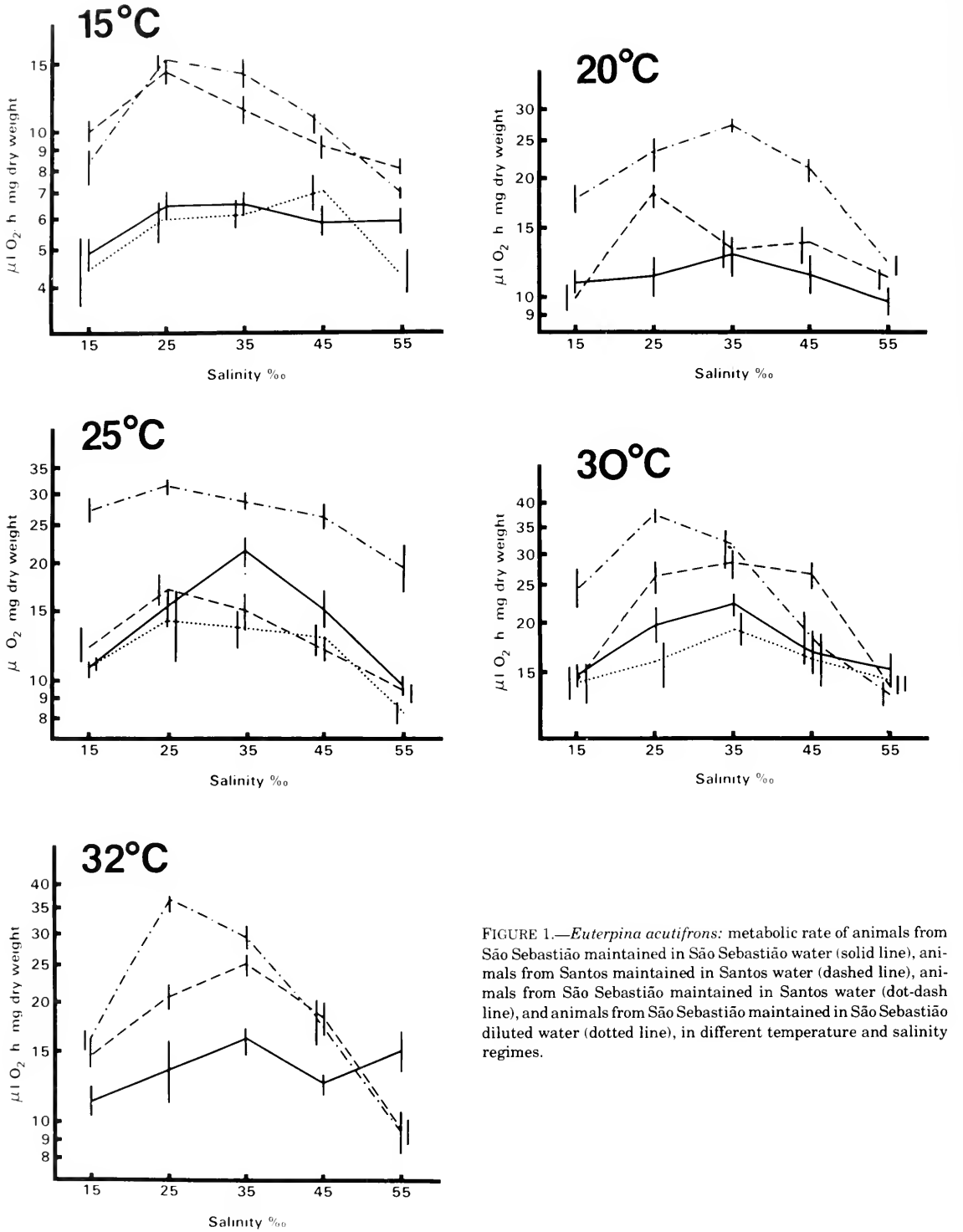

FIGURE 1.—*Euterpina acutifrons:* metabolic rate of animals from São Sebastião maintained in São Sebastião water (solid line), animals from Santos maintained in Santos water (dashed line), animals from São Sebastião maintained in Santos water (dot-dash line), and animals from São Sebastião maintained in São Sebastião diluted water (dotted line), in different temperature and salinity regimes.

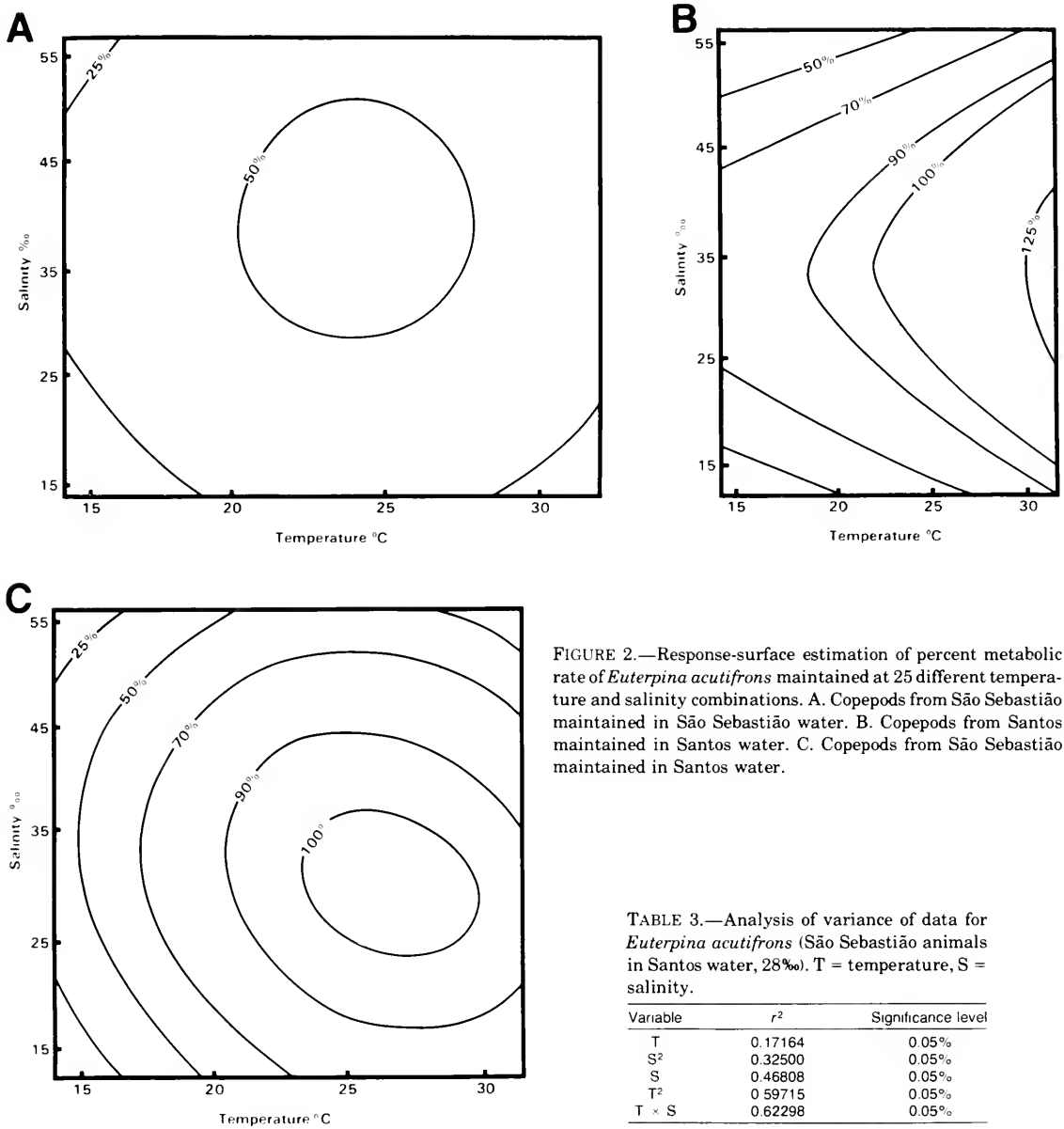

FIGURE 2.—Response-surface estimation of percent metabolic rate of *Euterpina acutifrons* maintained at 25 different temperature and salinity combinations. A. Copepods from São Sebastião maintained in São Sebastião water. B. Copepods from Santos maintained in Santos water. C. Copepods from São Sebastião maintained in Santos water.

TABLE 3.—Analysis of variance of data for *Euterpina acutifrons* (São Sebastião animals in Santos water, 28‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T	0.17164	0.05%
S^2	0.32500	0.05%
S	0.46808	0.05%
T^2	0.59715	0.05%
T × S	0.62298	0.05%

All of the analyzed factors, i.e., linear temperature and salinity, as well as the quadratic effect of these factors, and the temperature-salinity interaction, contributed significantly (0.05% level) to the observed variability in respiration rates (Table 3). A total of 62% of the variability could be explained by these various factors. Figure 2C shows the response surface contours fitted over the experimental design.

Animals From São Sebastião in São Sebastião Diluted Water

In this series the respiration experiments were run at three temperatures to test whether or not the results obtained for Santos animals were the result of acclimation to a lower salinity. The respiration rates at 28‰ were essentially the same as those for animals maintained in undiluted São

Sebastião water. At 15°, 25°, and 30°C, metabolic rates were not significantly different over the range of 15-45‰. The rates varied from a minimum of 4.32 to a maximum of 19.17 μl/mg h^{-1} dry weight (Figure 1).

DISCUSSION

In Brazilian waters, populations of *E. acutifrons* thrive over a wide range of salinities and variable salinity alone does not seem to be a limiting factor in their distributional patterns (Tundisi 1972; Moreira and Yamashita 1975). Indeed, of the various environmental variables tested, temperature alone significantly affected the metabolic rates of these copepods. The present data demonstrate that specimens of copepods from the unpolluted São Sebastião Channel have the capability of metabolic regulation over a wide range of salinities when tested using São Sebastião water. On the other hand, marked diminution in the capability to regulate metabolically at salinity extremes was noted in *E. acutifrons* from the Santos population and specimens from São Sebastião maintained in Santos water. For both groups of animals salinity, as well as temperature, proved to exert a statistically significant effect at the 5% level (or less) on their oxygen uptake rates. These marked changes in metabolic control in the copepods taken from or exposed to Santos water compared with that of copepods from São Sebastião are depicted in Figure 2.

While we did not measure population densities of the *E. acutifrons* in our two study areas (Santos Bay and São Sebastião Channel), there is some indication in the literature that population size is sensitive to polluted waters. Gabriel et al. (1975) reported a decrease in abundance of this species in the Milford Haven Estuary following its development into the largest oil port in the United Kingdom in the 1960's, and there are several examples that indicate that pollutants can affect the survival of copepods and planktonic larvae. Barnes and Stanbury (1948) have studied the toxic action of copper and mercury salts on the copepod *Nitocra spinipes* and verified that mercuric chloride is a very effective poison; in contrast, these animals are very resistant to copper. D'Agostino and Finney (1974) have found that copper and cadmium inhibit growth and development of the copepod *Tigriopus japonicus* at 0.064 mg/l and 0.044 mg/l, respectively. Heinle (1969) suggested that the high mortality rate of *Acartia tonsa* in a power plant effluent was due to the chlorination of the cooling water, correlating the apparent periodicity in the mortality rate with the chlorination schedule. Latimer et al. (1975) studied the toxicity of 30-min exposures of residual chlorine to two species of copepods, *Limnocalanus macrurus* and *Cyclops bicuspidatus thomasi*. The predicted "safe" concentrations were 0.9 mg/l for *L. macrurus* and 0.5 mg/l for *C. b. thomasi*. Roberts et al. (1975) studied the acute toxicity of chlorine to some estuarine species, including molluscan larvae, copepods, shrimps, and fishes. They found that molluscan larvae and *Acartia tonsa* were the most sensitive species tested, with 48-h TL_{50} values at chlorine levels <0.005 ppm. Gray (1974) demonstrated that lead ($Pb(NO_3)_2$) at 0.3 ppm reduced the growth rate of the marine ciliate protozoan *Cristigera* by 11.7% and at 0.15 ppm by 8.46%. Mercury was found to have an effect on survival, metabolism, and behavior of the planktonic larvae of *Uca pugilator* (DeCoursey and Vernberg 1972; Vernberg et al. 1973). Generally, larvae are much more sensitive to toxicants than are adults and very low concentrations of a toxicant can interact with environmental factors to cause increased mortalities among larvae (Vernberg 1975).

Detailed chemical analyses of Santos water obviously are needed, but the very high concentration of lead and nickel which were found in one sample, plus the oil and other industrial effluents that are being discharged, leave little doubt that the Santos Estuary is highly polluted. Data presented in this paper strongly suggest that specimens living in the Santos Estuary do so at a high cost energetically. This high metabolic cost for survival following exposure to salinity extremes would almost certainly be a factor limiting the distribution of *E. acutifrons* in polluted estuaries, since fluctuating salinity regimes are characteristic of this environment. Results obtained in this study highlight the fact that the physiological responses of marine organisms may be markedly modified if test animals are taken from or exposed to polluted waters.

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DESCRIPTION OF LARVAE OF A HIPPOLYTID SHRIMP, *LEBBEUS GROENLANDICUS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

EVAN HAYNES[1]

ABSTRACT

Larvae of *Lebbeus groenlandicus*, a hippolytid shrimp, were reared in situ in Kachemak Bay, Alaska, from the first zoea (Stage I) through the megalopa (Stage III). Each of the three stages is described and illustrated, and then compared with descriptions of larvae of *Lebbeus* spp. given by other authors.

Information on the larval stages of the genus *Lebbeus* is meager. Pike and Williamson (1961), in their summary of the generic characteristics of *Spirontocaris* and related genera, note that the only larva of *Lebbeus* known for certain is a larva of *L. polaris* dissected from a well-developed egg. During studies on rearing larvae of pandalid shrimp for descriptive purposes (Haynes 1976, 1978), I succeeded in rearing larvae of *L. groenlandicus* to the megalopa stage. This report describes and illustrates each of the two zoeal stages and megalopa of *L. groenlandicus*, and compares the stages obtained from rearing in situ and from plankton in Kachemak Bay with provisionally identified larvae of *L. groenlandicus* reported by other authors.

METHODS

A complete discussion of rearing technique, methods of measurement, techniques of illustration, and nomenclature of gills and appendages is given by Haynes (1976). Briefly, the rearing technique consists of obtaining Stage I zoeae from known parentage in the laboratory and then rearing the zoeae to postlarvae in 500-ml flasks suspended upright beneath the surface of the sea. Cast skins and larvae removed from the flasks were examined in the laboratory to determine sequence and morphology of each stage. Larval stage was also verified using larvae from plankton reared in the same manner as larvae obtained in the laboratory.

In the illustrations (Figures 1-3), for clarity, setules on setae are usually omitted but spinulose setae are shown. The terms are defined as follows:

setose - set with bristles (setae)
spinose - bearing many spines
spinous - spinelike
spinulose - set with little spines.

The figures are in part schematic and represent typical setal counts.

STAGE I ZOEA

Total length of Stage I (Figure 1A) 6.9 mm (range 6.4-7.4 mm; 10 specimens). Live specimens characterized by bright orange color extending along ventral surface of body from antennules to fourth abdominal segment, orange gut, small orange chromatophore at anus, and greenish internal thoracic organs; remainder of zoea translucent. Rostrum slightly sinuate, without teeth, about two-thirds length of carapace. Carapace with dorsal rounded prominence at base of rostrum and near posterior edge; no supraorbital spines. Usually at least two minute spinules occur along ventral margin of carapace immediately posterior to pterygostomian spine.

ANTENNULE (FIGURE 1B).—First antenna, or antennule, consists of an unsegmented cylindrical basal portion and two distal conical projections; largest conical projection bears four aesthetascs of various lengths; smallest conical projection bears a single heavily plumose seta.

ANTENNA (FIGURE 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum two-segmented, about twice length of scale; distal segment styliform and terminating in narrow projection. Two simple

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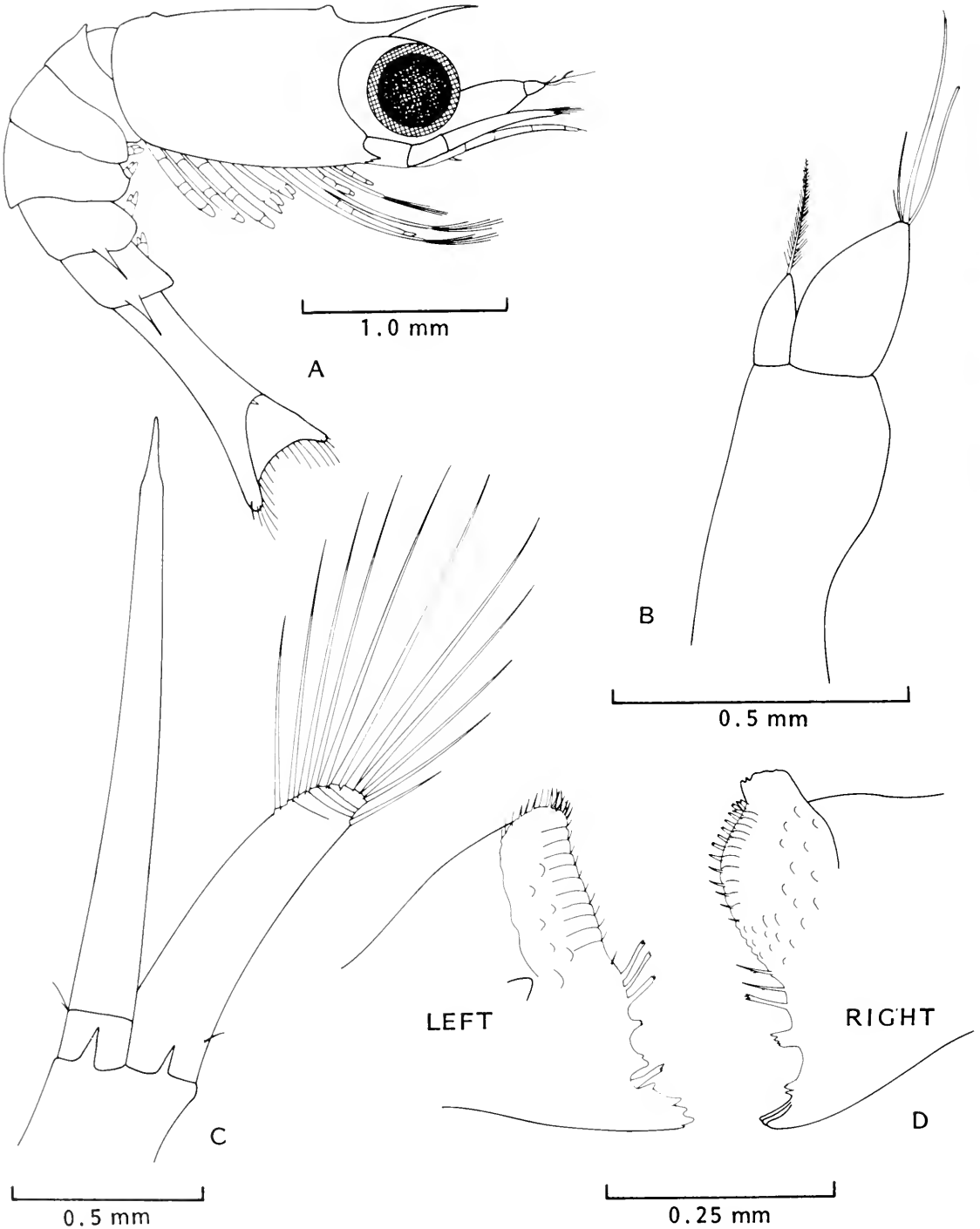

FIGURE 1.—Stage 1 zoea of *Lebbeus groenlandicus*: A, whole animal; B, antennule; C, antenna; D, mandibles (right and left).

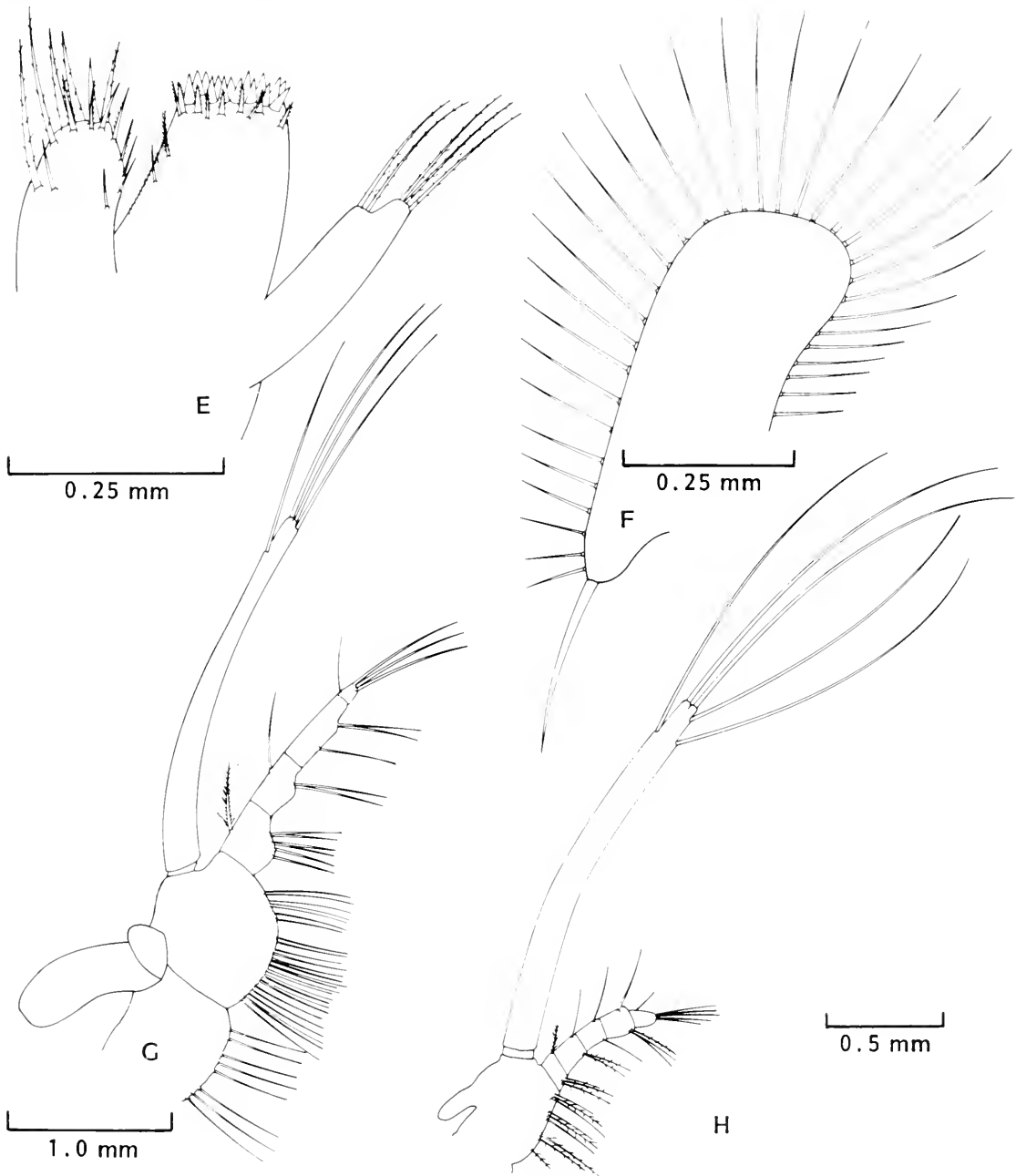

FIGURE 1.—Stage I zoea of *Lebbeus groenlandicus*: E, maxillule; F, scaphognathite of maxilla; G, first maxilliped; H, second maxilliped.

setae occur at joint. Antennal scale distally divided into four segments (proximal joint often incomplete) and fringed with 11 heavily plumose setae along terminal and inner margins. A small seta often occurs proximally near lateral margin. Protopodite bears two simple spines ventrally, one at base of flagellum and one at base of scale.

MANDIBLES (FIGURE 1D).—Without palps;

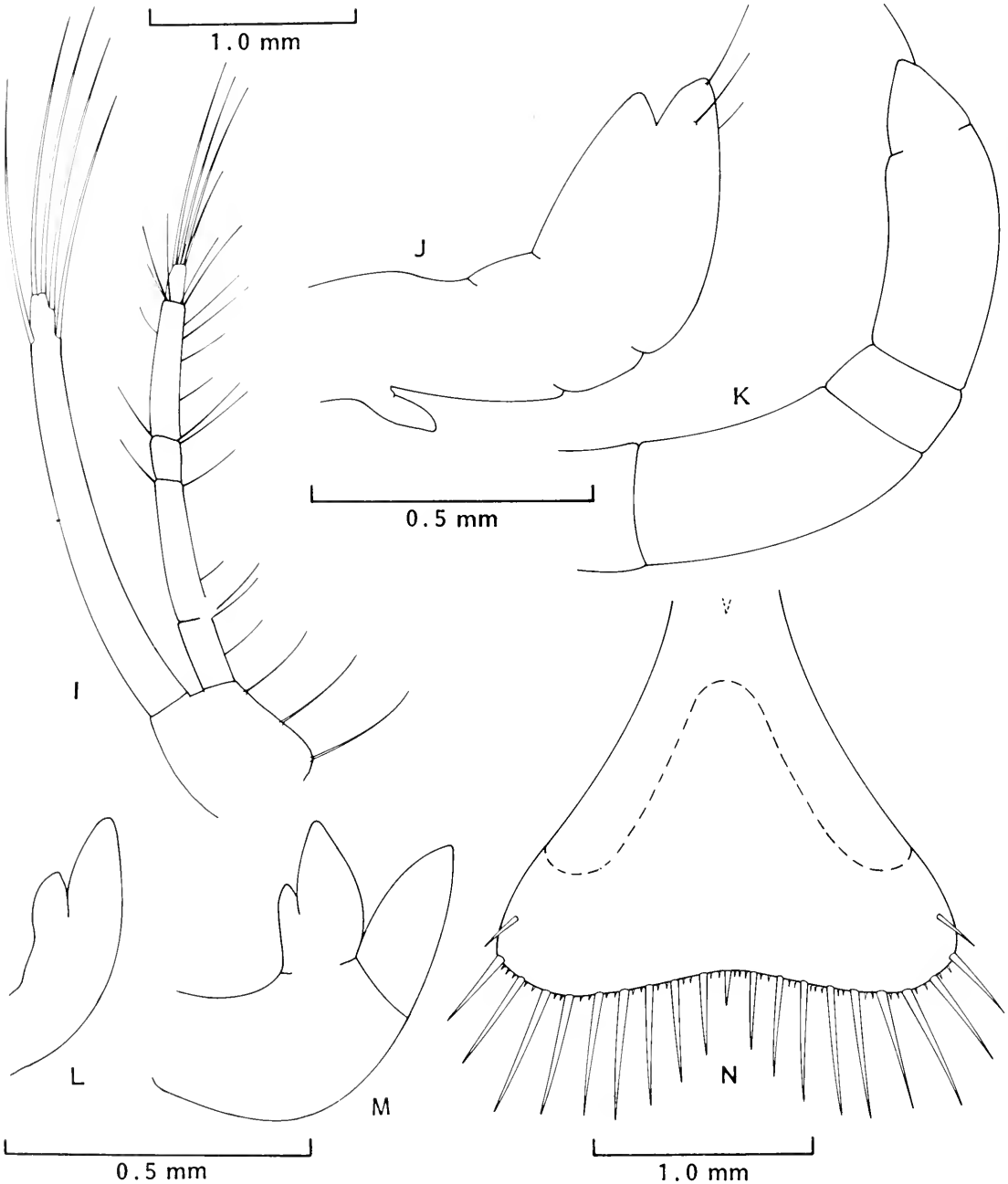

FIGURE 1.—Stage I zoea of *Lebbeus groenlandicus*: I, third maxilliped; J, first pereopod; K, third pereopod, L, first pleopod; M, second pleopod; N, telson.

well developed. Incisor process of left mandible bears five teeth, one of them located near movable premolar denticle (lacinia mobilis), in contrast to triserrate incisor process of right mandible. Both mandibles bear well-developed denticles along terminal margin. Truncated end of molar process of right mandible formed into curved lip. Only left mandible bears a subterminal process.

MAXILLULE (FIGURE 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) bears 15 setae, most of them spinulose. Median lobe (basipodite) bears 24 spines terminally, 9 of them spinulose; and 2 spines subterminally, 1 of them plumose and the other simple. A series of fine hairs occurs in vicinity of the simple spine. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal spinulose setae. No evidence of outer seta on maxillule.

MAXILLA (FIGURE 1F).—Bears platelike exopodite (scaphognathite) with 33 long, plumose setae along outer margin, and a longer, thick seta at the proximal end. Endopodite not segmented; setae spinous, setation formula 2, 2, 1, 2, 3. Both basipodite and coxopodite bilobed. Basipodite bears 29 setae, 14 on distal lobe and 15 on proximal lobe. Coxopodite bears 23 setae, 5 on distal lobe and 18 on proximal lobe.

FIRST MAXILLIPED (FIGURE 1G).—Protopodite segmented; bears 27 setae on distal segment and 8 on proximal segment, most of them spinulose. Endopodite four-segmented; setation formula 4, 3, 3, 7. Basal segment of endopodite bears conspicuous setulose spine. Exopodite segmented at base; bears four natatory setae. Epipodite distinctly bilobed.

SECOND MAXILLIPED (FIGURE 1H).—Protopodite not segmented; bears nine setae, five of them spinulose. Endopodite five-segmented; fourth segment expanded somewhat laterally; terminal segment tipped by five setae and bears single seta subterminally; basal segment bears conspicuous setulose spine like that on basal segment of endopodite of first maxilliped; setation formula 6, 4, 2, 3, 4. Exopodite about three times longer than endopodite; bears five natatory setae. Epipodite present but not bilobed.

THIRD MAXILLIPED (FIGURE 1I).—Protopodite not segmented; bears three setae. Endopodite five-segmented; as long as exopodite; number of setae somewhat variable. Exopodite bears five natatory setae. No epipodite.

FIRST PEREOPOD (FIGURE 1J).—Endopodite relatively short, wide, and partially segmented; chela partially formed; dactylopodite bears three simple spines. Exopodite a small lobe.

SECOND PEREOPOD.—Similar in shape to first pereopod except narrower, exopodite smaller, and chela more deeply cleft.

THIRD (FIGURE 1K) TO FIFTH PEREOPODS.—Each pair essentially identical except that they decrease slightly in size from third to fifth. No exopodites.

PLEOPODS.—First pleopod (Figure 1L) slightly cleft, without joints or setae. Second pleopod (Figure 1M) bilobed; outer lamella segmented; inner lamella usually only partially segmented but bears bud of appendix interna. Third to fifth pleopods essentially identical to second pleopod except both lamellae distinctly segmented.

ABDOMEN AND TELSON (FIGURES 1A, 1N).—Abdomen consists of five segments and telson (somite six is fused with telson in Stage I). Fourth and fifth abdominal segments each with pair of posterolateral spines nearly as long as segments themselves. Telson slightly emarginated distally; bears 19-21 densely plumose setae; small spinules occur between bases of all setae except two outermost pairs. Enclosed uropods visible. Anal spine present.

STAGE II ZOEA

Total length of Stage II 8.3 mm (range 8.1-8.7 mm; 8 specimens). Color similar to Stage I zoea but more diffuse. Rostrum (Figure 2A) arched upward; slightly blunter than in Stage I; without teeth. Carapace bears supraorbital, antennal, and pterygostomian spines in addition to several spinules along anteroventral margin.

ANTENNULE (FIGURE 2B).—Shows considerable change from Stage I. Largest conical projection segmented at tip; terminal segment bears three setae of different lengths; proximal segment bears six groups of five aesthetascs each in addition to row of four aesthetascs laterally and single seta distally. Smallest conical projection bears three nonplumose setae, one long and two short. Peduncle of antennule rounded laterally, not segmented, and bears five plumose setae that originate ventrally.

ANTENNA (FIGURE 2C).—Flagellum of antenna still two-segmented, but slightly stouter and projection at tip smaller than in Stage I; a few

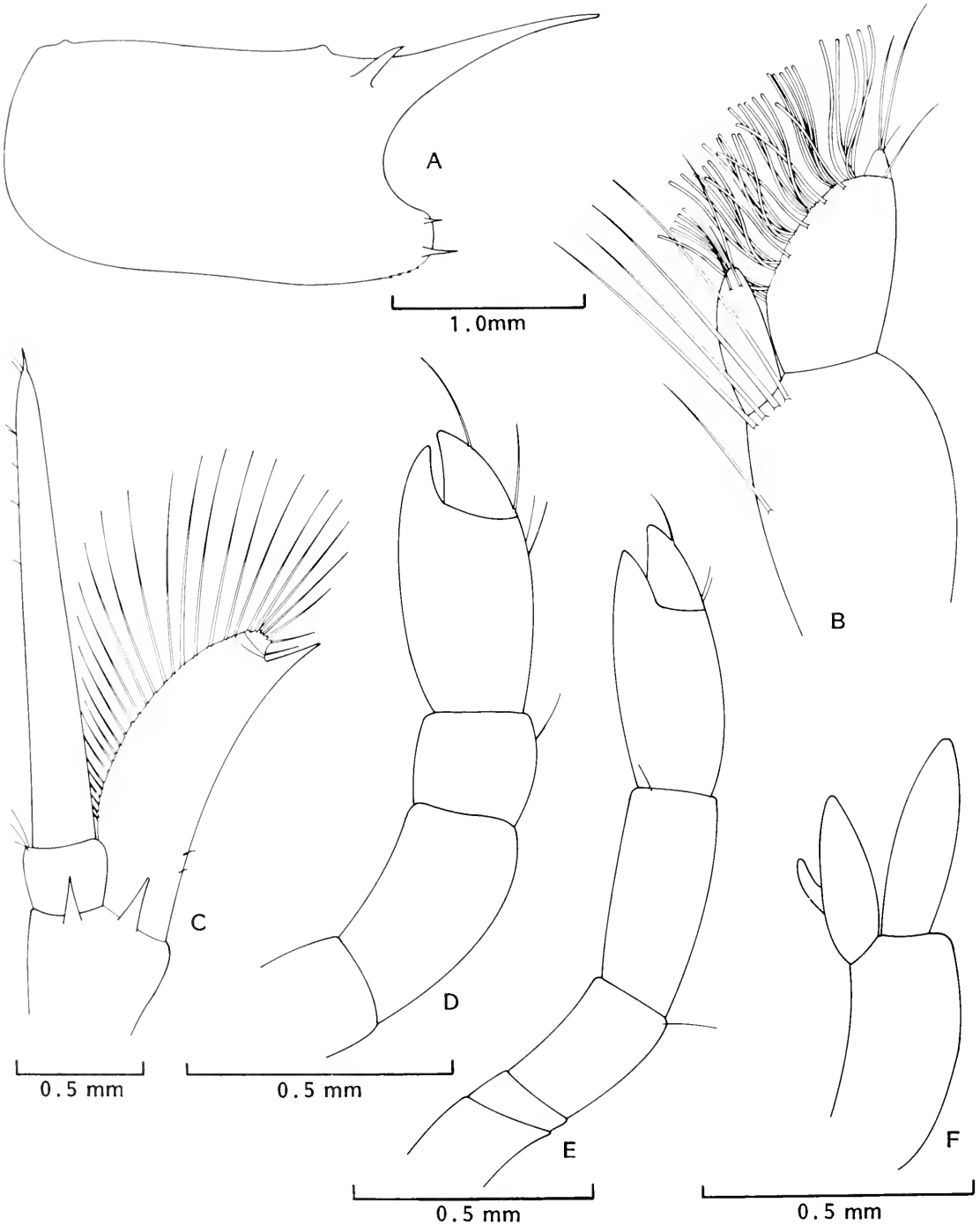

FIGURE 2.—Stage II zoea of *Lebbeus groenlandicus*: A, carapace; B, antennule; C, antenna; D, first pereopod; E, second pereopod; F, second pleopod.

small setae occur along lateral margin. Antennal scale distally divided into two segments and fringed with 29 or 30 thin, plumose setae along terminal and inner margins; distal outer projection a stout spine. Protopodite bears two stout spines, one at base of flagellum and other at base of scale.

MANDIBLES, MAXILLULE, AND MAXILLA.—Essentially identical to Stage I except scaphognathite of maxilla usually bears 35 setae along outer margin, in addition to the longer and thicker seta at proximal end, and proximal cleft slightly deeper.

MAXILLIPEDS.—Essentially identical to Stage I except exopodites of first, second, and third maxillipeds bear 5, 16, and 16 natatory setae, respectively.

FIRST PEREOPOD (FIGURE 2D).—Segmented; without exopodite; chela functional.

SECOND PEREOPOD (FIGURE 2E).—Adult in shape; chela functional; ischiopodite articulates somewhat laterally with basipodite. No exopodite.

THIRD TO FIFTH PEREOPODS.—Similar to Stage I except ischiopodite articulates somewhat laterally with meropodite and basipodite.

PLEOPODS.—First pleopod slightly more developed than in Stage I but still only about one-third length of second pleopod and without appendix interna. Second pleopod (Figure 2F) larger and narrower than in Stage I; outer lamella about one-fourth longer than inner lamella; both lamellae and appendix interna fully segmented at their bases. Third to fifth pleopods essentially identical to second pleopods.

ABDOMEN AND TELSON.—Posterolateral spines on fourth and fifth abdominal somites still present, those on fourth somite being only slightly shorter in relation to length of somite than in Stage I. Telson essentially identical to Stage I except segmented from sixth abdominal segment and bears 20 or 21 densely plumose setae. Uropods still enclosed.

STAGE III (MEGALOPA)

Total length of Stage III 7.5 mm (range 7.4-7.6 mm; two specimens). Antennal spine of carapace larger and pterygostomian spine smaller than in Stage II; no evidence of minute spinules along anteroventral margin. Rostrum (Figure 3A) short; bears single tooth at base in addition to dorsal protuberance. Antennules similar in shape to adult; outer flagellum six-segmented; inner flagellum five-segmented; peduncle three-segmented,

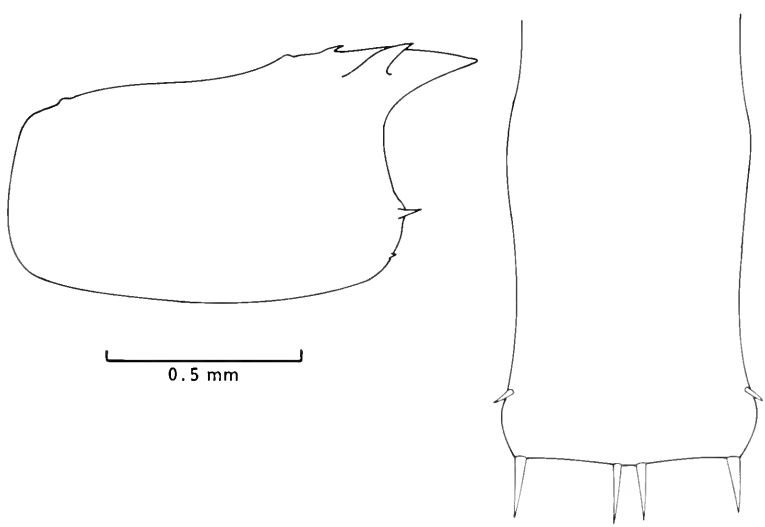

FIGURE 3.—Stage III (megalopa) of *Lebbeus groenlandicus*: A, carapace; B, telson.

lateral spine of proximal segment well developed. Antennal flagellum with at least 30 segments; about four times length of scale. Mandibles with unsegmented palps bearing four or five short teeth. Endopodite of maxillule reduced. Maxillipeds shaped as in adult, exopodites reduced. Dactylopodites of first and second pereopods well developed; carpopodite of second pereopod six- (sometimes seven-) segmented. Lateral margins of pleopods fringed with setae; appendix internae with minute cincinnuli. Posterolateral spines on abdominal segments four and five remnant or lacking. Telson (Figure 3B) rectangular in shape; bears two pairs of spines terminally and one pair laterally (one or two additional spines may occur centrally on terminal margin). Uropods exposed; fully developed except transverse hinge not complete.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Under the name "*Spirontocaris*-larva No. 1A," Stephensen (1935) included four specimens that were morphologically identical to zoeae provisionally identified by him as Stage I *S. polaris* (= *Lebbeus polaris* (Sabine)) except that they differed by lacking spines on abdominal segments four and five, exopodites on any pereopods, or free uropods. He regarded these four zoeae as belonging to either *Spirontocaris groenlandica* (= *L. groenlandicus*), *S. gaimardii* (= *Eualus gaimardii* (H. Milne Edwards)), or *S. spinus* (Sowerby). Pike and Williamson (1961) have shown that the absence of spines on abdominal segments four and five eliminates the zoeae from being either *E. gaimardii* or *S. spinus*. They agree with Stephensen that his specimens of "*Spirontocaris*-larva No. 1A" are closely allied to zoeae he tentatively described earlier (Stephensen 1917, 1935) as *S. polaris* (= *L. polaris*). They suggest, therefore, that Stephensen's "*Spirontocaris*-larva No. 1A" probably belongs to the genus *Lebbeus* and specifically to *L. groenlandicus*.

Comparison of my zoeae of *L. groenlandicus* with the descriptions given by Stephensen for "*Spirontocaris*-larva No. 1A" shows that "*Spirontocaris*-larva No. 1A" are not zoeae of *L. groenlandicus*. My Stage I zoeae bear remnant exopodites on the first and second pereopods and lateral spines on abdominal segments four and five, but Stephensen's Stage I zoeae bear neither the exopodites nor the spines. My Stage I zoeae do not bear supraorbital spines, the peduncle of the antennule is without joints or a ventral spine, and there is no indication of the carpopodite of the second pereopod being jointed; Stephensen's Stage I zoeae bear supraorbital spines, the peduncle of the antennule is three-jointed and bears a distinct ventral spine, and the carpopodite of the second pereopod is partially jointed. In addition, the chelae of the first and second pereopods are not as well formed in my Stage I zoeae as they are in Stephensen's Stage I zoeae.

Several of the morphological characteristics described by Stephensen as pertaining to "*Spirontocaris*-larva No. 1A" are typical of later stage zoeae, a fact already noted by Pike and Williamson (1961) in their discussion of the morphology of the zoeae of *L. polaris* and which prompted them to suggest that Stephensen's zoeae were actually in the second, or penultimate, zoeal stage. Even if Stephensen was mistaken in identifying his zoeae as Stage I rather than Stage II, the morphological differences between my zoeae and his are too great to consider them identical species. My Stage II zoeae bear spines on abdominal somites four and five and the telson is segmented from the sixth abdominal somite, whereas Stephensen's zoeae do not bear spines on abdominal somites four and five and the telson is not segmented from the sixth abdominal somite. Also, in my Stage II zoeae the peduncle of the antennule does not bear a ventral spine and is unsegmented but in Stephensen's zoeae the peduncle bears a ventral spine and is segmented.

I have no further evidence on the identity of Stephensen's "*Spirontocaris*-larva No. 1A." Of the three members of the genus recorded from Greenland waters, *L. polaris, L. groenlandicus,* and *L. microceros* (cf. Holthuis 1947; Squires 1966), *L. microceros* was not recorded by Stephensen. Apparently it is rare and its larvae have not been described. Also, the advanced development of Stephensen's "*Spirontocaris*-larva No. 1A" makes it unlikely that it belongs to another genus of the spirontocarid group (cf. Pike and Williamson 1961). Apparently Stephensen's "*Spirontocaris*-larva No. 1A" is either the zoea of *L. microceros* or that of another species of *Lebbeus* not yet recorded from Greenland waters.

On the basis of descriptions of "*Spirontocaris*-larva No. 1A" by Stephensen (1935) and a late stage embryo of *Hippolyte polaris* (= *L. polaris*) by Krøyer (1842), Pike and Williamson (1961)

characterized larvae of the genus *Lebbeus* as having two (or three) zoeal stages, five-segmented pereopods, and a small rostrum in Stage I, and pereopods without exopodites in the last zoeal stage. My description of larvae of *L. groenlandicus* confirms the generic characteristics for *Lebbeus* larvae as given by Pike and Williamson. As noted by Pike and Williamson, however, larvae are described for only a few species of hippolytids, including the genus *Lebbeus*, and further confirmation of the generic characteristics of the larvae is desirable.

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PREDICTING ABUNDANCE OF STRIPED BASS, *MORONE SAXATILIS*, IN NEW YORK WATERS FROM MODAL LENGTHS[1]

HERBERT M. AUSTIN[2] AND CLARENCE R. HICKEY, JR.[3]

ABSTRACT

The abundance of cohorts for any given year class of striped bass, *Morone saxatilis*, prior to their leaving Chesapeake Bay is inversely related to the modal length of fish in that year class 2 yr later in New York waters. The modal length of bass in their third year migrating into the New York area is a reliable index of the abundance of that year class. When back extrapolated modal lengths at the end of the second year of life are considered for the dominant year classes in the New York fishery (ages III-VI), a high degree of inverse correlation is found between age II and modal length and reported landings suggesting that this is an effective method of predicting the abundance of the stock for the fishery.

In discussing natural fluctuations in fish populations, Royce (1972) posed the question, "... can we forecast their occurrence to take maximum advantage of periods of high abundance and protect populations during periods of scarcity?" This question is pertinent to the striped bass, *Morone saxatilis*, stocks of the Atlantic coast of the United States. The Atlantic coast commercial catch of this species, while following a pattern of fluctuations, has been in an upward trend in recent years, apparently as a result of an increasing abundance of fish (Koo 1970; McHugh 1972). This increasing abundance has been reflected by an increased commercial harvest in the State of New York. Concurrently, although not as well documented, is an increase in the number of recreational fishermen utilizing the resource. Both phenomena necessitate the gathering of management information while the resource is still in good condition.

Most (>80%) of the New York commercial harvest of striped bass occurs in the waters of eastern Suffolk County (Figure 1) where the major fisheries are primarily with haul seine and pound net. Fish taken in this region are predominantly of Chesapeake Bay origin (Neville et al. 1939; Alperin 1966; Schaefer 1968, 1972; Koo 1970; Austin and Custer 1977; Austin and Hickey;[4] Texas Instruments, Inc.[5]).

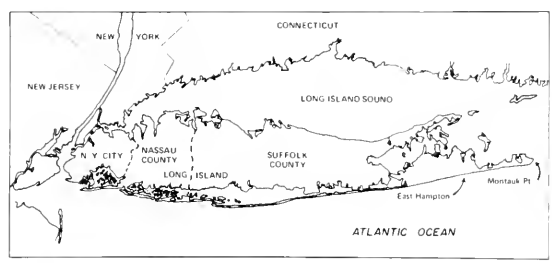

FIGURE 1.—Location of Long Island, N.Y., and the southeastern tip near Montauk Point where striped bass were collected during 1972 and 1974.

This study was designed as one phase of a program to tag and monitor "short" or prerecruit striped bass (less than the legal, 406-mm New York State limit). As stated by Talbot (1966), little is known of these fish outside of their nursery areas. Monitoring of these fish, then, permits study of the next year's catch, a segment of the striped bass population often overlooked in fishery investigations.

Prerecruit striped bass in New York waters of eastern Long Island are predominantly 2- and

[1]New York Ocean Science Laboratory, Contribution No. 82. Funded by a grant to the New York Ocean Science Laboratory from the State of New York, Project No. BR74-17F.

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[3]Environmental Specialists Branch, U.S. Nuclear Regulatory Commission, Washington, DC 20555.

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Manuscript accepted September 1977.
FISHERY BULLETIN: VOL. 76, NO. 2, 1978.

3-yr-old fish which are making their first annual migration from their Chesapeake Bay nursery areas to the northern summer feeding ground (Austin and Hickey see footnote 4). The concentrated study of one age-group of fish permits monitoring of the cohorts for successive years starting with first departure from their home grounds and, thereby, permits a description of differences or variations in migration and abundance on an annual basis, as well as an accurate evaluation of year class mortality in successive years.

METHODS AND MATERIALS

Prerecruit striped bass were randomly removed from the catches of commercial haul seine and pound net fishermen in the waters of East Hampton on the southeastern end of Long Island, N.Y. (Figure 1). Samples were collected during May and June 1972 and April-June 1974, thus the age II fish were of the 1970 and 1972 year classes, respectively. Fork lengths were measured in the field to the nearest millimeter and scale samples were removed for age determination. The fish were then tagged (Floy[6] FD-69B anchor tags) and released. The initial purpose of the study was tagging of prerecruit fish to monitor the seasonal migration and mortality of cohorts as they reached legal size in the different states. The feasibility study was focused on the 1970 and 1972 year classes. Large differences in the modal size of the fish in their third year (II+) existed between the two year classes (Figure 2). The smaller sized 1970 year class of fish were from the most abundant Chesapeake Bay year class on record (Schaefer 1972). Examination of the literature shows that the length of cohorts may be inversely proportional to the abundance or density of the fish (Stevens 1977; Texas Instruments[7]), suggesting to us that the length of the striped bass, when they first appear in New York waters, could be an indicator of year class strength and subsequently a means of predicting stock abundance in local waters. Consequently the focus of the study was redirected towards examination of these differences.

Schafer (1968, 1972) stated that most commercially harvested striped bass in New York are of four age-classes, III-VI. Based on this, Schaefer

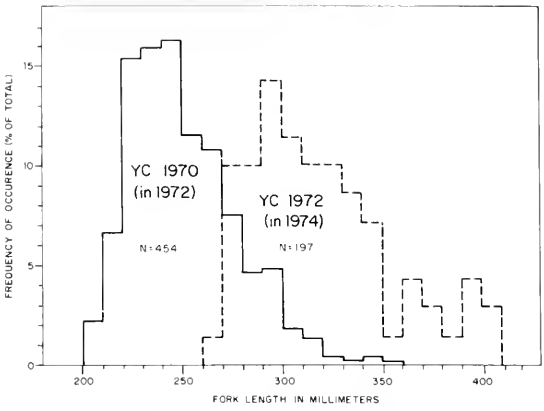

FIGURE 2.—Length-frequency distribution of age II striped bass captured by commercial fishing gear near eastern Long Island, N.Y., during 1972 and 1974.

(1972) related the New York harvest to a 4-yr mean brood production (year class strength; expressed as annual mean number of juveniles per standard seine haul in Chesapeake Bay, Md.) 3 to 6 yr prior to the harvest. He concluded that approximately 70% of the variability in annual New York landings could be explained by annual fluctuations in year class strength in Maryland waters of Chesapeake Bay.

We hypothesized that the growth rate of striped bass, and, therefore, the body length at the end of the 2-yr residence time in the Chesapeake Bay nursery grounds, is a density dependent function with the length inversely proportional to the year class abundance (number of fish). This hypothesis was tested via a correlation analysis using modal lengths at age II+ (our data combined with published data of Alperin 1966 and Schaefer 1968) and year class abundance indices supplied by the Maryland Department of Natural Resources. The analyses were performed using a Hewlett-Packard Model 9100B programmable calculator with an X-Y plotter, which provided both a regression line and a correlation analysis and coefficient.

The relationship resulting from the above analysis suggested that the density dependent hypothesis is true. Since Schaefer (1972) described a relationship between the annual New York harvest (reported commercial landings) of striped bass and the Chesapeake Bay year class abundance, and since we have described a probable relationship between year class abundance and modal length at age II+ in New York waters, it seemed reasonable to test the correlation between

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

[7]Texas Instruments, Inc. 1975. First annual report for the multiplant impact study of the Hudson River estuary. Unpubl. rep., vol. 1, p. VIII-8-VIII-12. Texas Instruments, Inc., Dallas, Tex.

the New York harvest and the modal length at age II+ via Model II correlation analysis.

These analyses were performed in an effort to describe a method for predicting the commercial harvest (and therefore the apparent abundance) of striped bass in New York waters. As each of the several steps in the analyses were dependent on the results of those previously calculated, they are discussed in more detail along with the results below.

The reliability of the suggested technique for predicting the abundance of striped bass in New York waters is dependent on several assumptions:

1) The Chesapeake Bay stock of fish is the major contributor of striped bass to the New York commercial fishery, as suggested by the several authors noted above;
2) The annual relative contribution of the several Atlantic coastal breeding stocks to the coastal stock of fish and, therefore, to the New York fishery remains constant or that it fluctuates or cycles in a consistent manner;
3) The commercial fishery for striped bass in New York effectively collects representative "samples" of the Chesapeake Bay stock of fish; this assumption appears to be valid based upon the relationships described by Schaefer (1972), Texas Instruments, Inc. (see footnote 5) and those described herein, and based upon our observations and those of Schaefer (1972) that many size classes of fish are present in the commercial catch—small age II prerecruits to large mature fish >16 kg total weight;
4) The forecast of commercial striped bass landings is based upon past historical landings in relation to past life history events of the species (year class abundance and length at age II+) and does not reflect changes in commercial fishing effort or any changes in the contributions to the reported landings by recreational fishermen; we have assumed a constant fishing effort, as did Schaefer (1972), and thus compared our results with his; while we recognize the weakness in this assumption, there is no alternative as there is no estimate of effort.

RESULTS AND DISCUSSION

Year Class Strength and Modal Size

The lengths of striped bass at age II+ near Long Island are probably related to ecological circumstances encountered by the fish during their first 2 yr of residence in the rivers of Chesapeake Bay (density, competition, amount of available food). Similarly, Cushing (1968) found a close relationship between the mean length of age III Atlantic herring, *Clupea harengus*, and the density of their food source in the sea, and Clark (1967) described reduced growth rates for sunfish, *Lepomis*, due to overcrowding, excessive competition, and reduced food supply. It has also been demonstrated by Anthony (1971) that the growth of young (age I and II) Atlantic herring is inversely related to their abundance, and Wagner (1969) has stated that in most fishes the growth rate per individual is inversely related to their density.

If an inverse relationship exists between the abundance of a year class of striped bass and the cohort length at age II+, a similar relationship should exist between the commercial harvest (as an index of abundance) and the length at age II+, assuming that fishing effort remains approximately constant. To test this hypothesis, age II+ modal length data for year classes 1970 and 1972 (Figure 2) were combined with other published modal length data for year classes at age II+ in New York waters from Alperin (1966) and Schaefer (1968) (Table 1), providing a total of eight annual data points. A correlation analysis was performed between these eight annual modal lengths of age II+ fish and their respective Chesapeake Bay year class strengths 2 yr earlier (Figure 3). The year class strength data (supplied by the Maryland Department of Natural Resources) are expressed as the annual mean

TABLE 1.—Comparison of observed and computed modal fork lengths for age II striped bass in New York waters.

Year class	Year class strength[1]	Observed modal length at age II (mm)	Computed modal length at age II[2] (mm)
1954	5.2	[3]313	318
1958	18.1	[4]285	278
1959	1.3	[3]335	330
1960	6.4	[3]310	314
1961	14.4	[3]290	289
1962	12.2	[3]300	296
1970	26.8	[5]245	251
1972	8.5	[5]295	307
Mean		297.9±53.0	297.9±50.4
Standard deviation		26.5	25.2
$t_r = 6.99$			
$n = 8$			
$P<0.001$			

[1]Courtesy Joseph Boone, Maryland Department of Natural Resources, Annapolis, Md., data expressed as annual mean number of age 0+ juveniles per standard seine haul.
[2]Based on the relationship $Y = 333 - 3X$, where Y is the modal length of age II+ fish and X is the strength of the year class (Figure 3).
[3]Extrapolated from Schaefer (1968).
[4]Extrapolated from Alperin (1966).
[5]Data from the present investigation.

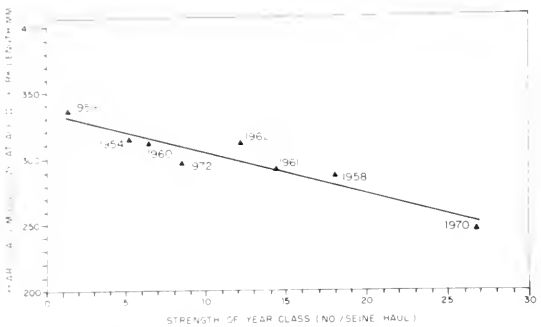

FIGURE 3.—Modal size (mm fork length) of age II striped bass from Long Island waters as a function of Chesapeake Bay year class strength. Year classes are indicated.

number of age 0+ juveniles per standard seine haul near the Maryland shores of Chesapeake Bay. These are the same data used by Schaefer (1972). The relationship ($Y = 333 - 3X$) yielded a correlation coefficient of -0.95 ($r^2 = 0.90$), suggesting that 90% of the annual variation in modal length at age II+ for striped bass in New York waters can be explained by annual fluctuations in year class abundance in the waters of Chesapeake Bay.

Modal Size and the New York Commercial Harvest

The equation described above ($Y = 333 - 3X$) was used to calculate (and thus to estimate) modal lengths of age II+ fish for those 8 yr for which actual modal lengths exist. A t-test comparison between the observed age II modal sizes and those computed using the correlation formula above showed no significant difference at the 0.001 probability level (Table 1). Since no significant difference existed between the observed and calculated modal lengths, the assumption was made that reliable modal lengths could be calculated for years in which no actual measurements exist. The equation described above was, therefore, used to estimate modal lengths of age II+ striped bass for all years between 1954 and 1972, using the corresponding year class abundance data. A correlation analysis was then performed (similar to that done by Schaefer 1972) between the New York landings of striped bass (Y) and a 4-yr mean of the computed modal lengths of age II+ fish 1 to 4 yr prior to harvest (X). The relationship ($Y = 15{,}205{,}309 - 46{,}859X$) (Figure 4A) yielded a correlation coefficient of -0.86 ($r^2 = 0.74$) significant at the 0.001 probability level ($t_r = 6.06$, $n = 13$). This expression permits the hindcasting of New York landings as well as a forecast 1 yr in advance, with 95% confidence limits. The hindcasts and 1-yr forecasts (for 1975) are superimposed on the actual New York landings in Figure 5A.

As stated by Schaefer (1968, 1972), the New York harvest is predominantly fish of ages III-VI. Close examination of his catch data for 1962, however, revealed that age VII fish, although <2% of the catch in number, could constitute a significant proportion of the catch by weight. Schaefer's (1968) age-frequency distribution shows that in 1962 the age III fish outnumbered the age VII by about 10:1. Using the mean age-weight relationships of Mansueti (1961) as 1.8 lb at age III and 12.5 lb at age VII, the age III fish in Schaefer's (1968) 1962 catch thus outweighed the age VII fish by less than 1.5:1. Similarly, the age VI fish (mean

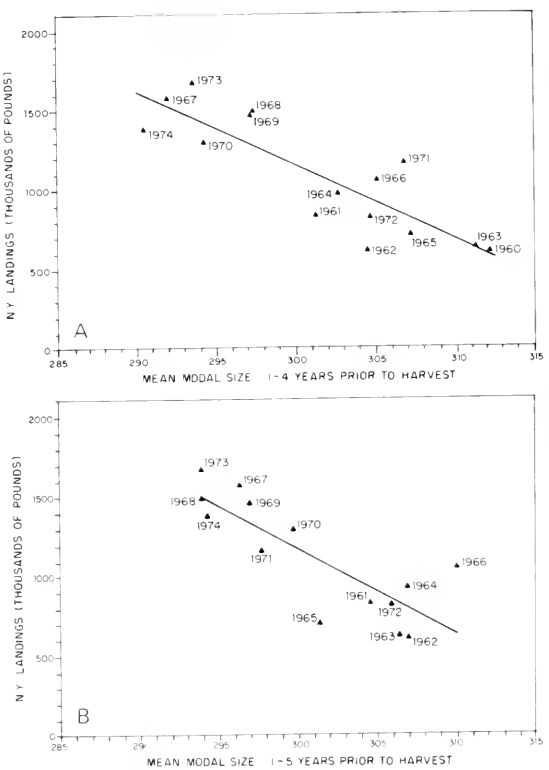

FIGURE 4.—Relationship of New York commercial landings of striped bass to the mean modal size at age II: A) 1 to 4 yr prior to harvest; B) 1 to 5 yr prior to harvest.

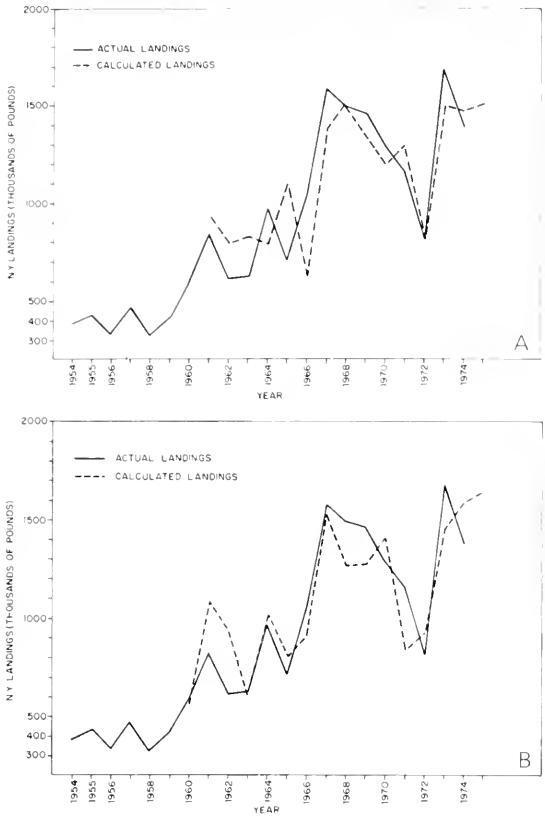

FIGURE 5.—Actual New York commercial landings of striped bass from 1954 through 1974 with calculated landings through 1975 superimposed using: A) 4-yr mean modal sizes of age II fish; B) 5-yr mean modal sizes of age II fish.

weight 8.1 lb) outnumbered the age VII fish by 2:1, but outweighed them by only 1.3:1.

It was apparent that during some years the New York harvest of striped bass may be dominated by five age-groups rather than four, as suggested by Schaefer (1972). Another correlation analysis was, therefore, performed between the New York landings (Y) and a 5-yr mean of the computed modal sizes of age II+ fish 1 to 5 yr prior to harvest (X). This 5-yr function was expressed as a linear relationship ($Y = 17{,}315{,}491 - 53{,}810X$) (Figure 4B) with a correlation coefficient of -0.83 ($r^2 = 0.69$), significant at the 0.001 probability level ($t_r = 5.05$, $n = 12$). Although this coefficient was reduced slightly from that of the 4-yr function above ($r = -0.86$), the fit of estimated-to-actual landings (with 95% confidence limits) was better for many years (Figure 5B) and was closer to the actual landings than the calculated predictions of Schaefer (1972) (Table 2).

Size, Age, and Migration

As stated, age II+ modal sizes may be computed. Another method of size determination at age II+ is by back calculation of scale radii from larger, older fish. Although no age II modal sizes determined by this method were used in the predictive models, our attempts to do so produced some interesting information. Mansueti (1961) described the body length-scale length relationship of striped bass as an allometric linear function, permitting the back calculation of size at each year of age using the scale radii method. Scales from 142 age III striped bass captured in eastern Long Island waters during 1973 (year class 1970) were made available to the authors by the New York State Department of Environmental Conservation. The ages were rechecked and the fork lengths at age II determined by back calculation from body length:scale radii ratios. The length-frequency distribution of back-calculated data was bimodal, with equal peaks at 205 mm and 235 mm. The second peak was 4.1% lower than the observed unimodal size of 245 mm. Although the back calculated values were slightly lower than the observed, the fit suggests that back calculations may be used for obtaining age II sizes of striped bass during years when these data are lacking.

Unpublished length-frequency data for age II striped bass of the year classes 1968, 1969, and 1971 taken in the Virginia rivers of the Chesapeake Bay System were made available to the authors by John V. Merriner of the Virginia Institute of Marine Science. These data showed bimodal distributions similar to that of the back-calculated age II lengths above (Merriner pers. commun.). Merriner suggested that multimodal frequencies occurred because the fish were from different river systems. Merriner's data were from Virginia rivers while our data (Austin and Hickey

TABLE 2.—Comparison of actual and calculated commercial landings of striped bass in the State of New York 1972-75.

Year	Actual landings[1]	Calculated landings 4-yr function[2]	Calculated landings 5-yr function[2]	Calculated landings by Schaefer (1972)
1972	818,150	926,903	852,860	908,000
1973	1,673,984	1,447,975	1,496,965	1,455,000
1974	1,378,529	1,592,301	1,477,594	1,607,000
1975	1,137,074	1,639,160	1,500,732	—

[1]Courtesy Fred Blossom, National Marine Fisheries Service, NOAA, Patchogue, N.Y.
[2]Forecasts using the linear regression formulae discussed in the text

see footnote 4) suggest that the bass we examined for back calculation of length were from both Maryland and Virginia rivers, which could explain the differences in the results of the back calculations and the observed lengths. These data suggest that the size-frequency distribution of age II striped bass on Long Island could be bimodal rather than unimodal. The fact that they were not may be due to striped bass migrating by size rather than by age. Two observations of prerecruit striped bass near Long Island lend support to this theory: 1) 100% of the small 454 sublegal fish tagged in 1972 were age-group II, and 2) only 28% of the 696 sublegal fish tagged in 1974 were age-group II (year class 1972), the remaining 72% were age-groups III (65%) and IV (7%). Those fish probably were the larger 1972 and the smaller 1971 and 1970 fish. This large overlap in length ranges permitted an intermingling of the age-classes during the migration of 1974.

Management Implications

The size increments between different year classes at the same age, and the size differences of individuals within the same year class have several implications:

1) Faster growing large individuals of any given year class or a less abundant year class of larger individuals are subject to earlier exploitation in Chesapeake Bay and along the entire Atlantic seaboard;
2) Slower growing individuals or small individuals of a large year class may be recruited several months later than normal in Chesapeake Bay, but perhaps not until a full year later among the northern Atlantic States; a late recruitment in the Chesapeake area might result in more available fish to the fisheries in the other coastal states when the fish migrate out of the bay;
3) Projecting sizes of fish on the basis of age or vice versa may be invalid, e.g., age II fish in 1972 compared with age II fish of Merriman (1941) or Mansueti (1961).

The use of a mean 4- or 5-yr modal function for prediction of landings treats all year classes equally. A weighted mean providing greater representation to more abundant year classes might result in more accurate predictions of landings. Such a method could be used by any State simply by monitoring the spring catches of age II+ prerecruit fish taken by commercial fishermen. This would require, in New York for example, annual monitoring of the spring run with measurements of sublegal fish. The use of observed modes rather than computed modes for prediction of landings will probably result in more accurate estimates, as suggested in Table 3.

TABLE 3.—Comparison of actual New York commercial landings of striped bass with those calculated using computed and observed age II modal values, for years in which sufficient empirical data exist.[1]

Item	1964	1965
Actual N Y landings	925,500	702,935
4-yr function:		
Landings calculated using		
Computed modes	1,021,090	807,881
Empirical modes	913,314	618,102
5-yr function		
Landings calculated using		
Computed modes	799,588	1,098,771
Empirical modes	—	849,631

[1]Computed and observed age II modal values are those on Table 1.

The eastern New York commercial harvest of striped bass is primarily dependent upon the year class abundance of the Chesapeake Bay stock. The harvest is influenced not only by the larger and older individuals, but also by the annual recruitment of age III fish, especially when dominant year classes are present.

Knowledge of Chesapeake Bay year class strength or age II+ modal sizes in New York waters offers a means of forecasting the New York commercial harvest, and thus the apparent abundance of striped bass in New York waters.

If, as suggested, the level of the New York harvest is primarily related to the Chesapeake Bay stock of fish, than the former can be used as a qualitative measure of the latter.

Such predictive tools as those discussed should be flexible to allow for the occurrence of more than four age-groups of fish in the catch. This may be especially important when dominant year classes are present for several years. Necessary, then, is the annual monitoring of the prerecruit fish in the commercial catch by age or year class, length, and weight. Age-weight data are especially important as commercial landings are recorded by weight of catch and not by numbers of fish. Differences noted between calculated and observed landings may be due to environmental variability, changes in fishing effort, the dominance of a particular year class in the fishery, and the fluctuation in the relative contributions of fish from the several At-

lantic coastal breeding grounds. Future research and managment efforts should take these into consideration.

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NOTES

OBSERVATIONS ON A WHITE-SIDED DOLPHIN, *LAGENORHYNCHUS ACUTUS*, PROBABLY KILLED IN GILL NETS IN THE GULF OF MAINE

On 20 July 1976, a white-sided dolphin, *Lagenorhynchus acutus,* was observed floating with its beak out of the water on Jeffreys Ledge, Maine (lat. 43°09'N, long. 70°04'W). The 201-cm long female weighed 113.2 kg and was freshly dead, still bleeding freely from symmetrical injuries to the left and right sides of both the upper and lower jaws and the flippers. The lungs contained foamy materials and were mottled white, indicating drowning as the immediate cause of death. Many gill nets were present in the area, and the symmetrical nature of the injuries indicated that the animal had become entangled in the mesh, drowned, and perhaps been freed or discarded during hauling of the net. A humpback whale, *Megaptera novaengliae,* was entangled in a gill net for 2 h before freeing itself on the same day in the same general area.

Gross autopsy revealed several cysts in the abdominal muscles of the lower left side and a 5 cm × 7.5 cm yellow, pussy abscess 15 cm anterior and dorsal to the right mammary gland, perhaps caused by a bladderworm stage (plerocercoid) of *Monorygma grimaldi* (Geraci et al.[1]). No other parasites were found, although all major organs except the brain were inspected. Tissue and organ weights are shown in Table 1. The length and weight of this animal fit well on a regression line developed for this species (Geraci et al. see footnote 1). From a length-age relationship (Geraci et al. see footnote 1), it is likely that this female was between 2½ and 3 yr old, and was immature.

The stomach contained 980 g of food, including four 25- to 30-cm herring, *Clupea harengus,* three partly digested (total weight 340 g) and one skeleton (15 g); and one partly digested short-finned squid, *Illex illecebrocus* (anterior mantle length 17.5 cm, weight 90 g), with remains of 10 other squid of this species (represented by 5 complete pairs of beaks plus 5 single anterior beaks). Mean length of anterior beaks (± SD) was 1.42 ± 0.03 cm, corresponding to mantle lengths from 17 to 19 cm (Testaverde[2]). Also 10 left and 11 right otoliths from silver hake, *Merluccius bilinearis,* (mean size ± SD = 1.15 ± 0.06 cm) indicated consumption of at least 11 fish of 22-26 cm fork length (Nichy 1969).

From these data and the literature it appears that *C. harengus* and *I. illecebrocus* are staples in the summer diet of white-sided dolphins. A 161-kg female collected on 14 September 1954, off Cape Cod contained 12 fresh herring, digested fish (apparently herring), and squid (Schevill 1956). A 180-cm long male driven ashore with pothead whales, *Globicephala melaena,* in Newfoundland on 30 July 1954, contained herring and short-finned squid (Sergeant and Fisher 1957). Short-finned squid was the most common food in the stomachs of white-sided dolphins which mass-stranded at Lingley Cove, Maine, on 6 September 1974; however, no herring were found despite the fact that "brit" herring were present in the cove (Geraci et al. see footnote 1). Smelt, *Osmerus mordax,* remains, were found in five individuals; silver hake had been eaten by one individual; and unidentified crustacean remains were found in another stomach.

Schools of white-sided dolphins were unusually common in the Gulf of Maine in 1976, perhaps because squid were abundant, possibly as a result of this year's unusually high sea temperatures

TABLE 1.—Tissue and organ weights of a *Lagenorhynchus acutus* from Jeffreys Ledge, Maine. Weights not corrected for blood loss.

Tissue or organ	Weight (kg)	Tissue or organ	Weight (kg)
Muscle	69.0	Left kidney	0.473
Blubber and fins	24.5	Right adrenal	0.011
Gastrointestinal tract	6.8	Left adrenal	0.010
Liver	3.2	Spleen	0.084
Heart	0.959	Right ovary	0.0051
Right lung	1.117	Left ovary	0.0047
Left lung	1.149	Bones[1]	5.4
Right kidney	0.476	Total	113.2

[1]Bones were bleached and dried in the laboratory

[1]Geraci, G., S. A. Testaverde, D. J. St. Aubin, and T. H. Loop. 1976. A mass stranding of the Atlantic white-sided dolphin, *Lagenorhynchus acutus:* a study into pathobiology and life history. Unpubl. manuscr., 166 p. submitted to Marine Mammal Commission by New England Aquarium, Boston.

[2]Testaverde, S.A. 1975. An informal discussion concerning the cestode *Phyllobothrium* sp. in squid, *Illex illecebrocus illecebrocus* and its possible relationship to marine mammals. Unpubl. manuscr., 20 p.

(Anonymous 1976; Prescott and Moore 1976). Silver hake, normally of variable abundance here (Bigelow and Schroeder 1953) was also abundant during 1976. On several different occasions, groups of 6-30 white-sided dolphins were seen by one of us (SKK) swimming close to pods of either finback whale, *Balaenoptera physalus*, or humpback whale, *Megaptera novaeangliae*, and apparently feeding with them.

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RECIPROCAL HYBRIDIZATION BETWEEN THE CALIFORNIA AND GULF OF CALIFORNIA GRUNIONS, *LEURESTHES TENUIS* AND *LEURESTHES SARDINA* (ATHERINIDAE)

The California grunion, *Leuresthes tenuis*, and the Gulf of California grunion, *L. sardina*, are the only fishes that temporarily leave the water during spring high tides to deposit their eggs in beach sand (Walker 1952). The eggs develop in the nearly dry sand and hatch when uncovered and agitated by the surf of the next series of high tides.

The grunions have an allopatric distribution. The California grunion ranges from Monterey Bay, Calif., to Bahia Magdalena, Baja California Sur. The Gulf grunion is endemic to the Gulf of California, ranging from Bahía Concepcíon, Baja California Sur, and Guaymas, Sonora, Mexico to the mouth of the Río Colorado (Moffatt and Thomson 1975).

Recent comparisons show that morphological, physiological, and behavioral differences exist between the grunions. Morphologically very similar, the most diagnostic characterictics distinguishing them are lateral scale row counts; the mean number in *L. tenuis* is 75 and in *L. sardina* is 55. Gulf grunion adults are also significantly longer, more slender, have a smaller eye diameter, and are more lightly pigmented than those of the California grunion (Moffatt 1974; Moffatt and Thomson 1975). Gulf of California grunion have wider embryonic and larval thermal tolerances, a higher larval preferred temperature, and wider larval salinity tolerances (Reynolds and Thomson 1974a, b, c; Reynolds et al. 1976, 1977; Moffatt 1977).

Light response remains positive in Gulf grunion through adulthood, whereas the response shifts from positive in the larvae to negative in the adults of the California grunion (Walker 1952; Reynolds and Thomson 1974c; Reynolds et al. 1977). In response to the shorter wave period in the northern Gulf of California, the duration of the spawning act of the Gulf grunion females is much briefer than that of the California grunion females (Thomson and Muench 1976; Muench 1977).

Only recently has the congeneric status of the grunions been recognized (Moffatt 1974; Moffatt and Thomson 1975). Evidence to date indicates that the California grunion, the less primitive of the two species, has adapted to the less fluctuating tidal and thermal regimes of the California coast, following isolation from an ancestral type by the

Baja California peninsula (Moffatt and Thomson 1975; Moffatt 1977).

Hybridization and hybrid survival experiments have been widely used as indices of divergence and have made valuable contributions as a tool in the definition of phylogenetic relationships (Hubbs 1967, 1970). In an attempt to further illuminate the relationship between the grunions, we made artificial and reciprocal crosses and we report on the first successful reciprocal hybridization of *Leuresthes tenuis* and *L. sardina*.

Materials and Methods

Adult grunions, although easily obtained in large numbers, are difficult to maintain and transport alive. On 18 March 1976 (2330 PST), milt from six California grunion males was collected at Scripps Beach, La Jolla Calif., mixed in the beaten yolks of two hen eggs (Bratanov and Dikov 1961), and transported to El Golfo de Santa Clara, Sonora, Mexico. The milt-yolk mixture, maintained between 16° and 20°C, was used to fertilize the eggs from 8 to 10 Gulf grunion females obtained at El Golfo on the following day (19 March) during a spawning run which began about 1700 MST. During this same run Gulf grunion milt was collected from 6 to 7 males, transported in the same manner and used to fertilize California grunion eggs from about 10 females obtained during a run that night at La Jolla at 0115 PST (20 March). One prior and four subsequent attempts to hybridize the grunions were made during the 1975, 1976, and 1977 spawning seasons, but these were unsuccessful because one or both grunions failed to spawn.

The female grunions were rinsed thoroughly in clean seawater before their eggs were stripped directly into the milt-yolk mixture. The mixture was diluted slightly with fresh seawater to increase sperm motility, gently agitated, and kept cool until the end of the spawning run. The eggs were then strained, rinsed with seawater, and placed in plastic refrigerator containers between moist paper towels for transport and incubation.

Conspecific control embryos of each species were obtained by mixing eggs and milt in a bucket of seawater, one-third full, and did not involve the transportation or preservation of milt in hen yolk. When spawning individuals were plentiful, as at the Gulf grunion run on 19 March, six to nine males were stripped per one female in order to achieve maximum fertilization levels (Moffatt 1977).

Both sets of hybrid fertilized eggs and the conspecific controls of *L. tenuis* (18 March) and *L. sardina* (19 March) were transported from San Diego, Calif., to the University of Arizona at Tucson aboard commercial airlines. Upon arrival (22 h postfertilization in *L. sardina* × *L. tenuis* and *L. sardina* controls; 13 h in *L. tenuis* × *L. sardina;* and 32 h in *L. tenuis* controls) each set of eggs was inspected. Their development was monitored daily thereafter.

Both California grunion spawning runs were sparse at La Jolla. Therefore, the greatest portion of eggs and sperm available were devoted to the hybridization experiments and a low conspecific *L. tenuis* sample size resulted. Consequently, the developmental and hatching data reported herein for these embryos are a compilation of these few controls and egg sets obtained on other occasions, incubated at 20°C from 12 h postfertilization (Moffatt 1977).

Yolk-sac larvae of the two hybrids and the conspecific controls were placed in separate tanks containing artificial seawater and raised on newly hatched *Artemia,* freeze-dried marine zooplankton, commercial staple food, and frozen *Artemia* nauplii. Larvae of the hybrids and controls were maintained for nearly 5 mo although initial mortality rates (first 2 mo) in all groups were high (>90%). On 19 August, 141 days posthatching, the aquaria air lines were fouled by compressor oil and the few remaining hybrids and controls died. Only two *L. tenuis* × *L. sardina* and nine *L. sardina* × *L. tenuis* individuals survived to a size (>12 mm) at which the scale rows could be counted. This is not to imply that scales might not have been present prior to this time, merely that no attempt was made to count them.

Results

At 22 h postfertilization, cleavage had progressed to the gastrula stage in *L. sardina* × *L. tenuis* embryos as it had in the *L. sardina* controls. The *L. tenuis* × *L. sardina* hybrids had reached a 32-cell blastodic stage at 13 h postfertilization as do *L. tenuis* embryos.

Artificial fertilization levels in the conspecific controls fell between 85 and 99% during the peaks of their spawning seasons when male to female ratios of 6 or 9:1 were available. The fertilization

levels of both hybrids ranged from 60 to 70%. These diminished levels in the hybrids may have resulted from a combination of several factors such as: the low male to female ratios used (<1:1); decreased sperm motility in the viscous hen-yolk medium; high sperm mortality due to time, starvation, temperature shock, handling, etc. or partial reproductive isolation between the species in the form of mild fertilization block to nonconspecific spermatozoa.

The grunions, *L. tenuis* and *L. sardina*, showed similar developmental rates (Moffatt 1977). Development proceeded normally in the hybrids and at about the same rate as the controls. No unusual embryonic mortality was observed in the hybrids, evidence that these embryos were not gynogenetic hybrids (Moore 1955).

Preliminary trials showed that hen's yolk and seawater alone will not initiate cleavage in Gulf grunion eggs. Precautions were taken to prevent conspecific milt contamination. Preliminary examination of cellular nuclei smears of developing embryos immersed in colchichine revealed somatic chromosome numbers of about 2n = 40 in all four sets of embryos (controls and hybrids), further evidence that these embryos were true diploid hybrids.

Grunion embryos will hatch after vigorous agitation in seawater. On 31 March at 284 h (11.8 days) postfertilization, 65.6% of the *L. sardina* × *L. tenuis* embryos hatched and 66.5% of the *L. tenuis* × *L. sardina* embryos hatched at 272 h (11.4 days). These hatch times are similar to those of the controls. Hatching can be induced in both grunions at 10.2 days postfertilization when embryos are incubated at 20°C (Moffatt 1977).

Newly hatched *L. tenuis* larvae are typically more darkly pigmented; they have a larger eye diameter; they are stronger swimmers; and they are more capable of escaping net capture than newly hatched *L. sardina* larvae (Moffatt 1977). *Leuresthes tenuis* larvae are 10% longer (mean total length = 7.70 mm) than those of *L. sardina* (mean total length = 6.93 mm). The greater length of the California grunion yolk-sac larvae occurs in the postanal region as in the adults. California grunion larvae are also 52% heavier (mean dry weight = 0.340 mg) whereas, the mean dry weight of *L. sardina* equals 0.223 mg (Moffatt 1977). The greater length and weight of the California grunion at hatching may be attributable to the 4.10 times greater ovum volume (Moffatt 1977; Moffatt and Thomson in press).

These differences which distinguish the prolarvae of *L. tenuis* and *L. sardina* were also observed in the hybrids. In most characteristics the *L. tenuis* × *L. sardina* larvae were not visibly distinguishable from the maternal controls (*L. tenuis*), e.g., size, pigmentation, and swimming ability. However, the *L. sardina* × *L. tenuis* larvae appeared to be somewhat intermediate to the controls in extent of pigmentation and swimming ability. At 2 wk after hatching the length and pigment differences between the larvae were more pronounced. Premaxillary teeth were visible in the *L. sardina* × *L. tenuis* larvae but not in the reciprocal hybrids. Again, hybrids closely resembled the maternal controls. Gulf grunion adults typically have much stronger dentition than do the adults of the California grunion (Moffatt and Thomson 1975).

As previously mentioned, the most diagnostic differences between the adult grunions are the lateral scale row counts. Scale counts of the 141-day-old controls were essentially the same as those of the adults (Table 1). The counts of the hybrids were intermediate and significantly different from each other. Those shown by both hybrids were significantly different from those of both parental species. The lateral scale rows of the hybrids were closer in number to those of the maternal controls. Mean counts of *L. sardina* × *L. tenuis* were 32% closer to those of *L. sardina;* and *L. tenuis* × *L. sardina* were 20% closer to *L. tenuis* than to those of the paternal parents, *L. tenuis* and *L. sardina*, respectively.[1] The intermediate counts indicate paternal genome influence and that these are indeed diploid hybrids.

[1]A mean hybrid count greater or less than 65 (the midvalue between the parental species) indicated the affinity to one parent or the other. The numerical affinities (percentages) were calculated as the ratio of the differences between 65 and the hybrid count and between 65 and the adult counts.

TABLE 1.—Means, ranges, *n*, and *P* values of lateral scale row counts observed in 141-day-old hybrids and controls and adults of the grunions, *Leuresthes tenuis* and *L. sardina*.

Parents ♂	♀ *L. tenuis*			♀ *L. sardina*		
	Juveniles	Adults	*P*	Juveniles	Adults	*P*
L. tenuis	$\bar{x}$ = 75.5 (75-76) *n* = 2	$\bar{x}$ = 74.6 (69-80) *n* = 143	>0.6	$\bar{x}$ = 61.8* (61-63) *n* = 9	—	—
L. sardina	$\bar{x}$ = 67.0* (66-68) *n* = 2 *P* < 0.01	—	—	$\bar{x}$ = 55.1 (54-57) *n* = 9 *P* < 0.001	$\bar{x}$ = 55.3 (51-60) *n* = 177 —	>0.7

*Student's *t*-test comparison of the lateral scale row counts between the two hybrids *P* < 0.001.

Discussion

Natural hybridizations are reportedly more common among freshwater fishes than among marine fishes (Hubbs 1955). Hubbs (1970) stated that, "teleost hybrids are relatively easily produced and if the parental morphology is similar the hybrids are easily reared." The results of natural and artificial amphibian and teleost crosses have been widely employed for estimating degrees of phylogenetic divergence, revealing systematic patterns, and explaining mechanisms controlling development and differentiation.

Davidson (1968) reports that the closer the phylogenetic relationship between the species hybridized, the less likely the hybrid genome control will be displayed early in development. This is because the mechanical aspects of early development tend to be similar in closely related species and may be primarily under the control of maternal RNA accumulated in the egg prior to fertilization. Davidson believes this, at least in part, accounts for the commonly observed resemblance of hybrids in early developmental stages to the maternal parent. The genetic influence of the paternal genes in the hybrid genome may not be apparent phenotypically until long after the onset of differentiation (Davidson 1968).

It is possible that such mechanisms account for the maternal resemblance pattern observed in the grunion hybrids as well. The hybrids resembled the maternal parents in overall size and body proportions, coloration, swimming ability, net-escape capability, and dentition until long after hatching. Only when the lateral scale rows were counted at 141 days after hatching did the influence of paternal genes become visibly and quantitatively apparent.

The numerous artificial and two natural hybridizations (interspecific and intergeneric) reported among the Atherinidae are reviewed by Hubbs and Drewry (1959), Rubinoff (1961), and Hubbs (1970). Natural hybrids reported between *Menidia menidia* and *M. beryllina* along the Atlantic coast of Florida (Gosline 1948) exhibit intermediate counts (i.e., scales and fin rays). Most of the experimental crosses between these atherinids resulted in low developmental success and low survival rates except those of *M. beryllina* ♀ × *M. menidia* ♂ (Rubinoff 1961). Rubinoff did not report whether any intermediate characteristics existed in these hybrids nor was the reciprocal cross attempted.

Geographically isolated species forms adapt to their respective environments by the evolution of appropriate gene complexes. Then, if sympatry reccurs and hybridization takes place, hybrid individuals will usually be selected against (Mayr 1963; Ford 1964). Hybrids not selected against will usually be successful over only a narrow geographical range, since in animals, natural hybridization is commonly associated with environmental perturbation (Mayr 1963; Manwell and Baker 1970).

The *Menidia* species are sympatric and hybridization does occur in northern Florida, a very narrow portion of the overlap in their ranges (Gosline 1948). Like these species, grunions are marine fishes with similar, but not identical, ecological preferences. However, the grunions are allopatric and natural hybridization is not possible.

According to Mayr (1963), some investigators argue that renewed sympatry with hybridization is required as a process of speciation in order to "perfect isolating mechanisms," and, therefore, unlike the *Menidia* species, the heterospecific status of the grunions may be questioned, especially in light of the hybridization success reported herein. We conclude that, despite our success at hybridizing *L. tenuis* and *L. sardina,* the morphological, physiological, and behavioral distinctions between them warrant their continued recognition as separate species.

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TYCHOPLANKTONIC BLOODWORM, *GLYCERA DIBRANCHIATA*, IN SULLIVAN HARBOR, MAINE

The bloodworm, *Glycera dibranchiata*, is distributed from the Gulf of St. Lawrence to the Gulf of Mexico and from central California to lower California and Mexico. It occurs from intertidal water to 402 m depth (Pettibone 1963), but it is more abundant in shallow coastal water. In Maine and Nova Scotia the worms are dug commercially along the coast from the upper layers of the intertidal sand-silt-clay strata (Dow and Creaser 1970; Anonymous 1974; Glidden[1]).

Spawning bloodworms are briefly pelagic occurring in large numbers as they swarm in the afternoon. Creaser (1973) observed swarming in Maine during June. Simpson (1962) reported swarming both in June and November-December, suggesting a biannual spawning in Maryland. Klawe and Dickie (1957) did not observe swarming by bloodworms in Nova Scotia, although other evidence indicated that the worms spawned in mid-May. They suggested that the worms had a short nocturnal swarming period making them difficult to observe. Simpson (1962) checked this possibility

[1]Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine: *Nereis (Neanthes) virens, Glycera dibranchiata, Glycera americana*. Rep. to Maine Dep. Sea Shore Fish., Augusta, Maine.

in Maryland by making 40 observations with a night-light between June and November. No worms appeared at the surface under the light.

Individual bloodworms occasionally are pelagic when not spawning. Pettibone (1963), when noting the sightings of others, reported a bloodworm swimming at the surface of Eel pond, Woods Hole, Mass., on the evening of 17 August 1943; another at the surface perhaps at the same pond on 28 January 1876; and another in Delaware Bay on 29 January 1957. No time was given for the two January sightings. On 2 October 1969, E. P. Creaser, Jr. sighted a bloodworm at the surface near a dock on McKown Point, Boothbay Harbor, Maine. The large nonspawner was observed at noon swimming during a flood tide. We have found that nonspawning bloodworms may also occur as fairly abundant members of the tychoplankton—bottom dwellers that are either swept upward with tidal currents or migrate upward at night. This study was originally designed to sample larval Atlantic herring, *Clupea harengus harengus* Linnaeus, and these results will be presented later. The implications of a large incidental catch of bloodworms prompted our writing this note.

Materials and Methods

The site of this investigation, Sullivan Harbor, is an embayment along the eastern coast of Maine. It is divided into northern and southern sectors by a constriction formed by an island, point of land, and ledges (Figure 1). The southern sector opens onto Frenchman Bay, which in turn opens onto the Gulf of Maine. At its upper end, the northern sector constricts into a tidal falls. A narrow channel extends north of the falls eventually bifurcating into broad extensive shallows. Only small streams enter these shallows about 5 km north of the highway bridge. Sullivan Harbor is thus relatively saline (31-32‰).

Six sampling stations were located within the northern sector of the harbor; two in the landward end of the channel (No. 3, 4), two in the seaward end (No. 1, 2), and one at each seaward entrance to the subtidal flats (No. 5, 6). At each station within the channel, four lines of buoyed and anchored nets were set (Graham and Venno 1968). On each line one net fished near the surface and a second at 3 m just above the edge (4 m) of the subtidal channel (Figure 1). A third net fished below the edge at 10 m and a fourth near the bottom (12-20 m). At the entrance to the subtidal flats, one net was suspended near the surface and another at 3 m just above the bottom.

The nets were set at each station at dusk and retrieved at dawn, fishing approximately one tidal cycle. Calibrated meters centered within the nets determined the amount of water strained. The contents of the nets were preserved in the field using a 5% Formalin[2] solution. The sexes of the worms were determined at a later date by inspection of the coelomic contents. Since variable shrinkage of the worms made length measurements unreliable, dry weight was obtained for each worm.

Results

The nets strained 72 bloodworms from tidal currents during 6 of 10 cruises in autumn and winter 1974-75. During 1974, the nets captured 2 worms on 14 October, 7 on 11 November, 2 on 5 December, 51 on 10 December, and 1 on 19 December. During 1975, the nets captured nine worms on 2 December. Only five worms were immature; their weights varied from 0.02 to 0.11 g. Mature females outnumbered mature males about two to one (41:24). The mean weights of the two sexes were similar, 0.57 g, and their range varied from 0.11 to 1.47 g.

Bloodworms were dispersed throughout the water column and over both the channel and subtidal flats. Nets at all stations and depths captured worms. The average number netted was three and ranged from one to seven. Of the 72 worms from all cruises, nets set in the channel contained 58 worms and those over the subtidal flats held 14. Their numbers decreased vertically: 33 near the surface, 17 at 3 m, 15 at 10 m, and 7 near the bottom.

An exceptionally large catch per unit effort was obtained on 10 December. During the 10 cruises the nets strained approximately 8,000 to 20,000 m^3 of tidal water per cruise. Five of the sets yielded catch rates varying from 0.1 to 0.7 worm/1,000 m^3. A sixth set (10 December) yielded 3.38 worms/1,000 m^3. This catch rate was sufficiently large to permit comparison of synoptic catch rates with location and depth. The four lines of nets in the channel strained 39 worms from 10,194 m^3, yielding a catch rate of 3.8 worms/1,000 m^3 Those nets

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

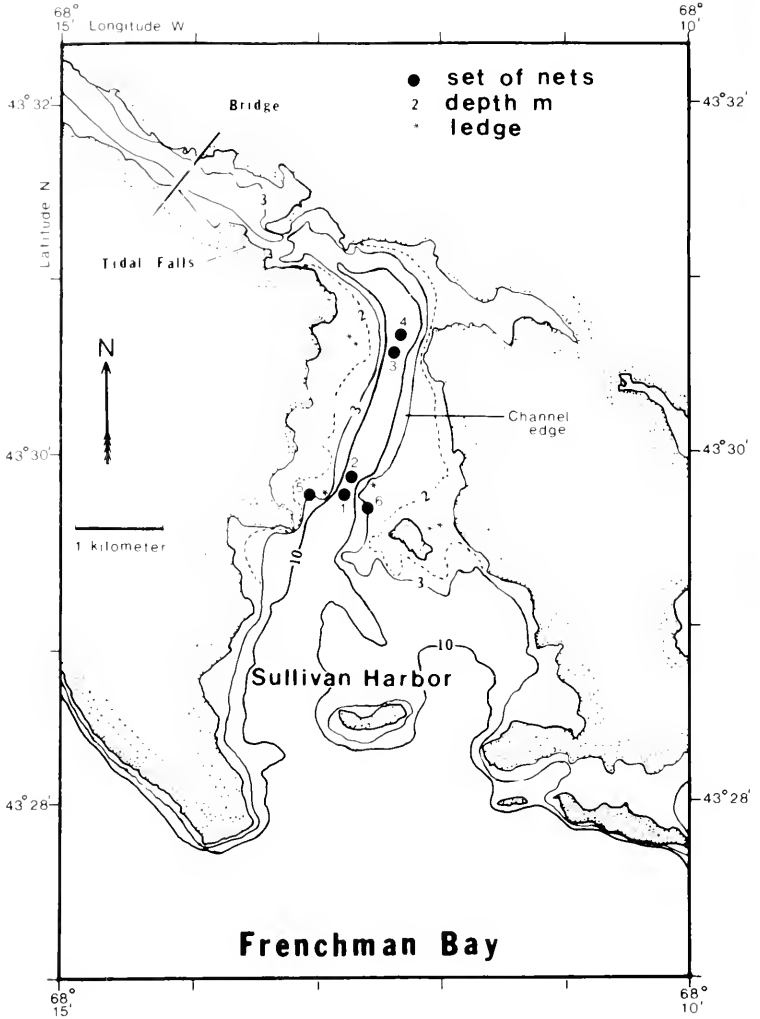

FIGURE 1.—Sampling stations (1-6) for larval Atlantic herring with sets of buoyed and anchored nets in Sullivan Harbor, Maine.

in the flats strained 12 worms from 4,889 m^3, yielding 2.4 worms/1,000 m^3. Shallow nets, above the channel edge and those near the surface of the flats, captured 37 worms by straining 9,614 m^3 for a catch rate of 3.8 worms/1,000 m^3. Deep nets, below the channel edge and those near the bottom of the flats, captured 14 worms by straining 5,469 m^3 for a catch rate of 2.6 worms/1,000 m^3.

The numbers of worms captured in the nets were few when compared with the numbers of smaller tychoplankters, such as amphipods. Each individual weight, however, was relatively large compared with those individuals of more numerous taxa and suggested that a large biomass of bloodworms sometimes enters the water column of the harbor.

Discussion

The mature bloodworms captured during winter in buoyed nets at Sullivan Harbor were not free-swimming spawners. Creaser (1973) sampled a small worm flat at Wiscasset, Maine, from November 1967 to August 1969. During that time, among the many worms dug, only three spawners occurred during winter. Analysis of his collections showed that egg diameters increased somewhat during December and January but ceased growth during the colder months of February and March. Spawning was triggered in June by formation of the epitoke, the growth of eggs to the spawning "range" and a water temperature of at least 13°C. These conditions were not found in the present

study. Also, we did not detect any morphological changes that accompany formation of the epitokes as described by Simpson (1962).

Swimming bloodworms at night have also been reported for two other Maine inshore waters. Dean[3] saw 22 bloodworms during observations made between 24 January and 29 March 1977 on 33 nights. The worms were present during five nights in March and 15 were collected under a night-light in the Damariscotta River, Maine—8 on 11 March and 7 on 12 March. The gametes of the worms were not sexually mature and the presence of the worms near the surface at night was not related to spawning. Dean also reported that buoyed and anchored nets set in Montsweag Bay and the Sheepscot estuary between 1970 and present captured 22 glycerids, some of which were *G. dibranchiata*. In contrast, the senior author of this paper did not capture bloodworms in buoyed and anchored nets set in the Sheepscot estuary over the same time period and in the same vicinity. Possibly, the swimming of bloodworms at night is sporadic.

A recent study of residual currents in Sullivan Harbor suggested that the relatively shallow nets above the edge of the channel (Figure 1) and at the surface over the tidal flats strained a residual seaward flow transporting tychoplankters and the relatively deep nets strained a residual landward flow. Distribution of bloodworms throughout the water column would, therefore, insure their wide dispersal by horizontal tidal currents, and it is unlikely that after a tidal cycle they would regain the location of their original burrows.

We hope to study further the bloodworms of Sullivan Harbor and do not wish to speculate on their origin or fate at this time. Rather, it is our purpose to suggest that researchers investigating bloodworms within their bottom habitat should also examine their possible role as tychoplankters for two reasons: populations of this important commercial species in separate flats may become intermixed, introducing problems in their management; and the reestablishment of worm populations previously destroyed by pollution or other environmental catastrophe might proceed more rapidly in those areas where there is winter transport of mature worms, as well as the "normal" dispersion of late spring larvae.

[3]Dean, D. The swimming of bloodworms (*Glycera* spp.) at night. Unpubl. manuscr.

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SIMULATED FOOD PATCHES AND SURVIVAL OF LARVAL BAY ANCHOVY, *ANCHOA MITCHILLI*, AND SEA BREAM, *ARCHOSARGUS RHOMBOIDALIS*

Survival rates of laboratory-reared marine fish larvae often are directly related to prey concentration. Best survival usually has been reported when prey are available at concentrations >1,000/l (O'Connell and Raymond 1970; Laurence

1974, 1977). Houde (in press) recently demonstrated that survival of three species of marine fish larvae from hatching to metamorphosis was 10% or higher when mean prey concentrations were only 34-130/l. But, he also found enhanced survival when food concentrations were increased. For significant numbers of larvae to survive the transition stage from yolk nutrition to active feeding, some researchers believe that dense patches of prey must occur in the sea (O'Connell and Raymond 1970; Hunter 1972). Such patches might occur at densities of 10 to 1,000 times above the mean prey density. Lasker (1975) has discussed the dense patches of the dinoflagellate *Gymnodinium splendens*, which serves as prey for larval northern anchovy, *Engraulis mordax*, in the California Current and their possible relationship to larval survival. Hunter and Thomas (1974) demonstrated that larval northern anchovies were able to remain in patches of *G. splendens* that were artificially created in laboratory experiments.

In two series of laboratory experiments we have examined the effect of two simulated patches of prey on survival in the bay anchovy, *Anchoa mitchilli*, and the sea bream, *Archosargus rhomboidalis*. Patches were simulated during the first 6 days after hatching, when these larvae are most susceptible to starvation mortality. The purpose of the experiments was to determine if prey at high density that were offered for more than some minimum period would result in survival rates of larvae that approached those obtained at a high, constant prey concentration. This would indicate that the larvae were able to obtain a daily ration suitable for maintenance and growth by increasing their feeding rate during the period of exposure to the patch concentration of prey. At the low prey concentrations usually found in the sea, a relatively great expenditure of energy would be required by larvae to obtain the minimum daily ration for maintenance and growth. Such larvae might weaken or fail to grow and thus be more susceptible to starvation or predation.

Methods

Larvae were hatched from fertilized eggs that were collected in plankton nets from Biscayne Bay, Fla. In each experimental trial 140 sea bream eggs were stocked (2.0/l) and 280 bay anchovy eggs were stocked (4.0/l) in a 76-l glass aquarium. Larvae were reared for 10 days at 26±1°C. Salinities ranged from 30.0 to 32.5‰ for bay anchovy and 33.0 to 33.5‰ for sea bream. Lighting was provided at 2500-2800 lx by 40-W, cool-white fluorescent tubes. A 13 h light-11 h dark schedule was maintained. Tanks were isolated in a black plastic enclosure and all light was extinguished during the dark periods. Sea bream and bay anchovy larvae do not feed in the dark. At the end of experiments, survivors were preserved in 5% Formalin[1] and measured using an ocular micrometer.

Prey were the nauplii and copepodid stages of copepods, approximately 50-100 μm in diameter, that were collected in 53-μm mesh plankton nets. Prey concentrations were determined by counting organisms in 100- to 200-cm^3 aliquots from the rearing tank (Houde 1975, 1977) several times per day during the 13-h feeding period. Background (i.e., nonpatch) prey levels were set at 25-50/l; this concentration was maintained when patch concentrations were not offered from 2-6 days after hatching and continuously from 7-10 days after hatching. The patch concentration was 500 prey/l. Patches were provided for periods ranging from 1.5 to 11 h (Tables 1, 2). Both 0 h, at which no patches were provided, and 13h, at which a constant 500/l prey concentration was maintained, also were included in the series of experiments for each species. The patch schedules were maintained for only the first 5 days of active feeding because larvae that survived that period had greatly increased their searching ability and were less dependent on high prey concentrations for successful feeding.

Patches were created by adding prey to obtain the 500/l concentration. After larvae had fed at the patch concentration for the desired period, prey were reduced to 25-50/l by siphoning them out of the system through a 280-μm mesh screen and replacing the siphoned water with 26°C filtered seawater from a 150-l header tank. Sea bream larvae had no difficulty avoiding the siphon and its screen during water exchanges, but precautions were necessary for bay anchovy larvae. A 280-μm mesh partition was used to "herd" anchovy larvae toward one end of the tank prior to each siphoning procedure. Siphoning procedures and water exchanges also were carried out in the 0-h and 13-h patch period experiments to insure that those larvae were exposed to the same procedural disturbances as larvae in experiments where prey concentration was being varied.

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

Larvae were exposed to the patch concentration twice during each 13-h feeding period to obtain the total desired time at the patch level. For example, for a 6-h patch exposure, the prey concentration was adjusted to 500/l from 0800 to 1100; it was then quickly reduced to 25-50/l, where it was maintained until 1800, when the prey concentration was readjusted to 500/l for the remaining 3 h of the light cycle.

Results

Anchoa mitchilli

Percent survival ranged from 0.36% at 0-h patch exposure to 22.86% at 13 h (Table 1). The steady increase in survival as patch exposure time was increased was described by an exponential function, $Y = 0.3038\, e^{0.3419X}$, where Y = percent survival and X = hours at 500/l prey concentration (coefficient of determination, $r^2 = 0.98$). For the 500/l patch concentration, there was no minimum time of exposure above which larval anchovy survival increased sharply or equalled the survival obtained when larvae were exposed throughout the day to the 500/l prey concentration.

Surviving bay anchovies at 10 days after hatching differed significantly in mean standard lengths (Table 1) among patch exposure times (analysis of variance, $P<0.001$). Mean lengths at 3-, 6-, and 9-h patch exposure times were significantly greater than those at 11 and 13 h (Student-Newman-Keuls test, $P<0.05$).

TABLE 1.—Survival and standard lengths of *Anchoa mitchilli* larvae at 10 days after hatching based on 280 eggs and variable patch exposure times. A patch is a prey concentration of 500/l. Nonpatch levels were 25-50/l. Patch conditions were presented to larvae on days 2-6 after hatching.

Patch exposure time (h)	Survival		Standard length (mm)	
	Percent	No.	Mean	SD
[1]0.0	0.36	1	6.75	—
3.0	0.70	2	7.79	0.17
6.0	1.79	5	7.50	0.68
9.0	9.29	26	7.18	0.64
11.0	13.93	39	6.41	0.76
[2]13.0	22.86	64	6.58	0.58

[1]Food concentration was held constant at 25-50/l during days 2-6.
[2]Food concentration was held constant at 500/l during days 2-6, then reduced to 25-50/l during days 7-10.

Archosargus rhomboidalis

Survival ranged from 3.57 to 66.43% for sea bream larvae over the range of patch exposure times (Table 2). The relationship between percent survival and patch exposure time was described by a power function, $Y = 25.0739X^{0.2878}$, where Y = percent survival and X = hours at 500/l prey concentration. Although the power function described the relationship reasonably well (coefficient of determination, $r^2 = 0.94$), an asymptotic regression might be better to describe the relationship because sea bream larvae exposed to a 500/l patch density for between 3 and 6 h daily apparently survived as well as when the 500/l prey concentration was offered throughout the day. The power function is retained here because fits to the data by asymptotic regressions gave lower coefficients of determination, due to the relatively high variability in observed survival as patch exposure times increased.

TABLE 2.—Survival and standard lengths of *Archosargus rhomboidalis* larvae at 10 days after hatching, based on 140 eggs and variable patch exposure time. A patch is a prey concentration of 500/l. Nonpatch levels were 25-50/l. Patch conditions were presented to larvae on days 2-6 after hatching.

Patch exposure time (h)	Survival		Standard length (mm)	
	Percent	No.	Mean	SD
[1]0.0	3.57	5	4.21	0.44
1.5	22.00	31	4.04	0.56
3.0	32.14	45	3.77	0.56
6.0	59.29	83	3.87	0.40
9.0	41.43	58	3.31	0.41
11.0	66.43	93	4.18	0.28
[2]13.0	42.00	59	4.21	0.31

[1]Food concentration was held constant at 25-50/l during days 2-6.
[2]Food concentration was held constant at 500/l during days 2-6, then reduced to 25-50/l during days 7-10.

Mean lengths of survivors at 10 days (Table 2) differed significantly among patch exposure times (analysis of variance, $P<0.001$), but there was no clear relationship between the mean lengths that differed significantly (Student-Newman-Keuls test, $P<0.05$) and the time of exposure.

Discussion

There was a marked difference in response of bay anchovy and sea bream larvae to the simulated patch conditions. Sea bream survival improved greatly when larvae were presented with prey at 500/l for more than 3 h/day, the observed survival then equaling that when they were offered a constant 500/l prey concentration. Bay anchovies were less successful in using the patch conditions to improve their survival, although increased survival rates did occur when larvae were exposed for more than 6 h to the patch concentration. Results imply that first feeding bay anchovy may require a high and stable prey density to attain best survival in the sea, but that sea bream

are better adapted to survive under fluctuating food conditions.

Survival observed in these experiments can be compared with that reported previously (Houde in press), when survival was related to prey densities that were held constant from day 2 to day 16. Predicted survivals at constant prey densities of 25-50/l and 500/l were 0.72-3.86% and 29.31%, respectively, for bay anchovy larvae; and 5.94-16.61% and 70.45% for sea bream larvae. Observed survivals at 0-h and 13-h patch exposures (Tables 1, 2), which correspond to the 25-50/l and 500/l constant prey concentrations, were only slightly lower than those reported in the constant prey level experiments (Houde in press). The small differences probably were caused by the siphoning and water exchange procedures which did subject larvae to some stress. The similarity of results in the two reports indicates that the patch simulation procedure was effective in demonstrating the impact of patches on larval survival.

Growth results were inconclusive. Significant differences in mean lengths were observed among patch exposure times for both species (Tables 1, 2). In sea bream there was no clear relationship between mean lengths and patch exposure times, but, unexpectedly, bay anchovy mean lengths were smallest at the longest patch exposure times. Presumably only the hardiest larvae survived when patches were presented for only a short time, and these larvae also may have had a relatively great potential for growth. At the long exposures to patch densities, survival was better, but no improvement in growth was noted, possibly because some larvae with relatively poor growth potential survived, or because of density-dependent effects on growth that have been previously observed (Houde 1975, 1977). Another compensating factor was that patches were only presented on day 2 to day 6 of the experiments, the prey concentrations in all experiments being held constant at 25-50/l from day 7 to day 10.

Only one possible patch regime was used in these experiments. It is possible that other patch densities or exposure schedules might alter results or conclusions. An infinite number of possible patch conditions could be simulated but future experiments should be delayed until the temporal and spatial scales of patchiness of organisms consumed by marine fish larvae are better known. Conditions that were simulated in these experiments do not discount the possible ability of larvae in the sea to maintain themselves within prey patches that retain their integrity for days or weeks. Hunter and Thomas (1974) demonstrated that northern anchovy larvae could maintain themselves within small patches of *Gymnodinium splendens* in laboratory tanks. Lasker (1975) found that feeding northern anchovy larvae were relatively more abundant in the chlorophyll maximum layer of the Los Angeles Bight, where *G. splendens* was abundant, than in surface waters, and he suggested that larvae might be able to maintain themselves in this rich source of food. Bay anchovy larvae in our experiments derived small benefits from the patch regime that we provided, but there may be stable patch conditions in the sea which could greatly increase their potential for survival.

Acknowledgments

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DISCOVERY OF JUVENILE PACIFIC SALMON (COHO) IN A SMALL COASTAL STREAM OF NEW BRUNSWICK

Three juvenile Pacific salmon (Figure 1) were discovered in a small coastal stream in southern New Brunswick (Figure 2) in October 1976 while young Atlantic salmon, *Salmo salar*, were being collected for laboratory experiments. The Pacific salmon were not recognized by the electrofishing team, and their presence among the Atlantic salmon was not realized until the fish were sorted in the laboratory some days or weeks later. Identification as either coho salmon, *Oncorhynchus kisutch*, or chinook salmon, *O. tshawytscha*, was later confirmed by W. B. Scott of Huntsman Marine Laboratory, St. Andrews, N.B. Positive identification to species of these juvenile fish was not possible, but they were almost certainly coho salmon because of recent introductions of this species to the Atlantic coast.

Coho salmon are not native to the Atlantic, and no populations reproducing in natural streams of the Atlantic coast are known. Two aquaculture operations using coho salmon are under way in Maine, and coho salmon smolts have been released in streams in New Hampshire and Massachusetts since 1969 and 1971, respectively (Figure 2, inset). Presumably, the parents were from one or more of these four operations. No adults have been reported from New Brunswick streams.

When the coho calmon were recognized, further trips were made to obtain an estimate of their numbers in the stream, their size, and habitat preference in comparison with Atlantic salmon and brook trout, *Salvelinus fontinalis*, which were also present.

The stream, known locally as Frost Fish Creek, drains into the estuary of the Digdeguash River about 250 m from the Digdeguash Falls. It is a small stream approximately 3 m wide in the lower kilometer where all fishing took place. Its drainage area is approximately 570 ha. Discharge during low summer flow reaches as little as 80 l/s (Symons and Harding 1974). The lowermost 0.25 km is steep with cascades and pools. The stream here is either open to the sky or overhung with alders. Most of the Atlantic salmon yearlings occur in this portion of the stream. Through the next 0.25 km upstream the gradient decreases; occasional riffles are separated by pools and slow-flowing water. Bankside cover consists of coniferous softwoods partially clearcut. Atlantic salmon yearlings and underyearlings occur in the riffles of this section while the pools and quieter water are inhabited by brook trout. Above this section the

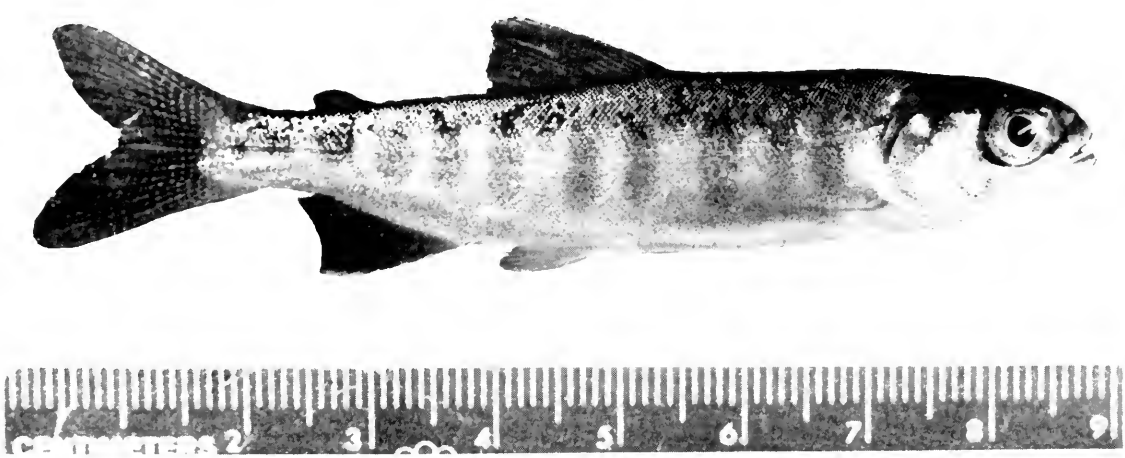

FIGURE 1.—Underyearling coho salmon captured on 28 October 1976 in Frost Fish Creek, N.B.

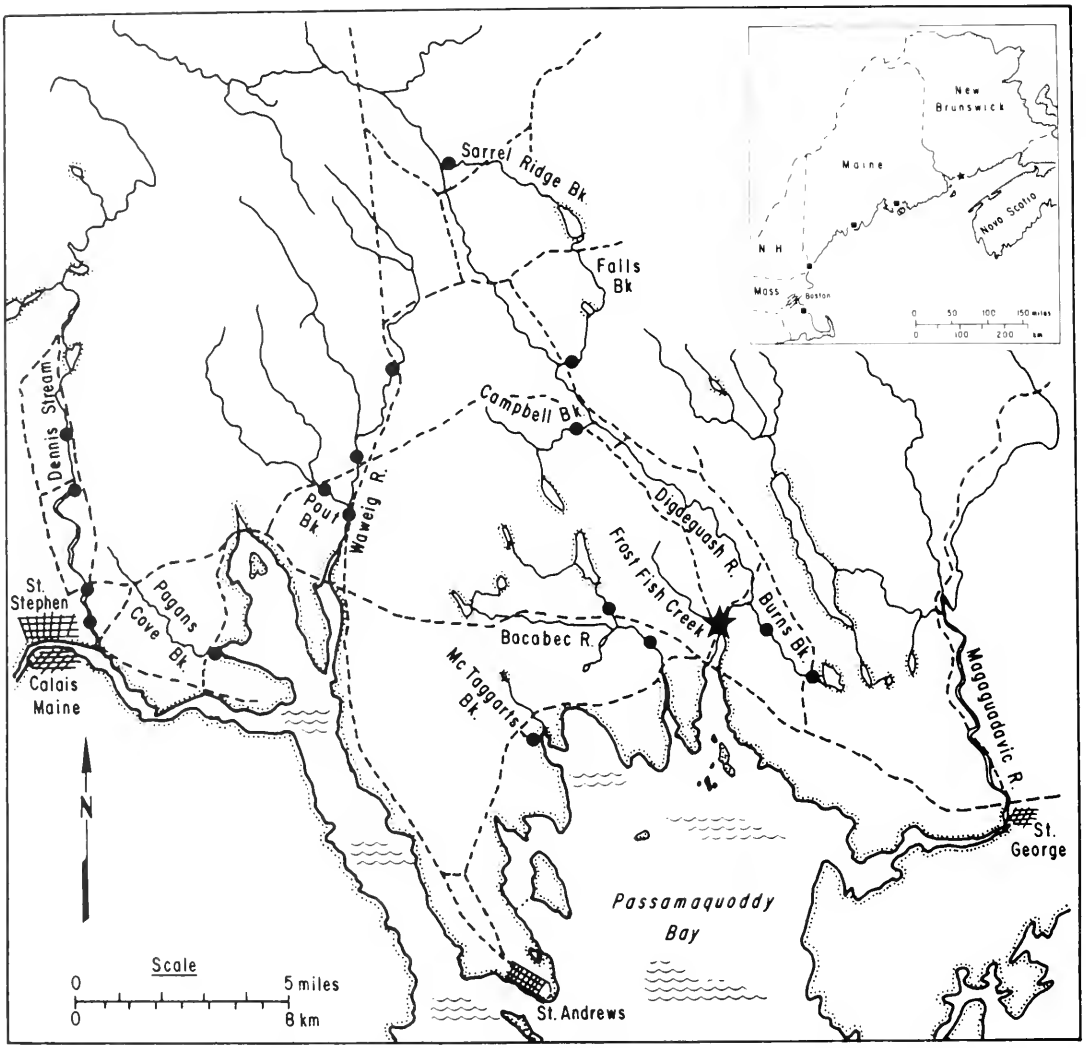

FIGURE 2.—Streams of southern New Brunswick and their access. Dots, sites of spot checks; star, site where coho salmon were captured. Inset, province of New Brunswick, Canada, and northeastern United States showing location of aquaculture operations (Maine) or release sites (N. H. and Mass.) of coho salmon (squares) with respect to location of underyearling coho salmon discovered in New Brunswick (star).

stream gradient becomes lower, the surrounding area is swampy, the stream is choked with alders and inhabited almost exclusively by brook trout. Coho salmon occurred through the middle riffle-pool section and extended in diminishing numbers into the swamp area upstream.

To estimate the numbers of young coho in the creek, two equal-effort electrofishings were performed through the riffle-pool section and approximately 50 m into the swampy section. The lower fast section was fished separately during the first trip (28 October), but since it contained no coho salmon it was omitted on the second 20 days later. Although some coho salmon might have moved downstream in the period between the two fishings, coho salmon were scarce in most upstream areas on both occasions, suggesting there were few above the point where fishing ceased. Twelve coho salmon were caught on the first trip and five on the second. The total population estimated by the depletion method (Seber and Le Cren 1967) was 21. Three coho salmon had been cap-

tured during the collection trip on 9 October, so that the total estimated population of coho salmon in the stream was 24.

During electrofishing, particular note was taken of the kind of habitat in which coho, Atlantic salmon, and brook trout were captured. Coho salmon were found where there was immediate or nearby overhead cover in the form of overhanging banks, tree roots, or fallen trees or brush, and where the water current was slow (<30 cm/s). This kind of habitat was also frequently occupied by brook trout. On at least one occasion, a brook trout and coho salmon were captured together. Atlantic salmon were scarce above the lowermost steep section of the stream. However, in October and November three or four Atlantic salmon were captured in slow water where they had never been seen in summer (Symons and Harding 1974). These observations suggested that summer habitat requirements of coho salmon were more similar to those of brook trout than of Atlantic salmon, although the latter may utilize brook trout-coho salmon habitat in winter.

All captured coho salmon were retained and taken to the laboratory for measuring and weighing. The average fork length of all coho salmon captured was 89 mm, ranging from 75 to 100 mm. There was no statistical difference between average lengths in October (89 mm) and in November (91 mm). Examination of scales revealed that these coho salmon were underyearlings. They were considerably larger than underyearling Atlantic salmon (60-70 mm fork length) and underyearling brook trout (40-60 mm) captured at the same time. The coho salmon were retained for use in laboratory experiments through the winter, and the 10-15 that survived were returned to Frost Fish Creek the following April.

To investigate whether coho salmon might be present elsewhere, spot checks were made in 17 nearby locations (Figure 2) between 28 October and 17 November. Spot checks consisted of 10-35 min of electrofishing with most effort being expended in parts of streams having habitat similar to that in which coho salmon were caught in Frost Fish Creek. No coho salmon were found at any of these sites. Brook trout were caught in all streams, and Atlantic salmon were caught in streams where they were known to occur. Brown trout, *Salmo trutta*, were caught in Frost Fish Creek (2 individuals), Burns Brook (1), and Sorrel Ridge Brook (1), all tributaries to the Digdeguash River. Brown trout were introduced to the Digdeguash as early as 1921 (MacCrimmon and Marshall 1968), and they continue to exist there in small numbers.

In sum, an estimated population of 24 underyearling coho salmon was found in Frost Fish Creek in fall 1976. No coho were discovered in neighboring streams during a cursory search. Although adult coho salmon are known to spawn in small, gravelly coastal streams (Scott and Crossman 1973), spawning may not have occurred in the creek. Atlantic salmon apparently do not spawn there despite the presence of young which are thought to arrive from the main Digdeguash River, having descended the falls into the estuary and then reentering the nearest available freshwater. The young coho salmon may have arrived by the same route. Regardless of the exact location in which coho salmon spawned, should they establish a run in the river system, it would probably be revealed by continued sampling of fish in the creek.

Acknowledgments

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SUBSAMPLER FOR ESTIMATING THE NUMBER AND LENGTH FREQUENCY OF SMALL, PRESERVED NEKTONIC ORGANISMS[1]

When many samples, containing large numbers of organisms, must be processed it is often necessary to take subsamples and assume that they are representative of the total sample. Frequently subsamples are taken in some arbitrary fashion which is described in such terms as "100 fish were randomly selected." However, it is doubtful whether any selection can be adequately random. Therefore, numerous devices have been designed in attempts to secure more representative subsamples and to increase the speed and efficiency of subsampling.

Most subsamplers have been designed for use with plankton, small benthos, and invertebrate drift samples and are generally unsuitable for larger organisms. However, Lewis and Garriott (1971) modified a Folsom plankton splitter for use on meter net samples containing larval fish up to 19 mm long, and Hightower et al. (1976) described a subsampler specifically designed for use with nektonic organisms.

In the present paper I describe the design, operation, and efficiency of a subsampler originally built for research on estuarine nekton (Herke 1971). The subsampler proved to be useful for estimating the number and length frequencies of small nektonic organisms such as the bay anchovy, *Anchoa mitchilli,* tidewater silverside, *Menidia beryllina,* and brown shrimp, *Penaeus aztecus,* as well as young of larger species such as gulf menhaden, *Brevoortia patronus,* and Atlantic croaker, *Micropogon undulatus.* Although different from most subsamplers, the design is fairly similar to that described by Hightower et al. (1976); it bears some similarities to those described by Hewitt and Burrows (1948) for subsampling live hatchery fish, by Cushing (1961) for plankton, and by Södergren (1974) and Hickley (1975) for benthos.

My sampler differs from that of Hightower et al. (1976) in at least four respects: 1) it has fewer moving parts; 2) fewer water jets are required to achieve through mixing of the sample; 3) a central pillar or cylinder prevents organisms from clumping in the center; and 4) the total sample is subdivided by raising vanes through the mixed sample, rather than allowing the sample to settle into baskets. Also, spin-dry weighing is required, but it takes <1 min to complete the subsampling process (after the organisms are placed in the subsampler), rather than several minutes as required for the subsampler described by Hightower et al. I have made no comparative tests between the two subsampler designs, however; individual circumstances may determine which would be most practical in any given situation.

Subsampler Construction

My subsampler can be constructed of various materials, and the same general design can be used for large and small models. A small Plexiglas[2] version (Figure 1) has an outside diameter of 305 mm, and Herke (1971) also illustrated one with a 580-mm outside diameter that utilized part of a 208-l steel drum for the outer cylinder, a 19-l bucket for the inner cylinder, and plywood for the false floor.

The subsampler in Figure 1 was constructed primarily of Plexiglas about 6 mm thick. Plexiglas joints were bonded with solvent (methylene chloride and trichlorethylene). The major parts and their functions are as follows (numbers refer to the parts labeled in Figure 1):

1. Base.
2. Brass hinge for attaching base to edge of table top.
3. Outer cylinder bonded to base; in addition to solvent, a suitable cement may be required to ensure a watertight seal to the base.
4. Central pillar of Plexiglas tube bonded to base at exact center of circle formed by the outer cylinder (3).
5. Rubber stopper in (4) to prevent material from falling inside the piller.
6. Inner cylinder, which slides smoothly up and down over (4).
7. Locking pin for holding (6) in the raised position. Rubber bands around (6) and over a peg through the shaft of (7) hold the pin in place (these are omitted from the diagram to avoid cluttering).
8. Vane bonded to (6); the outer edge almost touches the outer cylinder. In the raised posi-

[1]Contribution no. 24 of the Louisiana Cooperative Fishery Research Unit: Louisiana State University, Louisiana Wildlife and Fisheries Commission, and U.S. Fish and Wildlife Service cooperating.

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

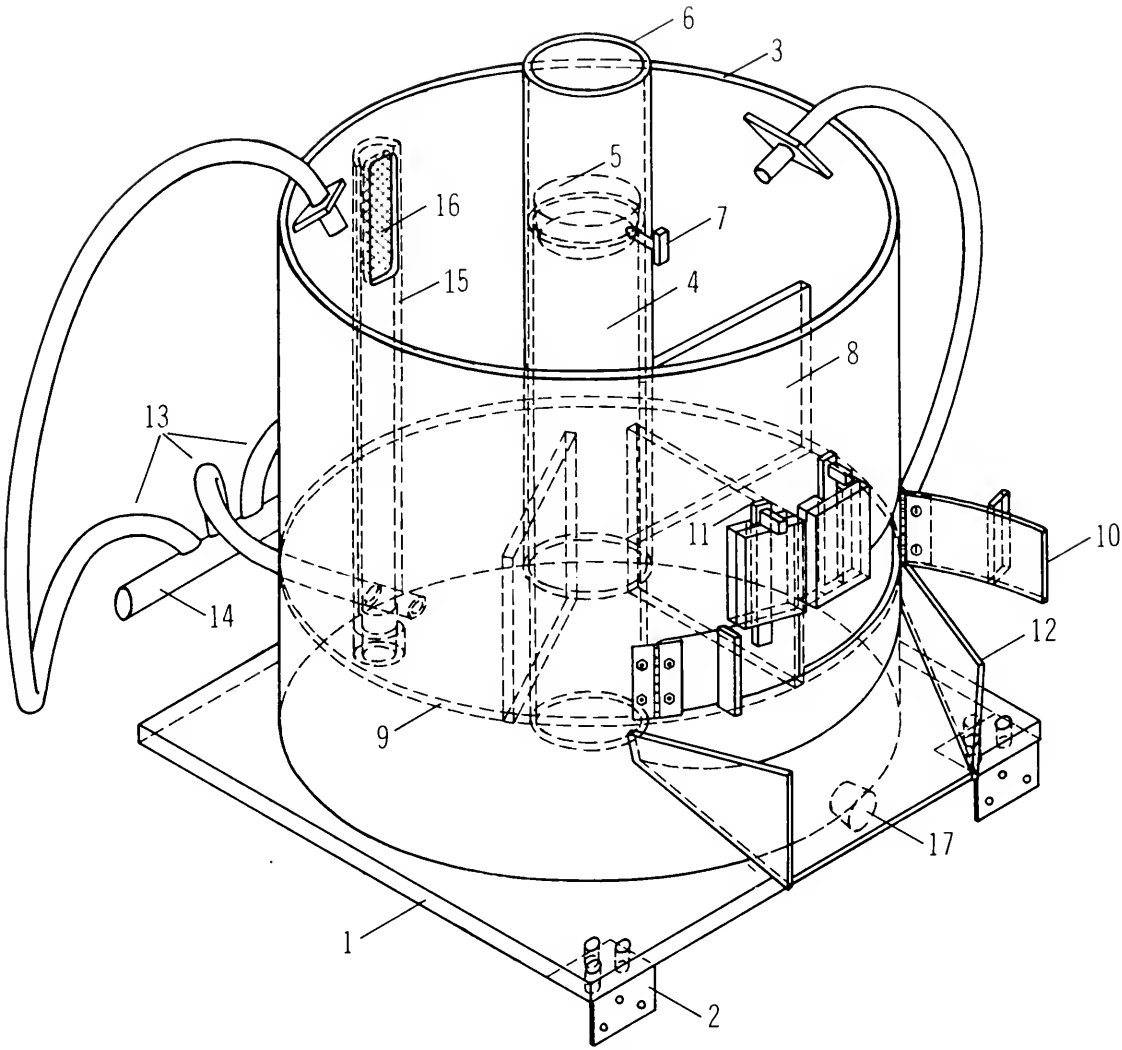

FIGURE 1.—Basic design of the nektonic subsampler; see text for explanation.

tion shown, the three vanes subdivide the sample into portions approximating 0.2, 0.2, and 0.6 of the total.

9. False floor consisting of three sections bonded to the inside of the outer cylinder (3) at a height so that the upper surface is exactly even with the upper edges of the vanes when (6) is lowered to the base. The vanes move up and down through the slits left between the sections of the false floor. Enough space must be left between the inner edges of the false floor and the inner cylinder (6) and its attached vanes to allow the inner cylinder and vanes to move freely up and down. Conversely, the clearance must be small enough to prevent organisms from falling into the space below the false floor. Omitted from the diagram are braces extending from the base to near the inner edges of the two smaller sections of false floor.
10. Hinged door for removing subsampled organisms.
11. Latch holding the other door closed.
12. One side of a spout into which the water and organisms pour when doors are opened; the organisms are collected in a sieve below the spout.
13. Rubber tubes to carry water; the middle one enters the cylinder (3) beneath the false floor (9).

14. Copper tube with outlets for each rubber tube (13). Water to operate the subsampler comes through a large-diameter garden hose and pistol-type hose nozzle (not shown) attached to this tube.
15. Overflow tube attached to the outside of the cylinder (3). The cut edges of a longitudinal section of Plexiglas tubing are bonded to the cylinder from the overflow intake to the bottom of the base (1). Below the base the tube is not sectioned (i.e., left intact) so a drain hose can be attached to it.
16. Aluminum window screen covering overflow intake; bottom of intake opening is level with the top of the vanes (8) when they are raised.
17. Rubber stopper in drain hole below spout.

Also omitted from the diagram are "stops" on the bottom edges of the vanes (which prevent the vanes from pulling through the false floor) and spongy, foam gaskets attached to the doors with rubber cement.

Subsampling Procedure

In subsampling, one pushes the inner cylinder (6) with the attached vanes down until it rests on the base; in this position the tops of the vanes are even with the top of the false floor so that the vanes and floor form a single flat surface. The entire sample is then placed on the false floor. The hose nozzle trigger is squeezed fully open, squirting water rapidly through the rubber tubing. (Normally, the space below the false floor is still filled with water from previous use.) Some of the water rises through the three vane slits in the false floor, thereby inhibiting downward passage of the smaller specimens; most of the water squirts out of the upper tubes, causing the water above the false floor to swirl rapidly. Turbulence thoroughly mixes the sample as both sample and water revolve. When the water almost reaches the bottom of the overflow intake, the inner cylinder (6) and attached vanes are quickly raised as far as possible so that the locking pin (7) slides farther through its hole in (6) and over the top edge of (4); simultaneously, the hose nozzle trigger is released. The sample has now been divided into three parts equal to about 0.2, 0.2, and 0.6 of the whole.

The entire subsampler is next tilted on its hinges (2) in preparation for emptying. If a 0.2 subsample is desired, only one door is opened and the contents of that compartment flow through the spout (12) into a sieve. (To avoid bias, the user should always open the same door first. Occasionally fish balance on top of the vanes; the user can avoid personal bias by always pushing the fish so it falls headfirst.) Opening both doors produces a 0.4 subsample and the remainder of the material in the subsampler constitutes a 0.6 subsample. The 0.6 subsample is removed by first taking out the 0.4 subsample and then lowering the vanes as far as they will go. The 0.6 subsample may then be washed into a sieve below the spout. (When removing any subsample, it is easier to wash the organisms out of the subsampler than to pick or push them out.) A wide variety of subsample ratios can be obtained by sequentially subsampling subsamples (e.g., $0.8 \times 0.2 \times 0.2 = 0.032$).

Small organisms do occasionally fall through the vane slits into the space between the base and the false floor. Such losses are normally insignificant compared with the total number being subsampled, but they are noticeable through the Plexiglas. These organisms may be recovered by washing them out through the drain hole plugged by the rubber stopper (17).

No special leveling of the subsampler is required for proper operation; it may be mounted on any reasonably level surface such as a table top or laboratory bench.

Discussion

The subsampler is useful for estimating both total numbers in a sample and the total length-frequency distribution. If the total sample is not first separated by species, one should at least make a thorough scan of the sample, before subsampling, to remove any unusually large or odd specimens. As stated by Hightower et al. (1976), these can later be added to the total estimate, which is derived by extrapolating the subsample results. However, subsampling can give erratic results for inconspicuous species present in small numbers. Therefore, I think it usually is best to first separate the total sample into individual species, and subsample only the abundant ones. For each of these species, a subsample is first taken, and its weight and that of the remainder are obtained by the spin-dry method described by Herke (1973). (In contrast to plankton, preserved fishes and many crustaceans can be easily and precisely weighed without damage by using the spin-dry method.) All organisms in the subsample are then

counted and the number in the total sample is estimated on the basis of the weights of the subsample and total sample. Since the estimate is based on weight rather than volume, the three vanes need not divide the subsampler into exactly 0.2, 0.2, and 0.6 segments.

If a length-frequency estimate is desired, the subsample can be further subsampled. Since the number in the first subsample is now known, any desired number for the length-frequency subsample can be closely approximated by selecting the proper sequence of subsamples. For instance, suppose the first subsample contains 3,371 anchovies and a length frequency is desired from approximately 100 fish; $3{,}371 \times 0.2 \times 0.4 \times 0.4 = 108$. Therefore, subsamples taken in this sequence should produce the desired number for measuring.

The consistency with which the desired number is obtained may be judged (Table 1) by comparing the "theoretical" and "actual" numbers obtained in 20 successive trials. The two subsamplers used in these trials had a tendency to slightly exceed the desired number; one or both of the smaller compartments in each subsampler probably contained a bit more than 0.2 of the whole. However, the increased subsample size actually improves the probability of obtaining an accurate length-frequency estimate. Also, with use, one soon learns whether the tendency is to obtain more or fewer than the theoretical number and can select the subsampling sequence accordingly.

How well the length-frequency estimates derived from subsampling groups of anchovies and menhaden represented the true length frequencies of the groups was examined by using the Kolmogorov-Smirnov one-sample, two-tailed test, which is a test of goodness of fit. The test involves comparing the observed cumulative frequency distribution from a subsample with the cumulative frequency distribution of the total sample. It is sensitive to any kind of difference between the two distributions—differences in location (central tendency), in dispersion, in skewness, etc. According to Siegel (1956) the Kolmogorov-Smirnov test is definitely more powerful than the chi-square test when samples are small, and may be more powerful in all cases.

The cumulative length-frequency distribution for only one subsample was significantly different ($\alpha = 0.05$) from its corresponding total sample (Table 1). In the other 19 tests, the probability was greater than 0.20 that a divergence of the observed magnitude would occur if the observations were really a random subsample from the total sample (0.20 is the highest probability listed in Siegel's table).

TABLE 1.—Results of 20 tests to determine the correspondence between: 1) the theoretical and actual number of bay anchovies or gulf menhaden in the subsample, and 2) the cumulative length frequency distribution of fish in the subsample and in the corresponding total sample. Subsamples were returned to the total sample after each trial. The cumulative distribution shown in italics (in the same row with the number in the total sample) was the true distribution obtained by measuring every fish in the sample.

Number in total sample	Subsample sequence	Final subsample no.		Standard length in millimeters[1]									
		Theoretical	Actual	15	20	25	30	35	40	45	50	55	60
3,371					*0.539*	*0.772*	*0.821*	*0.861*	*0.914*	*0.957*	*0.984*	*0.995*	*1.000*
anchovies	(0.2) (0.4) (0.4)	108	133		.481	.797	.835	.880	.947	.970	.977	.992	1.000
			124		.524	.758	.838	.863	.911	.960	.976	1.000	
			134		[2].418	.739	.791	.858	.932	.962	1.000		
			141		.489	.709	.773	.822	.894	.950	.979	.993	1.000
			146		.479	.740	.781	.856	.925	.938	.986	1.000	
1,505				*0.361*	*.553*	*.643*	*.774*	*.846*	*.908*	*.964*	*.991*	*.998*	*.999*
anchovies	(0.2) (0.2)	60	49	.347	.551	.571	.673	.734	.795	.917	.958	.999	
			59	.322	.576	.661	.729	.814	.848	.933	.967	1.001	
			77	.338	.520	.559	.676	.793	.832	.949	.988	1.001	
			70	.357	.528	.628	.728	.799	.885	.956	.985	.999	
			71	.389	.570	.598	667	.778	.875	.958	1.000		
Same 1,505 anchovies	(0.4) (0.2)	120	128	.328	.586	.672	.766	.836	.914	.992	1.000		
			125	.272	.544	.600	.776	.864	.920	.976	1.000		
			133	.353	.556	.654	.789	.842	.880	.940	.985	.993	1.001
			134	.306	.507	.589	.768	.843	.903	.970	1.000		
			152	.283	.526	.598	.710	.780	.881	.934	.987	1.000	
1,221								*.020*	*.273*	*.756*	*.980*	*.998*	*1.000*
menhaden	(0.4) (0.2)	98	90					.000	.278	.656	1.000		
			116					.026	.198	.733	1.000		
			115					.017	.252	.765	.991	1.000	
			128					.031	.242	664	.969	.984	1.000
			113					.027	.345	.796	1.000		

[1]Measured in 5-mm increments; i.e., 15 = 15.0–19.9, 20 = 20.0–24.9, etc.
[2]The probability of a divergence this large in a random subsample from the total sample was between 0.05 and 0.01. The probability for the 19 other subsamples was >0.20.

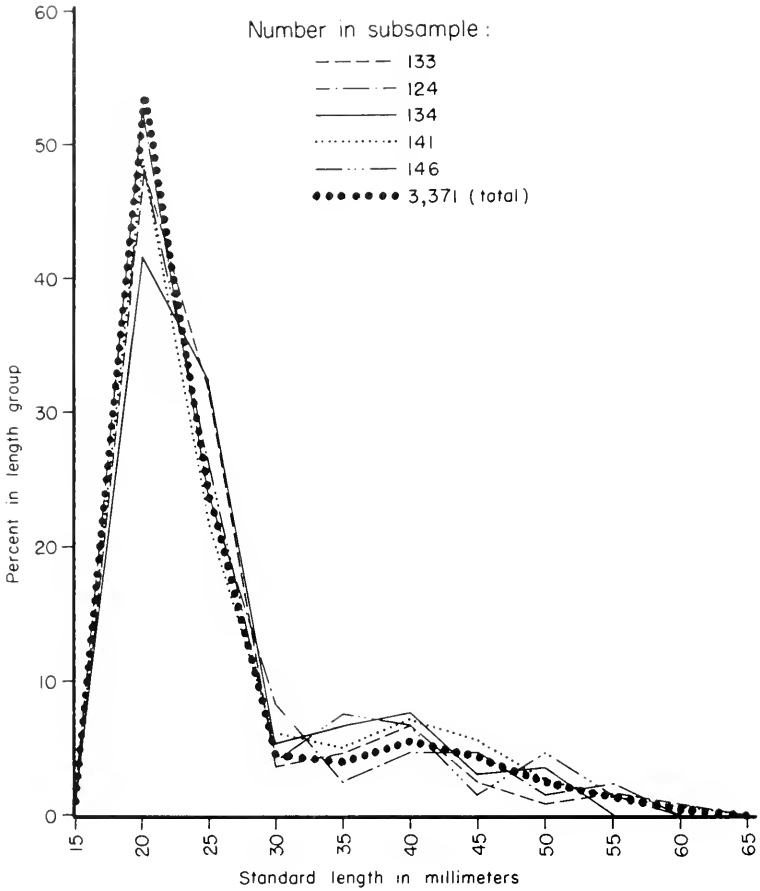

FIGURE 2.—Length-frequency distribution of a total sample of 3,371 bay anchovies, and of each of five subsamples taken from the total. (From Herke 1971.)

It is difficult to visualize, from inspection of the cumulative length-frequency distributions, how well the percentage of fish in each subsample length group represents the percentage in the corresponding length group in the total sample. Therefore, this comparison is shown graphically (Figure 2) for the first five subsamples listed in Table 1.

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Fishery Bulletin, Vol. 76, No. 1

Berrien, Peter L., "Eggs and larvae of *Scomber scombrus* and *Scomber japonicus* in continental shelf waters between Massachusetts and Florida," p. 95-115.

1) Page 99, left column, line 9, correct line to read:
or seven pterygiophores in the 2d through 5th (deleting the zero)

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CONTENTS

Vol. 76, No. 3 July 1978

Notes

(Continued on next page)

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DIEL FEEDING PATTERNS OF 16 SPECIES OF MESOPELAGIC FISHES FROM HAWAIIAN WATERS

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ABSTRACT

Diel patterns of stomach fullness, as percent of dry weight, were determined for 16 species of mesopelagic fishes. Nine species of myctophids and one melamphaid, all vertical migrators, appeared to feed solely or principally at night in the upper layers. These species encountered higher temperatures and prey concentrations at night. Four species of stomiatoid fishes appeared to feed during the day regardless of the extent of their migration or the absence thereof. Prey concentrations encountered by the stomiatoids during the daytime appeared to be higher than or similar to those encountered at night. One myctophid and one gonostomatid showed no diel pattern; diel changes in the environmental factors considered were relatively small in spite of the fact that both species undertook limited vertical migrations.

Crude estimates of instantaneous evacuation rate and daily ration were made from data for four species. These indicated that evacuation rate was increased at night in the upper layers and that daily rations of species which migrated into the upper layers were similar to values for shallow-living zooplanktonivores, while rations of deeper living species were lower. Thus while the adaptive value of upward migration in the species which feed at night is obviously related to feeding activity, the upward ascent by the daytime feeders may allow processing of larger daily rations than if they remained at low temperature all day.

The extensive diel vertical migrations of certain mesopelagic fishes have been well documented in a variety of oceanographic situations. While a number of theories have been proposed to explain the adaptive value of the behavior—in both fishes and migrating invertebrates as well—data to support any of them are few. One of the most frequently proposed hypotheses (e.g., Marshall 1960) is that the organisms ascend at night to feed in the upper layers where food is presumably at higher concentrations and descend during the day to avoid predation while the upper layers are well lighted. Several studies of mesopelagic fishes (to be cited below) have considered the relationship between feeding chronology and vertical distribution in an effort to support at least one-half of the hypothesis, but the results have for the most part been rather equivocal. Apparent diel trends in stomach fullness or details thereof are often questionable owing to low numbers of specimens examined, insensitive methodology, or incomplete diel coverage. Furthermore, all such studies on mesopelagic fishes, with the exception of Merrett and Roe (1974), have been conducted in high latitude or neritic situations and have dealt with only one or, at most, three species.

This study considered the feeding chronology of 16 species from 5 families of mesopelagic fishes from the north central Pacific Ocean. Vertical distribution and certain other apsects of the ecology of these fishes are covered in Clarke (1973, 1974) and Clarke and Wagner (1976); results from related investigations in the same study area are summarized in Maynard et al. (1975). Comparison of diel patterns of stomach fullness and diel changes in temperature and prey concentration allow consideration of adaptive value of the vertical migrations undertaken by most of these species. In four species, rough calculations of daily ration are possible using equations similar to those presented by Eggers (1977).

MATERIALS AND METHODS

Field Sampling

Specimens for this study were all collected with a 3-m Isaacs-Kidd midwater trawl ca. 20 km west of the island of Oahu, Hawaii (ca. lat. 21°20-30'N; long. 158°20-30'W) in waters 2,000-3,000 m deep. In order to reduce the concentration of zooplankton in the cod end of the net and thus

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minimize bias due to fishes' feeding after capture, the net terminated in a 1-m diameter cone of ca. 3-mm (⅛-in) knitted nylon mesh instead of the "normal" plankton netting.

Specimens were taken in oblique tows which sampled vertically migrating species at nine different periods of the 24-h cycle. At night, cable was paid out in increments over a period of 1.5 h such that the trawl fished roughly equal amounts of time at all depths between the surface and ca. 350 m. The trawl was retrieved immediately afterwards for a total towing time of about 2 h. Four such tows were made between last light at dusk and first light at dawn. During the day, 1,200 m of wire were paid out initially. This placed the trawl at ca. 350-400 m. Subsequently, cable was paid out in increments such that the trawl fished between this depth and ca. 1,100-1,200 m over a period of 1.5 h and then retrieved for a total fishing time of ca. 2.5 h below 350-400 m. Three such tows were made during the day. At dusk, 1,500 m of cable were paid out initially, placing the trawl at ca. 500 m. Cable was then retrieved in increments such that the trawl fished between 500 m and the surface over 1.5 h. The trawl reached maximum depth just before sunset and was on deck shortly after last light. At dawn, the process was reversed, and the trawl shot before first light, and fished from the surface to ca. 500 m over 1.5 h such that it reached maximum depth ca. 1 h after sunrise. Ship speed was ca. 1 m/s (2 kn) for cable retrieval and ca. 2 m/s (4 kn) for all other phases.

In order to collect sufficient numbers of specimens for as many species as possible, three 24-h series of nine tows each (dusk, four at night, dawn, and three during the day) were made 27-30 August 1973. These dates were chosen to bracket new moon (August 28) and minimize avoidance of the trawl at night (Clarke 1973). One day tow of this series was fouled and could not be repeated until 13 September 1973. The total range of time fished by equivalent tows of each series (Table 1) overlapped—considerably so for the night series due to one night's fishing proceeding ahead of schedule. The overlap was effectively less than shown in Table 1 since most of the fishes analyzed were probably taken below 50 m (based on previously cited studies of vertical distribution) and not during the first 15 min or the last 5 min of each tow when the trawl was shallower than 50 m. Consequently, equivalent tows from each 24-h series were considered replicates and specimens were combined for data from each period. The nine sampling periods will subsequently be designated as follows: SS for sunset and SR for sunrise; N1, N2, N3, N4 for the four night periods in chronological sequence; and D1, D2, D3 for the three daytime periods in sequence.

Danaphos oculatus, a nonmigrating species, was not taken in the shallow night tows described above. Nighttime data for this species were based on specimens from three night series of three tows each taken 30 August-1 September and 13-14 September 1973 (Table 1) using the same towing schedule described above for daytime (ca. 400-1,000 m). Thus only eight periods of the diel cycle were considered. The three nighttime periods for *D. oculatus* were designated dN1, dN2, and dN3.

In order to obtain more specimens of three species of stomiatoids, I utilized specimens taken 24-25 May 1974 in seven tows at the same location with the same net, and with the same procedure and timings as N1-4 and D1-3. The numbers of specimens used from this series will be noted in the results. All specimens of the other species came from 1973 collections.

The catch was immediately preserved in 4-5% formaldehyde in seawater. The specimens remained in this solution for up to 2 yr before processing, but since all specimens of a given species were processed within a period of 2-3 wk, any between-sample differences in weight loss due to leaching can be considered negligible.

Laboratory Analyses

The ratio of the dry weight of the stomach contents to that of the fish as percent was used as an index of stomach fullness. Where sufficient specimens of a given species were available, 20 from each of the nine sampling periods were examined. If possible, the least damaged specimens (or perhaps more appropriately—equivalently damaged specimens) were selected from a narrow size range. For many species, however, it was necessary to use specimens damaged to various degrees and of all sizes between recently (but fully) metamorphosed juveniles and mature adults. In cases where a specimen was damaged beyond loss of scales or fin rays, i.e., where tissue was missing, I used the median dry weight of other specimens of the same standard length.

Each fish was briefly rinsed with tapwater and gently blotted; standard length was measured to the nearest millimeter. The stomach (anterior end of the esophagus to the pyloric valve) was removed

TABLE 1.—Towing times (Hawaiian Standard Time) for three 24-h series of oblique tows to sample vertically migrating mesopelagic fishes and three all night series for deep-living nonmigratory fishes. Times given for dusk (SS), dawn (SR), and shallow night (N1-4) are for the entire tow; those for day tows (D1-3) and deep night tows (dN1-3) are for the time the trawl fished below ca. 350-400 m.

Period	27-28 Aug.	28-29 Aug.	29-30 Aug.	Midpoint	Period	30-31 Aug.	31 Aug.-1 Sept.	13-14 Sept.	Midpoint
SS	1754-1956	1815-1955	1820-2023	1910	dN1	2040-2300	2005-2233	2000-2235	2130
N1	2045-2240	2001-2155	2040-2233	2120	dN2	2352-0215	2325-0154	2330-0155	0050
N2	2315-0110	2207-0005	2255-0045	2340	dN3	0308-0540	0250-0515	0255-0525	0415
N3	0120-0320	0015-0210	0113-0310	0150					
N4	0330-0520	0220-0420	0318-0515	0350					
SR	0535-0742	0515-0725	0533-0745	0630					
D1	0822-1047	0807-1034	0820-1045	0930					
D2	1143-1425	1125-1350	1135-1410	1300					
D3	1510-1740[1]	1448-1710	1515-1740	1615					

[1]The D3 tow for 28 August was fouled; time given is for tow made on 13 September.

and its contents, if any, placed on a clean glass slide. The fish including the empty stomach was placed in a preweighed aluminum pan. After examination, the stomach contents were rinsed into a second preweighed pan using distilled water.

The stomach contents were examined only casually. A rough estimate of fullness was made and degree of digestion noted. Prosome length (PL) of copepods and total length (TL) of other prey were recorded from intact items. Intact prey items could usually be identified to genus, but no serious attempt was made to determine composition of the diet from these samples. The remarks below on types of prey include only the most frequently encountered items and are not meant to be taken as detailed analyses of diets.

Both fish and stomach contents were dried at 60°C for 24 h (somewhat longer for a few large fish) and allowed to cool under partial vacuum before weighing. The pans with stomach contents were weighed to the nearest 0.01 mg on a microbalance, and the content weight determined by subtraction. Both control pans and reweighing of several pans with dried stomach contents after a second period in the drying oven or desiccator indicated that the weighing and handling error was of the order of ±0.02 mg. There was no indication that error was proportional to the amount of material in the pan. Pans with fish were weighed on a semimicro balance; the reading was recorded to 0.01 mg on small fish and to 0.1 mg on those over ca. 100 mg. Based on changes in weight of control pans and reweighing of fish after a second period of desiccation, the error was <1% of the fish weight.

While the weighing and handling error was such that estimates of stomach fullness were affected only to the fourth or possibly third decimal place, other errors or biases inherent in the material should be mentioned. As noted above, an unknown fraction of the material was lost due to leaching. Damage to the fish positively biased the ratios since there was some loss of skin, scales, or fin rays in almost all specimens. Such errors were unrelated to the time of collection and were more likely to increase variability and thus to obscure rather than cause diel trends in the data. The intestinal contents, which were dried and weighed with the fish, may have varied with time and thus introduced a systematic error in fish weights. Based on visual examination, however, largest amounts of materials in the intestine were almost certainly <1% of the total fish weight, and, consequently, affected the stomach fullness index by <0.1%.

The 2-3 h durations of the tows were a possible source of bias and high variability. Bias in stomach fullness could result from evacuation of stomach contents between capture and death (Eggers 1977). It is likely that this was negligible since the fishes considered here were probably dead soon after capture by the net. The 2-3 h possible differences in capture time for fishes from the "same" period of the diel cycle almost certainly contributed to the variability in stomach fullness—particularly during periods when the latter was changing rapidly.

Stomach fullness could possibly be biased negatively by regurgitation after capture or positively by feeding in the net. (Either type of bias would tend to obscure rather than cause diel differences in stomach fullness.) Regurgitation apparently occurred infrequently in all species considered except *Lampanyctus nobilis*. Except for the latter (see below), specimens with partially digested food remains in the mouth or everted stomachs were not used. Hopkins and Baird (1975) showed that feeding in the net is an unimportant source of error even when a fine-mesh cod end is used, and there was little indication of net feeding in the present study. Zooplankton in good condition, usually crustaceans with appendages erect and extended, were infrequently found in the mouth. These were assumed to have lodged there during

capture and were not counted, but the fish and any other contents were used. Items part way down the esophagus with appendages flattened against the body or the body folded were assumed to have been eaten before capture and were included. I considered such "esophagus" items unlikely to have been eaten after capture because concurrent analyses of diet (Clarke in prep.) on the same species collected by the same net indicate that there is no difference in species composition between such items and items clearly in the stomach and partially digested.

Stomach fullness values for a single species and single time period were rarely distributed normally. Usually the values were skewed to the left, but variably so — the mean being sometimes close to the median and sometimes close to the 75th percentile. Consequently, the entire set of stomach fullness values for each species were ranked and tested for between-period differences by the Kruskal-Wallis nonparametric equivalent of analysis of variance (H-test). The test is mainly sensitive to differences in position (Tate and Clelland 1957), and significance implies differences among the medians for the separate time periods but does not single out which sets of data are different. Each adjacent (in time) pair of data sets was tested for differences in the median with the Mann-Whitney or Rank sum test (Tate and Clelland 1957); however, because of multiple testing on the same data, the significance levels from this cannot be taken rigorously.

Neither test used is sensitive to differences in variability, and no separate testing was done. Some idea of differences in frequency distribution can be gleaned from relative position of the mean and median. Other gross differences, e.g., bimodality vs. unimodality, will be pointed out in the results. Likewise, I did not test for possible correlations between sex or size of the fish and stomach fullness. The data from each period were, however, ranked and compared (by inspection) with sex and rank in length; no obvious correlations were found.

RESULTS

A total of 15 vertically migrating species (10 myctophids, 4 stomiatoids, and 1 melamphaid) and 1 nonmigrating stomiatoid were investigated. These included species for which 20 individuals were collected at most of the nine periods sampled plus a few, less frequently taken species selected to give broader coverage with respect to systematic position or vertical distribution pattern. In addition to graphical presentations (cited specifically below), ancillary data for all species are summarized in Table 2. In the subsequent presentation, stomachs were considered "empty" if stomach fullness was $<0.1\%$. This included both visually empty stomachs and those with only a trace of digested remains in the pyloric end of the stomach. Types of prey organisms, state of digestion, and other aspects not obvious from the figures or Table 2 are considered in individual species accounts below.

Comments on vertical distribution of prey items are based on preliminary analyses of opening-closing plankton tows taken in the study area and their general agreement with data in the literature for the same or closely related species in other central water mass localities. The plankton tows—16 taken in September 1973 and 20 in November 1974—covered the depth ranges of the fishes considered both day and night. Euphausiids from all samples have been counted and identified, and copepods either counted (shallow night samples) or sufficiently examined to at least roughly determine the depth ranges of the important prey species. The apparent depth ranges agree generally with those given by Brinton (1967) and Roe (1972). These two important types of prey can, with a high degree of certainty, be classified as shallow nonmigrators (above 200-300 m both day and night), vertical migrators (above 200-300 m at night and below this depth by day), and deep living (below 300 m day and night). Similar statements cannot be made for ostracods, the other important crustacean group, nor for other taxa of zooplankton.

Myctophidae

Benthosema suborbitale (Figure 1)

The H-test indicated highly significant ($P<0.005$) differences in stomach fullness over the diel cycle. The data from SS and N1 were characterized by low averages, narrow percentile limits, and high proportions of empty stomachs. Subsequently stomach fullness generally increased until SR and decreased throughout the day. The most frequent prey items were copepods of the genera *Pleuromamma, Candacia,* and *Paracandacia. Euphausia* spp. and occasionally small decapods contributed significantly to the weight of

TABLE 2.—Summary of data for each of the 16 species of fishes examined from each of the periods of the diel cycle. In each species/time block, the first line gives the number of specimens examined and the number with stomach fullness <0.1% of fish dry weight in parentheses; the second line, the size range of the specimens in millimeters standard length; and the third, the range of stomach fullness values in percentage of fish dry weight. All values of stomach fullness are rounded to the nearest 0.1%.

Species	SS	N1	N2	N3	N4	SR	D1	D2	D3
Benthosema suborbitale	20(12)	20(8)	20(3)	20(1)	20(5)	19(2)	20(2)	20(3)	20(2)
	24-30	15-32	18-31	19-29	22-31	17-27	16-30	18-32	17-30
	0-0.9	0-2.8	0-6.0	0.1-2.7	0.1-2.8	0-2.6	0.1-3.6	0-3.8	0-2.2
Bolinichthys longipes	20(7)	20(2)	20(2)	20(0)	20(1)	20(0)	20(0)	20(0)	20(0)
	24-46	21-46	20-51	17-49	18-43	21-32	16-50	17-46	19-48
	0-1.4	0.1-2.0	0.1-2.5	0.2-1.5	0.1-2.4	0.3-4.6	0.2-4.8	0.1-1.5	0.1-1.1
Ceratoscopelus warmingi	20(9)	20(1)	20(2)	20(2)	20(0)	5(0)	20(1)	20(0)	20(2)
	22-53	18-45	24-45	23-50	25-47	18-23	19-48	19-59	18-52
	0-2.8	0.1-9.8	0-8.1	0-5.0	0.1-7.6	0.9-4.9	0.1-2.4	0.1-4.5	0.1-7.4
Diaphus schmidti	20(2)	20(2)	20(0)	20(0)	20(0)	20(0)	20(0)	20(0)	20(2)
	25-39	20-41	19-41	19-40	17-38	20-38	14-37	15-38	19-38
	0.1-2.3	0.1-1.7	0.3-1.4	0.2-6.0	0.3-3.8	0.1-2.2	0.2-2.3	0.2-2.7	0-2.3
Hygophum proximum	20(14)	20(0)	20(2)	20(1)	20(0)	20(14)	20(16)	20(13)	18(11)
	26-33	19-32	18-38	18-42	18-37	19-43	19-42	19-40	18-46
	0-1.0	0.2-6.7	0-5.8	0.1-3.6	0.2-7.0	0-0.5	0-0.4	0-1.3	0-1.3
Lampanyctus niger	20(14)	20(11)	20(7)	20(8)	20(4)	0	20(10)	20(11)	20(10)
	65-84	65-85	63-83	64-85	51-85	—	52-87	68-85	64-85
	0-1.9	0-1.0	0-1.7	0-1.3	0-1.5	—	0-4.0	0-3.7	0-3.9
Lampanyctus nobilis	9(4)	20(3)	20(2)	20(4)	20(1)	0	14(2)	14(4)	18(6)
	24-84	29-81	27-88	24-80	26-98	—	25-94	25-90	25-94
	0-6.2	0-3.3	0-7.5	0-8.5	0-5.5	—	0-3.6	0-10.3	0-2.0
Lampanyctus steinbecki	20(2)	20(4)	20(3)	20(1)	20(0)	20(2)	20(0)	20(4)	20(2)
	25-39	22-48	22-41	21-39	22-42	18-36	22-42	23-44	27-42
	0-2.7	0-3.7	0-4.4	0-3.5	0.2-4.0	0.1-9.8	0.1-4.5	0-2.1	0-5.5
Notolychnus valdiviae	20(0)	20(1)	20(3)	20(0)	20(0)	20(0)	20(2)	20(1)	20(0)
	19-24	20-23	19-23	19-23	18-23	19-24	20-23	17-22	19-24
	0.2-3.4	0.1-2.9	0-3.0	0.3-4.7	0.3-3.6	0.3-3.5	0-1.7	0-2.5	0.1-3.5
Triphoturus nigrescens	20(3)	20(6)	16(3)	15(3)	19(0)	20(0)	20(4)	20(3)	20(4)
	18-34	17-31	15-34	15-35	16-33	15-36	16-34	18-33	18-34
	0-5.9	0-3.6	0-9.0	0-6.6	1.0-14.3	0.7-9.9	0-16.0	0-6.7	0-4.5
Melamphaes danae	3(0)	12(3)	14(2)	12(0)	9(0)	0	3(0)	2(0)	14(1)
	16-20	16-21	16-21	16-21	16-22	—	19-21	16	16-22
	0.4-0.6	0-3.2	0-3.0	0.4-3.5	0.5-4.0	—	0.3-1.5	1.1-1.5	0-1.6
Gonostoma atlanticum	4(0)	20(2)	20(1)	20(2)	17(4)	7(2)	9(0)	20(1)	8(0)
	48-58	36-62	32-65	31-64	26-62	48-65	22-64	50-68	48-57
	1.1-3.3	0-6.3	0-4.5	0.1-4.3	0-3.5	0.1-1.6	0.3-2.4	0.1-4.6	0.4-11.2
Gonostoma elongatum	20(2)	20(2)	20(1)	20(9)	20(3)	8(0)	20(4)	14(3)	10(1)
	26-112	31-126	30-135	30-132	32-79	30-150	24-125	30-149	29-87
	0.1-2.6	0-13.1	0.1-5.9	0-5.0	0-2.0	0.2-8.0	0-16.6	0-5.2	0.1-7.3
Vinciguerria nimbaria	20(0)	20(0)	20(3)	20(3)	20(13)	20(15)	20(9)	20(1)	20(2)
	21-34	24-35	24-36	25-32	23-34	24-33	20-35	20-33	20-30
	0.7-8.9	0.2-8.9	0-7.9	0-3.1	0-0.6	0-1.8	0-12.7	0.1-6.3	0.1-14.2
Danaphos oculatus	15(0)	9(0)	11(0)	11(0)		15(2)	20(2)	4(0)	10(0)
	27-40	27-39	29-40	29-36		28-42	31-40	28-38	27-39
	0.5-2.5	0.6-2.3	0.3-1.0	0.3-1.8		0-0.8	0-1.0	0.6-1.7	0.2-2.3
Valenciennellus tripunctulatus	6(0)	20(0)	12(0)	9(2)	10(1)	3(2)	7(2)	5(0)	10(0)
	25-30	22-32	23-32	21-32	21-32	21-31	25-30	21-30	22-33
	1.2-4.5	1.2-3.6	0.9-2.2	0-2.2	0.1-1.0	0-0.2	0-0.6	0.9-2.5	1.0-3.5

food. The food from specimens taken by day samples was generally well digested; except for the thoracic spots or "buttons" from *Pleuromamma*, prey was rarely recognizable beyond general category.

Bolinichthys longipes (Figure 1)

Analyses of *B. longipes* were complicated by the frequent presence in the stomachs of digenetic trematodes. These were 1-10 mm long (most were 1-5 mm) and occurred in 41% of the stomachs examined. They were mingled with the food and appeared to have been fixed while wrapping around or holding to items. As a probable consequence, whole prey were rarely found in *B. longipes*' stomachs. The parasites were, however, easily separated from the food; they were not included with either the fish or stomach content weight.

The number of trematodes was roughly a function of size of the fish. Fish < ca. 30 mm SL usually had 0-2 individuals while several > 40 mm contained 10-20. Since there was little between-period difference in size composition of the fish examined, there was no apparent correlation of trematode number with time of day. Also there

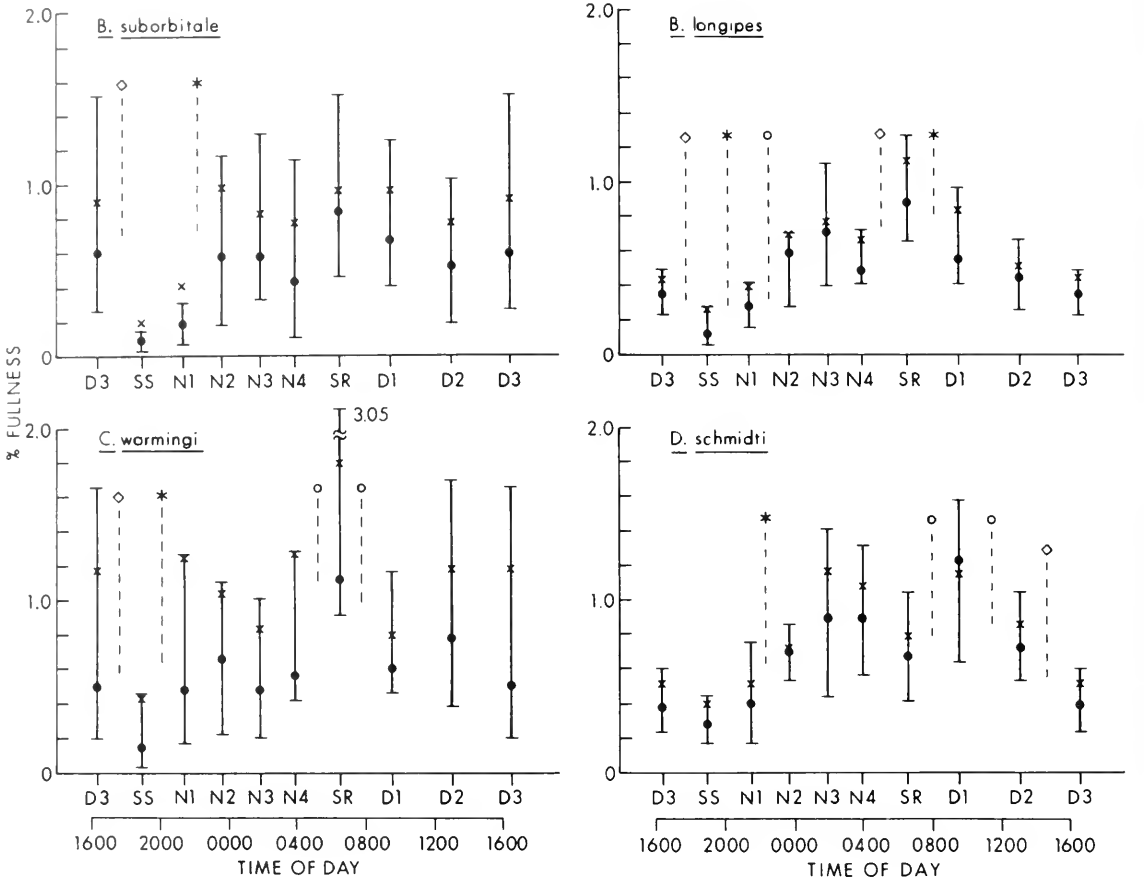

FIGURE 1.—Medians (dots), means (×'s), and ranges between 25th and 75th percentiles (solid vertical lines) of stomach fullness as percentage of body weight throughout the diel cycle for four species of myctophids: *Benthosema suborbitale, Bolinichthys longipes, Ceratoscopelus warmingi,* and *Diaphus schmidti.* Values are positioned at the midpoint of each sampling period (Hawaiian Standard Time). Dashed vertical lines indicate significant differences between adjacent pairs (circle—$0.05<P<0.10$, *—$0.01<P<0.05$, diamond—$P<0.01$; two-tailed probabilities, Rank Sum test).

was no apparent correlation between number of trematodes and amount of food in the gut.

There were highly significant differences ($P<0.005$) in stomach fullness over the diel cycle. The medians and means both showed a trend similar to that of *B. suborbitale* but more of the adjacent pairs showed significant differences and the changes in variability were not as great as with the latter species. The percentage of empty stomachs was <10% at all periods except SS (35%).

Small euphausiids, *Pleuromamma,* and a variety of small (< ca. 2 mm PL) copepods occurred in the stomachs. Even though the stomach parasites apparently broke up the prey items soon after ingestion, there were identifiable pieces of prey in the stomachs from night or dawn. In contrast, contents from day-caught specimens (particularly D2 and D3) were usually amorphous pink material; even the apparently resistant *Pleuromamma* buttons occurred infrequently.

Ceratoscopelus warmingi (Figure 1)

There were significant ($P<0.01$) diel differences in stomach fullness for *C. warmingi*. Similar to the above two species, median stomach fullness was lowest at SS and peaked at SR with an apparent decline in between. The peak at SR, based on only five specimens, differed marginally ($P<0.10$) from values before or afterwards. Day values were comparable with those at night and showed no clear

trend. Except for SS, the percentage of individuals with empty stomachs was low, and there were some fish with very full stomachs (>2%). Because of the latter, ranges and percentile limits were broad, and means were much higher than medians.

Ceratoscopelus warmingi fed on a wider variety of taxa and sizes of prey than did the other species covered here. The most frequent items were copepods, ostracods, and small euphausiids, but heteropods, siphonophores, and other zooplankton also occurred. Intact items of such relatively small prey were recorded mostly from specimens collected at night; remains from day-collected specimens were usually well digested. *Ceratoscopelus warmingi* also took items up to 10% of bodily weight; squid, other fishes, and large euphausiids or decapods occurred in specimens >35-40 mm. Such single large items accounted for nearly all the fish with high values of stomach fullness, and intact prey of this size occurred at all times of the day. Most such items were vertically migrating species that could have been taken at night, but remains of nonmigrating *Cyclothone* spp., which could have only been encountered between dawn and dusk, were found in 11 specimens. Thus, while the overall trend of the data indicates that *C. warmingi* feeds principally on small zooplankton in the upper layers at night, it probably takes large prey whenever encountered.

Diaphus schmidti (Figure 1)

Diel differences in stomach fullness for *D. schmidti* were highly significant ($P<0.005$), and the trend was similar to that of the preceding myctophids except for timing; the maximum value occurred at D1 instead of SR. Empty stomachs occurred only in a few specimens from D3, SS, and N1. *Diaphus schmidti* took a large variety of prey items; the dominant taxa were small crustaceans (ca. 0.5-3.0 mm PL or TL): ostracods, copepods, and larval and juvenile malacostracans. Heteropods, pteropods, polychaetes, and chaetognaths were also noted. Excepting chaetognaths, few items were >4-5 mm. Frequency of intact items was highest at SR, and lowest at D3 and SS.

Hygophum proximum (Figure 2)

Diel differences in stomach fullness for *H. proximum* were highly significant ($P<0.005$), and the trend quite different from those of the other species examined here. Most stomachs were empty, and even 75th percentile values were zero or nearly so between SR and SS; the peak value occurred at N2. *Hygophum proximum* fed principally on medium-sized copepods (1-3 mm PL) and occasionally other crustaceans. Less than 10% of the stomachs were empty for any of the night periods, but intact items were found frequently only in stomachs from N1. By N2 most of the prey were unrecognizable, and only six items were recognizable to even general category in all the other samples.

Lampanyctus niger (Figure 2)

This species, one of three forms of the *L. niger*-complex which occur near Hawaii, has minute pectoral fins and lower AO counts than the others; it was designated as "Form B" in Clarke (1973). Zahuranec[2] has recently identified the form as *L. niger* (sensu stricto). There was evidence from deep night tows taken during the same sampling period that a fraction of the population of *L. niger* did not vertically migrate; consequently, some of the day-caught specimens may not have ascended to the upper layers the previous night. (Such "non-migration" was also recorded in previous studies, see Clarke 1973.)

The *H*-test indicated no significant diel differences in stomach fullness ($P>0.10$), and none of the adjacent pairs differed significantly. The medians from nighttime show a trend similar to that of other myctophids, but the means were highest during the day. No specimens were available from SR. Values of stomach fullness were overall much lower than observed in other species. Stomach fullness exceeded 1% in only 21 of the 160 specimens, and over 50% of the stomachs were empty at all periods except N2, N3, and N4.

The most frequent food items were large copepods of the familes Metridiidae, Euchaetidae, and Aetideidae and small (<10-15 mm TL) euphausiids. Occasionally small fishes were found. Intact prey items were found in stomachs from all periods. Deep-living copepods such as *Metridia* and *Pseudochirella* were noted in day-caught specimens indicating that at least some feeding occurs during the day.

[2]B. J. Zahuranec. Oceanic Biology Program, Office of Naval Research, Arlington, VA 22217. Personal communications, June 1977.

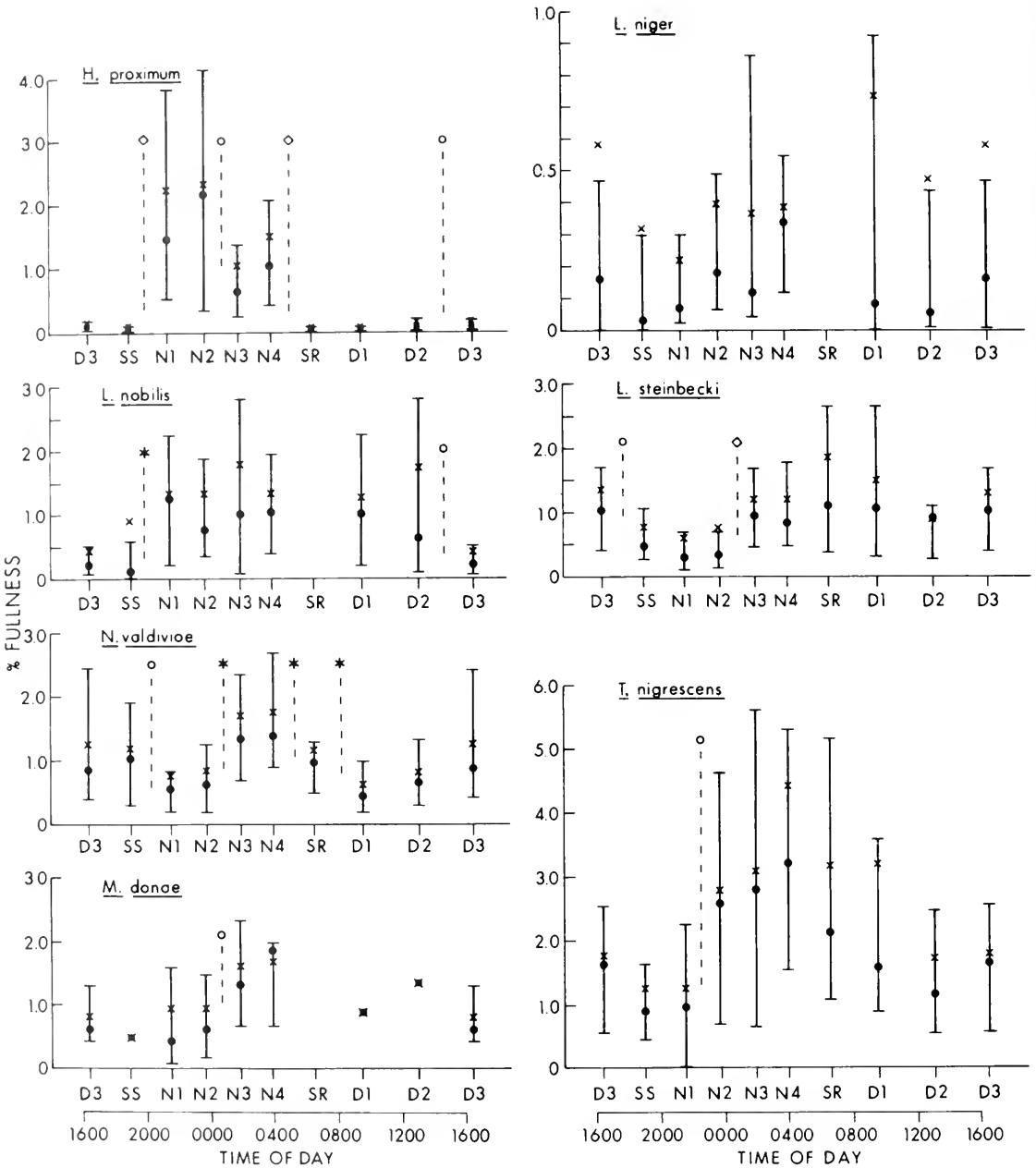

FIGURE 2.—Stomach fullness throughout the diel cycle for six species of myctophids and one species of melamphaid: *Hygophum proximum*, *Lampanyctus niger*, *Lampanyctus nobilis*, *Lampanyctus steinbecki*, *Notolychnus valdiviae*, *Triphoturus nigrescens*, and *Melamphaes danae*. Symbols and format as in Figure 1.

Lampanyctus nobilis (Figure 2)

Lampanyctus nobilis appeared to regurgitate food more frequently than other species examined. Because few specimens of *L. nobilis* were collected (none from SR and <20 from four other periods), I included in the analyses data from 19 specimens that had some partially digested food in the mouth

or esophagus. In all of these specimens, the stomach also contained food and was not everted; the remains from the esophagus or mouth were picked out as carefully as possible and added to the stomach contents. (No specimens with everted stomachs were included.) Use of these 19 specimens had the desirable effect of increasing the numbers upon which statistical estimates were based, but, as pointed out earlier, possibly biased the data because some of the regurgitated food may not have been recovered. The data were treated with and without these 19 specimens. Inclusion of the latter either had no effect or increased the significance of differences indicated without them. Thus bias, if any, that was introduced was insufficient to obscure between-period differences in stomach fullness.

Diel differences in stomach fullness were significant ($P<0.05$) and resembled the trends of other myctophids. There was, however, no clear indication of a peak value at dawn; no specimens from SR were available and the medians for N3, N4, and D1 were similar to each other. The percentage of empty stomachs was low throughout most of the night and increased steadily between D1 and SS.

The size-frequency distribution of the specimens was bimodal; 45% were <40 mm SL and 47% >60 mm. The small specimens had eaten mostly copepods and amphipods 1-3 mm and *Euphausia* spp. <10 mm, while the large ones had taken large copepods (>3 mm PL) and euphausiids, mysids, sergestiids, and fishes 10-30 mm long. Intact prey were found frequently in night specimens and occasionally in those caught by day. The latter were, with the exception of a single *Lophothrix humilifrons* (apparently a deep-living copepod), migrating species that could have been taken at night. One specimen from N4 contained; among the remains of a euphausiid, crab megalopa, and copepods; a partially digested insect (probably a hymenopteran).

Lampanyctus steinbecki (Figure 2)

Stomach fullness values for *L. steinbecki* differed significantly ($P<0.005$) over the diel cycle. The medians generally increased from SS to SR and thereafter stayed at about 1% until a sharp decrease between D3 and N1. The percentage of fish with empty stomachs was low for all periods. The principal prey of *L. steinbecki* were copepods > ca. 2 mm PL—mostly aetideids, *Pleuromamma*, and *Candacia*—and euphausiids. A few intact items were found in specimens from D1 and D2 but all were shallow-living or migrating species that could have been taken the previous night. With the exception of a single *Pareuchaeta* sp. (probably a deep-living nonmigrator), the prey from D3 and SS were all well digested.

Notolychnus valdiviae (Figure 2)

The *H*-test indicated highly significant ($P<0.005$) diel differences in stomach fullness for *N. valdiviae*. Median values were low early in the night and increased to a peak at N4. The minimum value at D1 was slightly below the early night values. Stomach fullness increased slightly until SS and then decreased at SS-N1. The percentage of fish with empty stomachs was low at all periods. The positions of the 75th percentiles indicated higher percentages of fish with relatively full stomachs at N3, N4, SS, and D3.

Notolychnus valdiviae had taken a wide variety of sizes (ca. 0.5-4.0 mm PL) and species of copepods, but the bulk of the food in terms of weight was made up by large (relative to the weight of *N. valdiviae)* items such as *Pleuromamma xiphias, Candacia longimana,* and 2-4 mm aetideids. Intact prey were more frequently noted in specimens from N3 and N4 than in those from the apparent "secondary peak" in stomach fullness at D3 and SS. Considering only those specimens with stomach fullness >2% (whose numbers distinguish the peak periods from others), only three of the nine from D3 and SS contained intact or partially intact *Pleuromamma*. The other six contained remains that were either unrecognizable or barely so. In contrast, of the 15 specimens from N3 and N4, 12 contained 1-3 intact items, while only 3 contained unrecognizable remains. This plus the absence of any apparent significant differences associated with the D3/SS peak indicate that the latter was due to a chance collection of a few more specimens that had taken large meals the previous night rather than to extensive daytime feeding.

Triphoturus nigrescens (Figure 2)

Overall diel differences in stomach fullness were highly significant ($P<0.005$). Both medians and means rose from low values at SS and N1 to a peak at N4 and then, except for a slight increase at D3, declined until SS. Due to the broad overlap in

ranges and percentiles for most pairs, only the large increase between N1 and N2 was even marginally significant. The percentage of empty stomachs was highest at N1 and zero at and just after the peak at N4.

Triphoturus nigrescens fed principally on *Pleuromamma* and *Euphausia* spp. Intact prey were recorded more frequently during N2-N4 than in other periods. As in the case of *N. valdiviae*, the apparent peak at D3 was due to a few fishes' containing large amounts of well-digested material rather than freshly taken items.

Melamphaidae

Melamphaes danae (Figure 2)

Few *M. danae* were taken at any period. None were taken at SR, and only two or three were taken at SS, D1, and D2. The data indicate a diel trend similar to that of several myctophids, but the H-test indicated that diel differences were only marginally significant (P = ca. 0.10). If the data from SS, D1, and D2 were not included, the H-test indicated significance at P = ca. 0.05 and the N4 and D3 values differed at $P<0.05$. This latter, and statistically dubious, manipulation indicates that the apparent trend in the data is real, but that more specimens would be needed to confirm it properly.

Melamphaes danae fed on a wide variety of zooplankton including polychaetes and chaetognaths as well as crustaceans—mostly small copepods and ostracods. The copepods identified were all either vertical migrators or shallow-living, nonmigrating species. Intact items were present in nighttime specimens; those from daytime contained remains barely identifiable to general taxon.

Gonostomatidae

Gonostoma atlanticum (Figure 3)

Relatively few *G. atlanticum* were available from four periods even though 23 additional specimens from the May 1974 collections were included. Still there were significant ($P<0.05$) differences in stomach fullness over the diel cycle. Median values rose steadily from SR to D3, remained at ca. 2% between D3 and N2, and then dropped sharply between N2 and N3. Though the median for N4 was slightly higher than that for either N3 or SR, the percentage of empty stomachs was highest at N4 and SR, indicating an overall trend for decrease during the late night.

Gonostoma atlanticum fed on large copepods—mostly *Pleuromamma xiphias, Candacia longimana,* and aetideids and scolecithricids of several genera—and small (<10-15 mm) euphausiids. Intact prey were found in stomachs from all periods, but were mostly from the period between D1 and N2. The majority of the contents from N3 and N4 were well digested.

Gonostoma elongatum (Figure 3)

Relatively few *G. elongatum* were available from three periods and the size range of individuals used was extremely broad (26-150 mm). There is evidence from past studies that fractions of the population occasionally do not migrate (Clarke 1974), but catches from deep night tows taken during the same sampling period did not clearly indicate whether or not this occurred during this study.

The H-test indicated marginally significant differences ($0.05<P<0.10$) in stomach fullness over the diel cycle, and there was no clear trend in any of the parameters. Medians for all periods except SR (only 8 specimens) and D3 (10 specimens) were <1%. The means were well above the medians for several periods due to a few fishes' having very full stomachs. *Gonostoma elongatum* fed on the same copepods and euphausiids noted for *G. atlanticum* and on ostracods, amphipods, small sergestiid shrimps, and fish as well. Fresh or intact items were noted most frequently in specimens from SR, D1, D3, and N1.

Photichthyidae

Vinciguerria nimbaria (Figure 3)

Although previous evidence (Clarke 1974) indicated that a fraction of the population of *V. nimbaria* does not always migrate, catches of deep night tows from the same cruise indicated that only an insubstantial fraction, if any, remained at depth during the shallow night sampling periods.

Diel differences in stomach fullness were highly significant ($P<0.005$). The median was highest at SS and decreased steadily throughout the night to nearly zero at N4 and SR. The values were only slightly higher during the day, but increased sharply between D3 and SS. A clearer picture of changes between D2 and SS is given by the means

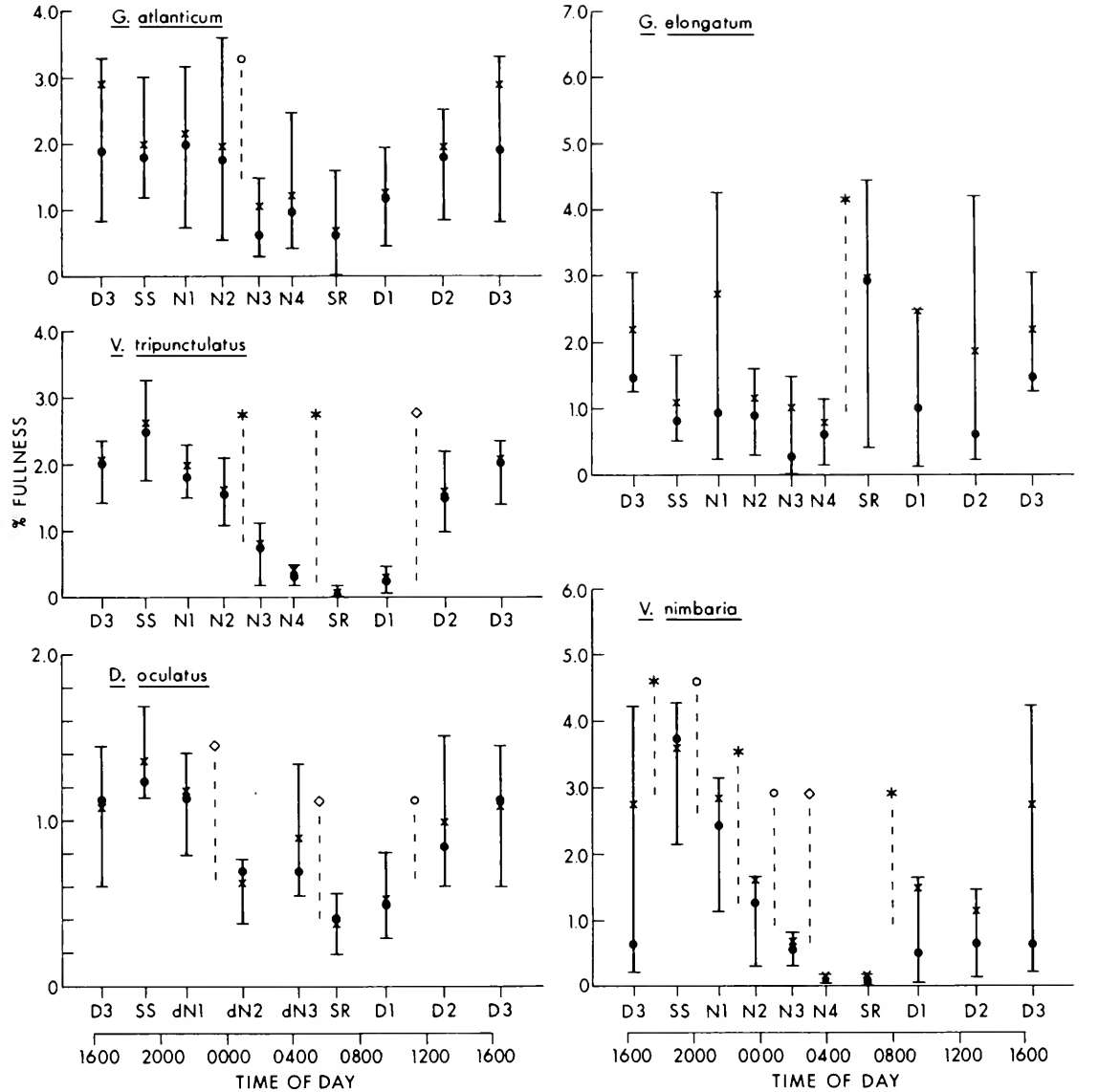

FIGURE 3.—Stomach fullness throughout the diel cycle for five species of stomiatoids: *Gonostoma atlanticum*, *Gonostoma elongatum*, *Valenciennellus tripunctulatus*, *Danaphos oculatus*, and *Vinciguerria nimbaria*. Symbols and format as in Figure 1.

rather than the medians, because there were marked differences in frequency distribution for these periods—differences to which the median is not sensitive. At D2 the data were skewed to the left with most values <1% and very few full stomachs. At D3 the data were bimodal; 7 values were higher than the mean of ca. 2.75% and 11 <1%. By SS, the data were again unimodal and skewed slightly to the right with 16 values >2% and only 2 <1%. Thus the trend between D2 and SS was one of a gradual change in percentages of the fish with very full stomachs, and the abrupt increase in median values between D3 and SS occurred as the high values became the dominant mode. The percentages of empty stomachs showed a trend opposite to that of the average values, i.e., an increase during the night and a decrease between SR and D2.

Vinciguerria nimbaria fed upon a wide variety of sizes and taxa of prey. Small (< ca. 2 mm PL) copepods and ostracods were most frequent, but larger copepods and small euphausiids occurred regularly. Both the number of prey items and absolute values of stomach fullness for the peak period were higher than for most of the the other species examined here; in several instances the remains of 20-40 prey items were found in a single stomach. Intact items were most frequent at SS and common in specimens from day samples. Some intact items were noted from N1 and a few from N2, but stomachs from N3, N4, and SR contained practically nothing but well-digested remains.

Sternoptychidae

Danaphos oculatus (Figure 3)

Few *D. oculatus* were available for any period except D1, and numbers were particularly low for D2. Nine of the specimens used came from the May 1974 series. In spite of this, there was an evident and highly significant ($P<0.005$) diel trend in stomach fullness. Median values rose steadily from a minimum at SR to a maximum at SS and declined nearly constantly throughout the night. There were a few empty stomachs at SR and D1 and none at other periods. *Danaphos oculatus* fed almost exclusively on *Pleuromamma xiphias*, *Euchaeta media*, and similar-sized juveniles and adults of several aetideid species. Intact items were most frequently noted in D3 and SS specimens; some were found in those from D1 and D2. Almost none of the night specimens contained any but well-digested remains.

Valenciennellus tripunctulatus (Figure 3)

Few *V. tripunctulatus* were available from any period except N1; 31 of the total examined came from the May 1974 collections. Still, like *D. oculatus*, *V. tripunctulatus* showed a clear and highly significant ($P<0.005$) diel trend in stomach fullness. Medians rose from zero at SR to a maximum at SS and declined throughout the night. The principal prey items were *P. xiphias*, *P. abdominalis*, *E. media*, and similar-sized aetideids. The stomachs from D2 to SS were nearly uniformly packed with intact prey while those from late night and SR were either empty or contained only traces of well-digested remains.

DISCUSSION

Feeding Chronology

Interpretation of data on stomach fullness is limited because observed fullness is a function of two rate processes—feeding rate and stomach evacuation rate. Diel changes in stomach fullness indicate that one or both rates vary over the diel cycle, but without independent estimates of one or the other, the only certain statements that can be made are that feeding exceeds evacuation during periods when fullness increases, the opposite when fullness decreases, and that both rates are zero when the stomach is empty. Notes on state of digestion of stomach contents are helpful, but must be interpreted with caution. Absence of intact items indicates that feeding rate is zero, but presence of intact items does not necessarily mean feeding rate was positive during a given period since some items may remain intact for an unknown time after feeding ceases. Still, it is possible within these limits to qualitatively consider changes in the two rates and to relate them to environmental changes which the fishes encounter over the diel cycle.

The species considered here undergo diel changes in numerous environmental factors, some of which are likely to affect either feeding or stomach evacuation rate in a qualitatively predictable manner. The migrating species encounter higher temperatures at night. Diel temperature changes for each species (Table 3) were determined using temperature-depth profiles from the study area (Maynard et al. 1975 give profiles from several seasons of three different years) and depth ranges of the fishes (Clarke 1973, 1974; Clarke and Wagner 1976). Because all species considered occur below the steepest part of the thermocline during the day, the magnitude of the diel temperature change is mostly a function of nighttime depth range and not day depth or absolute range of migration. For the same reason, juveniles, which occur shallower than adults in most species (Clarke 1973), incur greater temperature change than adults of the same species. The migrating species also encounter lower pressures and higher oxygen concentrations at night (oxygen-depth profiles for a site near the study area are given in Gordon 1970).

Unless the fishes are able to regulate metabolism over the range of diel changes, the day-night

TABLE 3.—Depth ranges, estimated diel changes in temperature, and probable day-night differences in prey concentration for the 16 species of fishes considered. (See text for sources of estimates.)

Species	Depth range (m) Night / Day	Temperature change (°C) Night-day	Prey density Night vs. day
Benthosema suborbitale	0-100 / 500-600	18-19	N >D
Bolinichthys longipes	50-150 / 500-700	16-19	N >D
Ceratoscopelus warmingi	0-150 / 600-1,000	16-20	N > >D
Diaphus schmidti	0-75 / 500-600	17-19	N >D
Hygophum proximum	0-150 / 500-700	15-19	N >D
Lampanyctus steinbecki	75-200 / 600-1,000	10-17	N > >D
Lampanyctus nobilis	50-150 / 600-1,200	16-20	N > >D
Notolychnus valdiviae	80-150 / 500-650	15-16	N >D
Triphoturus nigrescens	25-100 / 550-750	17-19	N >D
Melamphaes danae	75-200 / 750-1,200	10-18	N > >D
Danaphos oculatus	450-650 / 450-650	0	N << D
Valenciennellus tripunctulatus	200-330 / 400-500	5-6	N < D
Gonostoma atlanticum	150-300 / 500-550	6-14	N ≤ D
Vinciguerria nimbaria	0-125 / 400-560	13-17	N ≥ D
Gonostoma elongatum	60-265 / 550-725	10-19	N ≥ D
Lampanyctus niger	100-300 / 650-900	7-15	N >D

differences in temperature and oxygen concentration both predict lower rates of metabolic processes in general and in particular lower feeding or stomach evacuation rate during the day. Childress (1975) and Childress and Nygaard (1973) indicated that mesopelagic organisms can regulate over a wider range of oxygen partial pressures than these fishes encounter off Hawaii. Thus temperature changes are more likely to affect rate processes. Teal (1971) showed that increased pressure can stimulate metabolic rates and thus mediate or cancel effects of temperature; however, it seems likely that temperature effects are predominant for the species considered here since these fishes migrate through a much stronger thermocline than did the shrimps studied by Teal.

As a consequence of vertical migration—by the fishes and by many of their prey—the fishes encounter diel differences in prey concentration, with which feeding rate is likely to be positively correlated. As noted above, the depth distributions of all prey species in the study area are not known in detail; however, general, qualitative features were evident from the available plankton samples (see above). Most of the important prey species were either shallow-living nonmigrators that occurred above ca. 200 m day and night or were vertical migrators with maximal concentrations at ca. 300-450 m by day. Some important genera, e.g. *Euphausia*, *Pleuromamma*, and *Euchaeta*, occurred as deep as 600 m during the day but not at high densities. At night, most copepods and many of the euphausiids occurred at highest densities above ca. 150-200 m. Many prey species occurred between 200 and 300 m at night, but except for a few euphausiid species, concentrations were much lower than in the upper 200 m. Below ca. 600 m by day and below ca. 300 m at night, total zooplankton concentration was low and that of important prey species nearly zero. Based on the above features and the fishes' depth ranges, qualitative estimates of day-night differences in prey concentration were made for each species (Table 3).

Nine species of myctophids and probably *Melamphaes danae* had similar diel patterns in that median values of stomach fullness were minimal at or near dusk and increased only at night, but details of the patterns were variable. Six species, *Benthosema suborbitale*, *Bolinichthys longipes*, *Ceratoscopelus warmingi*, *Diaphus schmidti*, *Lampanyctus steinbecki*, and *L. nobilis* (Figures 1, 2), had two periods of increasing stomach fullness during the night separated by a decline. Maximum stomach fullness occurred at or near dawn, and the fish reached day depth with relatively full stomachs. Stomach fullness appeared to decrease during the day in some species and showed no clear trend in others, but in most there was a significant decrease at or near dusk. In *Notolychnus valdiviae*, *Triphoturus nigrescens*, and possibly *Melamphaes danae* (Figure 2), median stomach fullness appeared to increase steadily throughout the night to a peak value just before dawn. In the first two of these species, stomachs were partially evacuated by the time they reached day depth. In *Hygophum proximum* (Figure 2) median fullness reached a peak value early in the night, and stomachs were completely evacuated by dawn.

For most of the above species there was no evidence of significant feeding at depth during the day. Intact items were more frequent at night, and stomach contents of day-caught fish were usually

well digested. *Lampanyctus nobilis* and *L. steinbecki* occasionally take deep-living copepods during the day, and *C. warmingi* apparently takes large items whenever it encounters them. Still, the instances of definite day feeding were so few in even the latter three species that the medians and, therefore the diel patterns, were only marginally affected.

All of these myctophids undergo diel changes in temperature and prey concentration (Table 3) that correlate with the observed pattern of feeding solely or mostly at night while in the upper 200 m. All are at much higher temperatures at night. Although some species occur as shallow as ca. 500-600 m during the day and thus partially overlap the daytime depth ranges of certain of their prey, all occur below daytime maxima of prey concentrations and almost certainly encounter higher concentrations at night. Certain details of the patterns of stomach fullness indirectly indicate that stomach evacuation rate may be lower during the day as predicted by temperature differences. In many species, stomach fullness did not clearly decrease during the day; since feeding rate was apparently zero then, the evacuation rates must have been low or zero. The sharpest declines in stomach fullness occurred at or near dusk in most species, near dawn in *N. valdiviae* and *T. nigrescens*, and during the night in *H. proximum*—not during periods when the fishes remained within their day depth ranges. In all cases except *H. proximum*, however, something related to vertical migration itself, e.g., activity, could be responsible for the apparent increases in evacuation rates.

Four species of stomiatoids, *Gonostoma atlanticum*, *Danaphos oculatus*, *Valenciennellus tripunctulatus*, and *Vinciguerria nimbaria*, fed only during the day. The last three species occur somewhat shallower by day then do the myctophids and are consequently at or near depths of maximum concentration of their prey then. The upward migration of *V. nimbaria* is similar in extent to that of its prey. Thus this species encounters little or no diel change. *Danophos oculatus* does not migrate, and *Valenciennellus tripunctulatus* migrates less than do its prey. Consequently, both species occur below high concentrations of prey at night. The adults of *G. atlanticum* (as were most specimens used here) occur near the lower depth limits of most prey species both day and night, and the day-night difference is probably minor. Thus in these species, the day depth ranges, rather than the occurrence or upward extent of migration, seem more related to observed feeding pattern.

All four species feed at nearly the same, low temperature. Diel temperature change is zero for *D. oculatus*, and relatively small for *V. tripunctulatus* and large *G. atlanticum* because they penetrate only part way through the thermocline. *Vinciguerria nimbaria* undergoes a change similar to that of the myctophids. The temperature changes or lack thereof obviously have no effect on feeding periodicity; however, the steepness of the nighttime decline in stomach fullness seems roughly correlated with nighttime temperature indicating an effect on stomach evacuation rates. This trend is considered in more detail below.

Lampanyctus niger and *G. elongatum*, the two species which showed no diel pattern in stomach fullness, do not undergo large diel changes in either temperature or prey concentration in spite of the fact that they migrate. The large individuals of both species (as were all the *L. niger* and most *G. elongatum*) undergo a relatively small temperature change. Likewise, only the smallest juveniles of either species encounter markedly higher prey concentrations at night. The relatively low values of stomach fullness in both species and the presence of deep-living, nonmigrating zooplankton in *L. niger* indicate that these two species feed at a low rate whenever and wherever they encounter prey.

Relationship to Previous Studies

Comparison of the present results with those of previous studies is restricted because methodology in all cases was different from that of the present study and in many cases equivocal or probably not sensitive enough to discern diel trends or lack thereof. With the exception of the study by DeWitt and Cailliet (1972), appropriate statistical testing was not done, and it is impossible to do so from the published data.

The most directly comparable study is that by Holton (1967) on *Lampanyctus* (= *Triphoturus*) *mexicanus*. Using 10 fish from each of eight periods of the day, he determined dry weights, but for some unknown reason weighed the entire alimentary canal with the food. The minimal values observed, presumably from empty stomachs, indicate that his "% nutrition" values should be decreased by about 2.5-3 to make them roughly comparable to those of the present study. Though

the ranges and standard deviations of the data are broad relative to the differences in means, the diel trend in the latter is similar to that observed here for *H. proximum*, i.e., peak value was reached early in the evening and then dropped to low values and probably zero before the dawn descent.

Most previous studies have used visual estimates of fullness with a scale of 3-5 ranks. Because of the lack of "intercalibration" between investigators, only the rank for "empty" can be compared unequivocally, and it is not certain in what manner the ranks might correlate with percentages of the fishes' dry bodily weight. Finally the validity or absence of trends and details thereof are questionable because scales of only 0-3 or 0-4 are rather insensitive. (Had only visual estimates of fullness been used for the present study, only in a few cases, e.g., *H. proximum* or *Valenciennellus tripunctulatus*, would the diel trends have been obvious.)

Anderson's (1967) data on *T. mexicanus* indicate a peak in stomach fullness just before sunrise, but his data on degree of digestion indicate that fresh food items were most frequent between sunset and midnight. His data for *Bathylagus stilbius* (cardiac portion of the stomach only) indicate two separate periods of increasing fullness at night and the sharpest decrease prior to ascent at dusk. This pattern correlates with frequency of less-digested prey items and is very similar to that observed for several myctophids in this study.

Similar indices were used in the studies of four species of high latitude myctophids: *Benthosema glaciale* (Gjösaeter 1973) and *Stenobrachius leucopsarus*, *Diaphus theta*, and *Tarletonbeania crenularis* (Tyler and Pearcy 1975). Both studies examined large numbers of specimens from each of a few, very broad time periods. Their data indicated highest percentages of full or nearly full stomachs at night and highest percentages of low values during the day. The occurrence of some full stomachs during the day led Gjösaeter to conclude that diel variation in feeding was not great and Tyler and Pearcy to conclude that there was no evidence against diurnal feeding. Both studies noted a higher degree of digestion during the day. These results are, however, consistent with the possibility that like many of the myctophids in the present study, their species descended at dawn with full stomachs and did not evacuate them completely until the dusk ascent. The latter may well have not been detected in these studies due to the broad time periods used.

Data on myctophids from recent studies by Merrett and Roe (1974) and Baird et al. (1975) are consistent with nocturnal feeding but are equivocal to varying degrees due to low numbers of specimens, incomplete diel coverage, or methodology. Both studies based stomach fullness estimates on counts of identifiable prey items. Apparently, the presence of a single resistant part, e.g., a *Pleuromamma* button, was counted the same as an intact, whole individual of the same taxon. Because of this and the likelihood that some prey taxa or parts of prey are digested—and concomitantly rendered unrecognizable—at different rates (e.g., Pandian 1967; Gannon 1976), such counts seem to be insensitive or possibly biased estimates of gut fullness—especially so when the counts are used to back-calculate dry weight as done by Baird et al. Furthermore, neither study corrected the fullness estimate for fish weight, which (using standard length ranges given by these authors and assuming that weight is roughly porportional to the cube of the length) varied by factors of ca. 7-15 in the myctophids covered by Merrett and Roe and ca. 2.75 in *D. taaningi*, the species studied by Baird et al.

Merrett and Roe's data for *L. cuprarious* indicated peak fullness in the middle of the night and a decrease before the dawn descent—a pattern similar to that of *H. proximum*. Their data for *Lobianchia dolfleini* and *N. valdiviae* include no samples between dusk and near dawn, but show fuller stomachs at dawn. Data of Baird et al. for *D. taaningi* are also similar to that for *H. proximum*. The rise in fullness from empty or nearly empty stomachs in the afternoon to fairly high values in early evening is evident and based on 39 and 9 specimens, respectively; however, the subsequent decline is based on a single specimen from late night and 4 from just after dawn (1 which contained a fair amount of food).

Fewer stomiatoids have been examined elsewhere, but much of the data available is consistent with diurnal feeding. Perhaps the most convincing data (because of good diel coverage and numerous specimens) presented by Merrett and Roe (1974) is that for *Valenciennellus tripunctulatus*, which does not migrate in their study area. The pattern is clearly similar to that observed for the Hawaiian specimens. Hopkins and Baird (1977) cited their own unpublished data also indicating diurnal feeding for the same species. Merrett and Roe (1974) interpreted dusk peaks of numbers of items/nonempty stomach as

an indication of dusk feeding activity in two species of *Argyropelecus;* however, the data for *A. hemigymnus* seem to me more consistent with increasing stomach fullness throughout the day and a nighttime decline. Except for high dawn values (based on only three specimens from two tows), *A. aculeatus* shows a similar trend.

DeWitt and Cailliet (1972) found no diel trend in feeding of *Cyclothone signata*, but, based on fewer empty stomachs in fish caught in the upper part of the depth range, proposed that this species, although it does not undertake diel vertical migrations, may ascend irregularly to levels of higher prey concentration to feed. Their data also indicated that a deeper living species *C. acclinidens*, had a higher percentage of empty stomachs by day; as noted by the authors, the latter seems to defy any reasonable explanation.

Legand et al. (1972) considered feeding chronology of 14 species of mesopelagic fishes from the South Pacific. Though trends in stomach fullness of some species are similar to those noted here, e.g., that for *Triphoturus microchir* (which almost certainly = *T. nigrescens)* is very similar to that for *T. nigrescens* near Hawaii, a number of species show patterns quite different from those reported by either the present or other studies. Interpretation of the validity of such "exceptions" is difficult owing to the sparse presentation of Legand et al. Though total numbers of specimens are fairly high, it is not clear that they were equitably distributed among diel periods, from the same area, or from the same season, etc. The percent fullness values are obviously based on wet weights—an imprecise measurement, particularly for stomach contents—and it is not clear whether all fish and stomach contents were weighed or some sort of averaging or regression procedure was employed.

The feeding patterns shown by previous studies cannot be compared in detail with those presented here; however, there is general agreement in data on the two dominant groups of mesopelagic fishes. Myctophids feed mostly at night, while stomiatoids tend to feed by day. My interpretations indicate that near Hawaii, the differences are at least partially related to different diel relationships of the fishes to vertical distributions of their prey. Other interpretations are obviously possible, e.g., the feeding patterns may prove to be characteristic of the two taxa regardless of relationship to prey distribution. It would be of particular interest to investigate myctophids with vertical distribution patterns similar to those of the stomiatoids, i.e., with shallow day depth ranges at or near high daytime concentrations of zooplankton. (Certain *Myctophym* and *Diaphus* spp. from Hawaii meet this criterion [Clarke 1973], but were not captured in sufficient numbers to be included in this study.)

The diel feeding patterns of mesopelagic fishes could well be related to light rather than (or in addition to) temperature and prey concentration. No data on diel light changes near Hawaii are available; however, data of Kampa (1970) from a similar area of clear oceanic water in the North Atlantic show that during full moon the diel change in depths of relevant isolumes is of the order of 300-350 m. Even allowing for considerable differences in extinction coefficients between Hawaii and Kampa's study area, the diel change in isolumes at new moon (when the present samples were taken) off Hawaii is probably at least 300-350 m and could be as great as 500 m. The absolute diel change in depth for most of the myctophids is over 500 m while that for the 4 day-feeding stomiatoids is ca. 400 m or less (Table 3). Thus it is possible that feeding in both groups occurs when higher light levels are encountered—at night for the myctophids and by day for the stomiatoids.

Estimation of Rates

As mentioned previously, neither feeding rate nor stomach evacuation rate can be considered quantitatively without an independent estimate of the other. Because of the difficulty in keeping mesopelagic fishes alive for grazing or evacuation experiments, it will likely be a long time before independent estimates are available. For a few species considered here it is, however, possible to derive "quasi-independent" estimates of evacuation rate given certain plausible assumptions. These allow, with further assumptions, rough estimates of feeding rate and daily ration.

For any period where feeding rate is zero, changes in stomach fullness are due to evacuation alone, and, if temperature, pressure, etc., remain essentially constant during that period, the rate of evacuation can be assumed to be proportional to the amount of food in the stomach (Kjelson and Johnson 1976; Eggers 1977). The change in stomach fullness would then be described by:

$$dS/dt = -kS \text{ or } S_t = S_0 e^{-kt} \qquad (1)$$

where S is stomach fullness as percentage of fish weight; S_0 and S_t, the values at the beginning and end of a period of t hours; and k, the instantaneous evacuation rate in per hour.

For most of the species considered here, there is no extended period of decline in stomach fullness where the above assumptions are met, but a rough estimate of k is possible for *H. proximum* and three species of stomiatoids. *Hygophum proximum* apparently ceases feeding early in the night, and stomach fullness declines from N2 to SR under essentially constant conditions, i.e., the fish remain in the upper layers. Stomach fullness declines from SS to SR in *Vinciguerria nimbaria*, *Valenciennellus tripunctulatus*, and *Danaphos oculatus*, and except for relatively brief periods of migration in the first two species, they remain at the same temperature, etc., for this period.

The values of k for these four species were calculated by simply using the integral form of Equation (1) and the median values of S for the beginning and end of the periods mentioned above (Table 4). (Other fitting procedures, such as least square methods, require that a number of questionable statistical assumptions be made.) The values of k are inversely correlated with night depth and thus positively with temperature being lowest for *D. oculatus*, highest for *Vinciguerria nimbaria* and *H. proximum*, and intermediate for *Valencienellus tripunctulatus*.

For each of the four species, prey concentration and temperature, pressure, etc., were essentially constant throughout the period when feeding occurred (SS to N2 for *H. proximum* and SR to SS for the stomiatoids). It is not unreasonable to assume, as a first approximation, that feeding rate was constant during the periods of increasing stomach fullness. Changes in fullness would then be described by:

$$dS/dt = F - k'S \tag{2}$$

where k' is the instantaneous evacuation rate during the period of feeding, and F is the feeding rate in percentage bodily weight per hour. Integrating and rearranging gives an equation for F in terms of k', the duration of the feeding period t' in hours, and median fullness at the beginning (S_0') and end (S_t') of the feeding period:

$$F = \frac{k'(S_t' \times S_0' e^{-k't'})}{1 - e^{-k't'}}. \tag{3}$$

(In some cases, there were a few relatively high values of stomach fullness among the data for a given period; consequently, the feeding rate of some individuals may have been lowered due to satiation. Such values had little effect on the median, and thus the assumption of constant feeding rate is probably not seriously violated as long as medians are used in the calculations.)

Estimates of feeding rate and daily ration ($= Ft'$) were calculated (Table 4) using median values of stomach fullness at SR and SS as S_0' and S_t', respectively, for the stomiatoids and, similarly, SS and N2 for *H. proximum*. Since both *D. oculatus* and *H. proximum* feed at the same temperatures as those under which the instantaneous evacuation rates were estimated above, k' in Equation (3) was assumed equal to k calculated from Equation (1). The daytime or "feeding" temperatures of *Vinciguerria nimbaria* and *Valenciennellus tripunctulatus* are lower than those under which k was estimated from Equation (1). During the day both species occur at nearly the same temperature as does *D. oculatus* both day and night. Consequently, for each of the two migrating stomiatoids, two values of feeding rate and daily ration are given in Table 4—one calculated using

TABLE 4.—Estimates of instantaneous stomach evacuation rates, feeding rates, and daily rations for four species of mesopelagic fishes based on changes in median stomach fullness over the diel cycle. The first three columns give the sampling periods (Table 1) between which feeding rate was assumed to be zero, the duration of this interval (t), and the calculated instantaneous stomach evacuation rate (k). The last five columns give the sampling periods between which feeding rate was assumed constant and positive, the duration of this interval (t'), the instantaneous stomach evacuation rate assumed for the feeding periods (k'), and calculated feeding rate (F in % of bodily weight per hour) and daily ration ($R = Ft'$ in % of bodily weight per day). For both *Valenciennellus tripunctulatus* and *Vinciguerria nimbaria*, two values of k', F, and R are given: the higher values under the assumption of constant stomach evacuation rate night and day ($k' = k$), the lower under the assumption that stomach evacuation rate during the feeding period was lower and equal to that estimated for the nonmigrating, deep-living, *Danaphos oculatus*. See text for formulae and further explanation.

Species	Nonfeeding period	t (h)	k (h^{-1})	Feeding period	t' (h)	k' (h^{-1})	F (%/h)	R (%/d)
Hygophum proximum	N2-SR	6.8	-0.52	SS-N2	4.5	-0.52	1.26	5.7
Danaphos oculatus	SS-SR	11.3	-0.10	SR-SS	12.7	-0.10	0.15	1.9
Valenciennellus	SS-N4	8.7	-0.22	SR-SS	12.7	-0.22	0.57	7.3
tripunctulatus						-0.10	0.34	4.3
Vinciguerria	SS-SR	11.3	-0.38	SR-SS	12.7	-0.38	1.42	18.1
nimbaria						-0.10	0.51	6.5

$k' = k$ from Equation (1) and the other using $k' = 0.10$, the value for *D. oculatus*.

The estimated ration for *Vinciguerria nimbaria* seems inordinately high (18%) if k' is assumed equal to k, the nighttime estimate of evacuation rate. Such values have been estimated for very young, rapidly growing zooplanktonivorous fishes, e.g., *Alosa aestivalis* (Burbidge 1974) and *Oncorhynchus gorbuscha* (Parsons and LeBrasseur 1970). Data from Kjelson and Johnson's (1976) study of postlarval *Lagodon rhomboides* and *Leiostomus xanthurus* feeding rates on zooplankton yield estimates of daily ration of only 9.4 and 8.6%, respectively, in terms of wet weight (my calculations from their data). The estimated ration for *V. nimbaria* using the low value for k' and that for *H. proximum* lie within the range of values observed for larger individuals in the first two studies cited above and for *Morone chrysops* juveniles feeding on zooplankton (Wissing 1974). The daily ration of the California sardine, *Sardinops caerulea*, which is a larger zooplanktonivore, is apparently slightly lower; judged from Lasker's (1970) estimates of metabolic and growth requirements, the daily ration is probably about 3-4% (in terms of calories) for the sizes considered.

The above comparisons are admittedly stretched and ignore, among other things, possible differences due to environmental temperature, but the similarity of estimated daily rations of *H. proximum* and *V. nimbaria* to those of shallow-living planktonivores is not entirely unexpected. Childress and Nygaard (1973) have shown that the chemical composition of mesopelagic fishes which migrate to the upper layers at night is more similar to that of epipelagic species than to non-migrating, deep-living forms.

Differences between estimates for the three stomiatoids are correlated with the extent of vertical migration. Nighttime stomach evacuation rate is highest in *V. nimbaria*, lowest in *D. oculatus*, and intermediate in *Valenciennellus tripunctulatus*. Feeding rate and daily ration estimates show the same trend regardless of whether or not daytime stomach evacuation rates are assumed lower. The absolute values of stomach fullness at the end of the feeding period (Figure 3) are also highest in *Vinciguerria nimbaria* and lowest in *D. oculatus*. These trends indicate a possible adaptive value for the upward migrations of some stomiatoids. The higher temperatures encountered at night by migrators could allow processing of larger meals and presumably faster growth, turnover, etc., rates than for species which remain at depth day and night.

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ON THE RESTRUCTURING OF THE PELLA-TOMLINSON SYSTEM

R. IAN FLETCHER[1]

ABSTRACT

The time-dependent analysis of an earlier work is extended to the equilibrium case of the Pella-Tomlinson system, and the relationships between the equilibrium and nonequilibrium versions of the restructured system are developed. The dual formulations of the conventional analysis are avoided and maximum sustainable yield is separated from the indeterminacy of the system. All arbitrary coefficients are eliminated and the management components incorporated directly into the system equations. The source of the statistical degeneracy in the model is revealed and explicitly formulated, and in the companion article by D. Rivard and L. J. Bledsoe (this issue of the *Fishery Bulletin*) the restructured model is treated by a new statistical method that subdues the estimation failures associated with past treatments of the Pella-Tomlinson system.

Because the equilibrium versions of all stock-production models follow from steady-state integrations, the strategy of fishery regulation becomes a strategy of accommodation, so to speak, as determined by a pattern of balanced model states where removals just equal the productivities otherwise surplus to the maintenance needs of the stock. Population status usually enters the process in the simple, robust form of integrated numbers or biomass, and the removals of fishing constitute direct fractions of the whole fishable stock without reference to age or weight distributions. Since the appearance of Schaefer's work (Schaefer 1954) the strategy has been applied to the management of many fisheries. Schaefer devised a rational, linearized method for estimating the parameters of Graham's equilibrium model (Graham 1935) from the actual nonequilibrium yields and effort expenditures of a fishery, a contribution that is often misunderstood. In applying Schaefer's method or like schemes of synthesis, it is not so much that one hopes to observe a pattern of equilibrium levels in a fishery or even expects them to come about, but rather, by knowing the response history of a stock to various exploitation pressures, one might then be guided by the model in bringing a stock, through a sequence of management actions, into a state where some desired level of sustainable yield most likely abides. The philosophy is widely accepted in fisheries management but its application is often censured, either on economic or biological grounds (see, for example, Larkin 1977).

The exploitation model of Pella and Tomlinson (1969), as it is customarily thought of, extends the more "basic" model of Graham from a system of second degree in nonlinearity to a flexible or more "general" system of indeterminate degree. The increased flexibility comes into the Pella-Tomlinson model through the addition of a single exponential parameter, but the analytical peculiarities that accompany the improvement often lead to paradoxical ends since the equations of the system then permit the simultaneous generation of good data fits and poor parameter estimates (see the commentary of Ricker 1975:323-326 and the treatments of Fox 1971, 1975). This disturbing trait of the statistical model arises from the conflict between the variable (or parametric) curvature of the analytical model and the coupling of that curvature, in the conventional formulations, with all the coefficients of the system. As shown in a prior work (Fletcher 1978), those effects may be separated in the time-dependent analysis by restructuring the system equations so as to accommodate directly the critical-point coordinates of the system graphs. In this paper we extend the analysis to the equilibrium version of the Pella-Tomlinson system, and we show the relationships between the equilibrium model and the (restructured) time-dependent equations.

For a stock of mixed age classes, the most difficult problem in applying any equilibrium model will lie, essentially, in the interpretation of time-dependent transitions between idealized states (however momentary, long-enduring, or

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unobserved such states may be), since the stock will include simultaneously the young and the old, the older having accumulated a probabilistic history of mortality, fecundity, and growth which may differ considerably from the current schedule that affects both. Various tactics for adjusting the parametric mechanics of stock-production models to such long-term, delayed influences are given by Gulland (1969), Fox (1975), Walter,[2] and others, but in the case of the Pella-Tomlinson system the difficulties have been compounded by artifacts of the conventional analysis and by an instability inherent to the mathematical indeterminacy of the system itself. With the critical-point analysis, most of those impediments will convert to tractable relationships or vanish altogether. We can suppress the troublesome dual formulations associated with the conventional casting of the system, we can uncouple the indeterminate exponent and the coefficients of the governing equations, and we can make explicit the relationships between parametric graph curvature and the management components of the system.

THE REFORMULATED GOVERNING EQUATIONS

Stock-production models, as they are usually defined, arise from the common premise that a fish stock, when reduced by exploitation to a level below some prior abundance, will always strive to recover its former size in accord with some latent, self-regulating mechanism of restoration. Irrespective of the compensatory details, any such recovery must accrue directly from the productivity of the stock, and in the conventional representation of the Pella-Tomlinson system, the latent capacity for biomass production in a stock of fishes is given the dual formulation

$$\dot{P}(B) = \pm aB^n \mp b\,B, \qquad \begin{matrix}(1a)\\(1b)\end{matrix}$$

$\dot{P}(B)$ being the production rate of the stock at stock size B. Equation (1a) applies when exponent n falls on the range $0<n<1$, and Equation (1b) applies when $n>1$. In either case, all the critical components of the system—maximum stock size, maximum productivity, the stock level where maximum productivity occurs—depend in some way on the numerical value assigned to exponent n. That is, root B_∞ is given by

$$B_\infty = \left(\frac{a}{b}\right)^{1/1-n},$$

the critical ordinate p (which corresponds to the stock level where maximum productivity occurs) is determined by

$$p = \left(\frac{an}{b}\right)^{1/1-n},$$

while extremum coordinate m (which corresponds to productivity $\dot{P}_{\max}$) must be determined from the formula

$$m = \pm \frac{b(1-n)}{n}\left(\frac{an}{b}\right)^{1/1-n},$$

the plus sign applying to Equation (1a) and the minus sign to Equation (1b).

Although exponent n controls the graph curvatures of Equations (1a) and (1b), the nonzero roots and extrema are controlled by B_∞ and the coordinate pair (p, m). As shown by Fletcher (1975), coordinate m has no essential dependence on exponent n, and with the appropriate transformations the dual formulation (Equations (1a, b)) may be suppressed. In consequence, either of the parametric sets $\{m, p, B_\infty\}$ or $\{m, n, B_\infty\}$ will constitute a complete set of independent governing parameters for latent productivity in the Pella-Tomlinson system, and the dual formulation (Equations (1a, b)) converts to the single differential equation for latent productivity

$$\dot{P} = \gamma m\left(\frac{B}{B_\infty}\right) - \gamma m\left(\frac{B}{B_\infty}\right)^n, \qquad (2)$$

with γ a purely numerical factor wholly prescribed by n as

$$\gamma = \frac{n^{n/n-1}}{n-1}. \qquad (3)$$

With the coefficients so cast, the sign reversals at turning point $n = 1$ become automatic, and the consolidated interval of definition for n becomes $0<n<\infty$ (the point $n = 1$ being a removable singularity). With parameter m thus separated from n in Equation (2), the undetermined exponent n can be defined solely by the ratio p/B_∞ in the relationship

[2]Walter, G. G. 1975. Non-equilibrium regulation of fisheries. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/IX/131, 12 p.

$$\frac{p}{B_\infty} = n^{1/1-n}. \quad (4)$$

When n takes any value between zero and unity, coordinate p falls on the range between zero and $B_\infty e$; when n takes any value greater than unity, coordinate p falls on the range between B_∞/e and B_∞. Wherefore, with $\{m, p, B_\infty\}$ as the parametric set for Equation (2), p and B_∞ determine n; with $\{m, n, B_\infty\}$ as the parametric set, n and B_∞ determine p. In the complete exploitation model, maximum productivity m becomes maximum sustainable yield (MSY) and biomass level p becomes the equilibrium level (the "B_{opt}") where MSY occurs.

For any stock-production system, we may enter exploitation into the productivity formulation by the direct difference $\dot{P} - \dot{Y}$, with $\dot{Y}$ signifying the rate of biomass removal attributed to exploitation. Therefore, in writing

$$\dot{B} = \dot{P} - \dot{Y}, \quad (5)$$

we interpret $\dot{B}$ as being the resultant productivity that nets to the stock for its growth. When removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$, then net productivity $\dot{B}<0$ and the stock declines; when $\dot{P}$ exceeds $\dot{Y}$, then $\dot{B}>0$ and the stock increases. Should $\dot{Y} = \dot{P}$, then $\dot{B} = 0$ and biomass trajectory $B(t)$ exhibits an extremum, which is the necessary condition for equilibrium fishing. Yield rate $\dot{Y}$ customarily takes the form

$$\dot{Y}(t) = F(t) \cdot B(t) \quad (6)$$

with the assumption that all fish of the fishable stock share equal probabilities of capture. By admitting Equations (2) and (6) into Equation (5), the differential equation that governs net productivity in the restructured system becomes

$$\dot{B} = \gamma m \left(\frac{B}{B_\infty}\right) - \gamma m \left(\frac{B}{B_\infty}\right)^n - FB \quad (7)$$

and over any time interval, however brief, that mortality F might be presumed to have a fixed value, biomass variable B in Equations (6) and (7) has the general time-dependent solution

$$B(t) = \left(B_*^{1-n} + C \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right)^{1/(1-n)}, \quad (8)$$

$$B_* = \left(\frac{\gamma m}{\gamma m - F B_\infty}\right)^{1/(1-n)} B_\infty.$$

With initial time t_0 set at zero, the integration constant C in Equation (8) becomes

$$B_0^{1-n} - B_*^{1-n}.$$

The quantity B_*, when positive in Equation (8), becomes the adjustment level such that $B(t) \to B_*$ over time. When, for certain ranges of n and F, quantity $B_*<0$, then the zero root of Equation (7) applies and $B(t) \to 0$. When mortality F takes the value

$$F_{\text{MSY}} \equiv \left(\frac{n-1}{n}\right) \frac{\gamma m}{B_\infty}, \quad (9)$$

irrespective of the value of parameter n, then $B(t) \to p$ and $\dot{Y} \to m$ (which are the conditions, in the equilibrium limit, for maximum sustainable yield). In terms of the parameter set $\{m, p, B_\infty\}$, Equation (9) becomes, simply,

$$F_{\text{MSY}} = \frac{m}{p}.$$

Figure 1 gives a summary of the general constraints on the time-dependent system; for a more detailed treatment of system behavior, see Fletcher (1978).

THE RESTRUCTURED EQUILIBRIUM SYSTEM

By Equations (2) and (5), the time-varying rate of yield in the reformulated Pella-Tomlinson system takes the form

$$\dot{Y} = \gamma m \left(\frac{B}{B_\infty}\right) - \gamma m \left(\frac{B}{B_\infty}\right)^n - \dot{B}, \quad (10)$$

and when, for given F and n, governing Equation (7) exhibits a positive root, then $B(t) \to B_*$ and $\dot{B} \to 0$ in Equation (10), and yield rate $\dot{Y}$, over sufficient time, approaches a constant value. In the steady-state (or "equilibrium") limit, yield then accumulates as

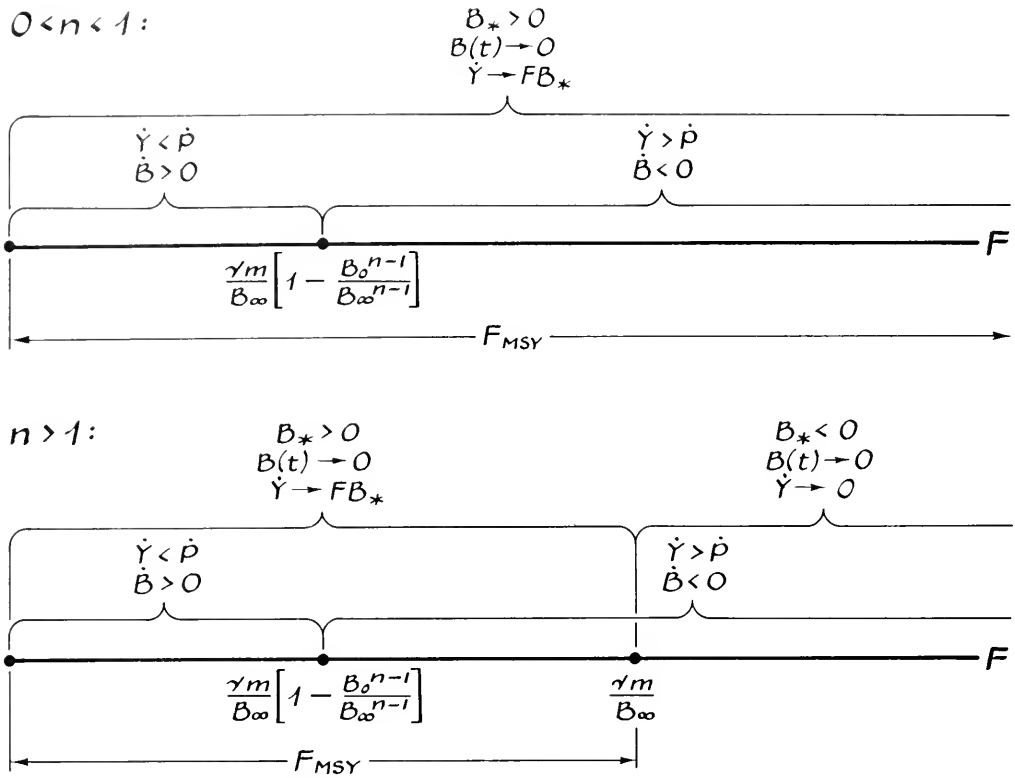


FIGURE 1.—Time-dependent response of the Pella-Tomlinson system to parametric variations of exponent n and mortality F. The upper diagram summarizes system response when n falls on the range $0 < n < 1$. The adjustment level of biomass is never zero for this range of n however great the value of F, and mortality F_{MSY} has no absolute constraints; such a stock cannot be fished to extinction. The lower diagram summarizes system behavior when n falls on the range $n > 1$. Mortality F_{MSY} is then constrained to the interval indicated by the diagram. When F exceeds the critical value $\gamma m/B_\infty$, then the stock, over sufficient time, trends to extinction.

$$\int dY = \int \left(\gamma m \left(\frac{B_*}{B_\infty} \right) - \gamma m \left(\frac{B_*}{B_\infty} \right)^n \right) dt = 0,$$

and for any such equilibrium interval τ, the integrated yield rate (Y_*/τ) takes on the parametric formulation

$$\frac{Y_*}{\tau} = \gamma m \left(\frac{B_*}{B_\infty} \right) - \gamma m \left(\frac{B_*}{B_\infty} \right)^n, \qquad (11)$$

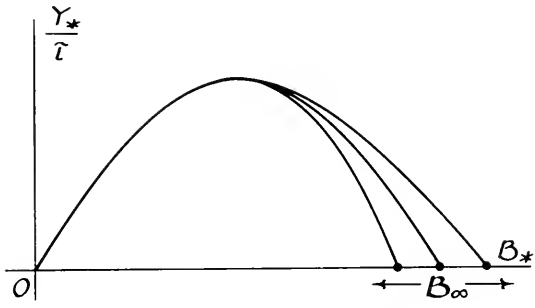
with maximum latent productivity m of the time-dependent system becoming the maximum sustainable yield rate (the MSY) of the equilibrium system. With B_* as the parametric variable in Equation (11), a zero left endpoint exists for Y_*/τ when $n > 1$ and $F = \gamma m/B_\infty$. Should F exceed the critical value $\gamma m/B_\infty$ when exponent $n > 1$, no equilibrium state exists; such conditions in the time-dependent system correspond to extinction trends. But when n has any value on the range $0 < n < 1$, no left endpoint of Equation (11) exists; a positive equilibrium level of biomass and a non-zero yield rate may be defined for any value of F, however great.

The equilibrium biomass level p where MSY (or m) occurs can be regulated in Equation (11) by relationship (4). And once designated in (4), the corresponding value of n determines the value of coefficient γ, as given by Equation (3). Either of the parametric sets $\{m, p, B_\infty\}$ or $\{m, n, B_\infty\}$ (augmented by the auxiliary parameters F and B_* or F and B_0) will constitute a complete, independent set of controls for equilibrium yield in the Pella-Tomlinson system. Collectively, the parameters control the behavior of equilibrium model Equation (11) but the influence of any one parameter remains independent of the remaining

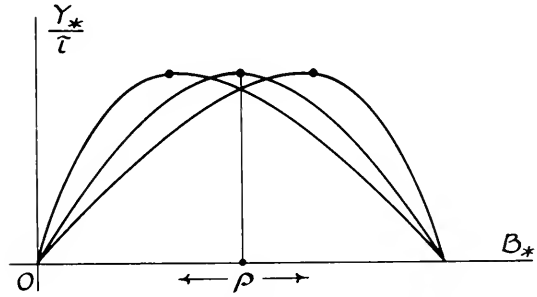
two. Figure 2 illustrates the individual effects of set $\{m, p, B_\infty\}$ on the graph of Equation (11).

In equilibrium model (11), biomass level B_* varies parametrically as a function of equilibrium fishing mortality F. In terms of parameters m, n, B_∞, the relationship becomes

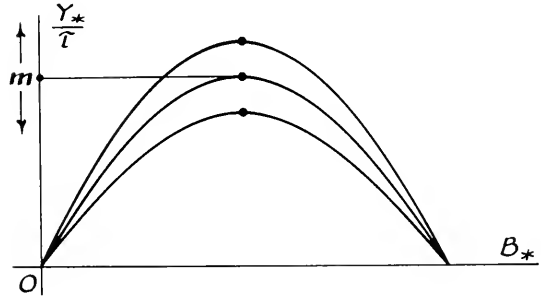
$$B_* = \left({B_\infty}^{n-1} - \frac{{B_\infty}^n}{\gamma m} F\right)^{\frac{1}{n-1}}. \qquad (12)$$



B_∞: Unexploited stock level



p: The biomass level for MSY



m: Maximum sustainable yield

FIGURE 2.—The graph of Equation (11), equilibrium yield vs. equilibrium stock size in the Pella-Tomlinson system, as controlled by independent parameters m, p, B_∞.

When exponent n of the system takes any value on $0<n<1$ then $\gamma<0$, in which case we can see by Equation (12) that $B_*>0$ no matter how great the value of F. That is, when $0<n<1$ there exist equilibrium adjustment levels of stock biomass for all magnitudes of fishing mortality large and small; such a stock defies annihilation. Should exponent $n>1$, however, the corresponding stock can have nonzero adjustment levels B_* only when $F<\gamma m/B_\infty$. That is, when $n>1$ and when fishing mortality exceeds the critical value $\gamma m/B_\infty$, the "adjustment" level corresponds to extinction and Equation (12) does not apply.

Upon the substitution of Equation (12) into Equation (11), the direct relationship between equilibrium yield and equilibrium fishing mortality becomes

$$\frac{Y_*}{\tau} = \left(F^{n-1} - \frac{B_\infty}{\gamma m} F^n\right)^{\frac{1}{n-1}} B_\infty, \qquad (13)$$

and the fishing mortality that maximizes Equation (13) is given by Equation (9). That is, with the substitution of F_{MSY} into Equation (13) then $Y_*/\tau = m$.

Under the equilibrium conditions, the conventional quantity U (which signifies accumulated catch per unit of fishing effort as a function of fishing intensity f/τ) can be cast into the restructured form

$$U = \left({U_\infty}^{n-1} - \frac{{U_\infty}^n}{\gamma m} \frac{f}{\tau}\right)^{\frac{1}{n-1}}, \qquad (14)$$

which eliminates the explicit appearance of catchability coefficient q, permitting instead the direct quantification of maximum sustainable yield m. Quantities U and U_∞ have the customary meanings

$U \equiv \frac{Y_*}{f}$ (Y_* being the yield accumulated over time interval τ as a consequence of effort f).

$U_\infty \equiv qB_\infty$ (q being the individual probability of capture per unit of fishing effort f).

Should the accumulation interval τ be a year, the variable U becomes annual CPUE (catch per unit of effort) and the variable f/τ becomes effort per annum. With exponent $n>1$ in the Pella-Tomlinson system, no steady-state CPUE exists for a fishing intensity in excess of critical value $\gamma m/U_\infty$. But if n

has any value on the interval $0<n<1$, then steady-state CPUE will exist for all magnitudes of effort (save $f = \infty$). Trajectories of Equation (14) are similar to those of Equation (12), and any graph of (12) will represent the corresponding graph of (14) (CPUE as a function of fishing intensity) with the substitution of U for B_*, f/τ for F, and the ratio $\gamma n / U_\infty$ for $\gamma n / B_\infty$.

DISCUSSION

For all its adaptability, the Pella-Tomlinson system has serious, inherent limitations and it cannot be viewed as a perfectly generalized model of exploitation-productivity relationships. It is, instead, a nonlinear, first-order, wholly empirical system of open degree that admits of a convenient flexibility in a minimum number of terms. Properly regarded, a particularization of the system will accommodate an arbitrary prototype to the extent that the system graphs might be geometrically accommodating to the data.

Experience with the model has shown that unrealistic estimates of coefficients are likely to occur when the data lie in confined or badly scattered patterns over ranges of effort and yield. The tendency to unrealistic estimates arises from the conflict between graph curvature, as controlled by exponent n, and the coupling of n with the coefficients of the system. Heretofore, the exact relationships between exponent n and the management components have been obscured by the conventional casting of the system. But with the independent parameters and the restructured equations, much of the parametric uncertainty associated with previous statistical treatments can be circumvented. As we have seen, maximum sustainable yield m bears no essential relationship to exponent n, and m may be wholly separated from n in all the system equations. And despite the fact that parameters m, p, B_∞ share no interdependence (any one may be varied without change in the value of the others), the parametric ratio p/B_∞ determines n in the relationship (4). But n in turn prescribes the curvature (hence the fit) of every graph of the system. As indicated by Figure 3, exponent n exhibits a dismaying sensitivity to perturbations in ratio p/B_∞. The variational response in n, for a perturbation of 10^{-1} in p/B_∞, is of the order of n near $n = 1$, and the instability increases as $p/B_\infty \rightarrow 1$. Therefore, when an estimation procedure depends solely on a general curve-fitting statistic, poor parameter estimates are likely to follow, owing to stochastic displacement of datum points at biomass levels remote from locations p and B_∞. In the article that follows, Rivard and Bledsoe (1978) address such problems directly and their work illustrates certain advantages of the restructuring treated here.

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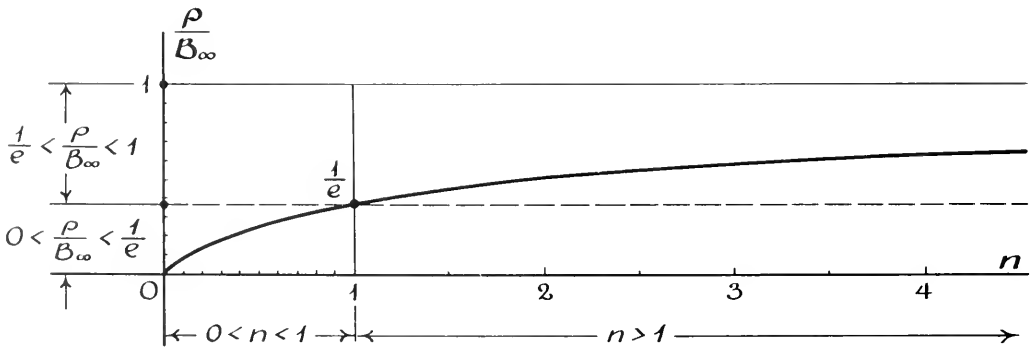

FIGURE 3.—Graph of the relationship between parameter ratio p/B_∞ and exponent n of the Pella-Tomlinson system, which indicates the slow convergence of the ratio for increasing n.

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PARAMETER ESTIMATION FOR THE PELLA-TOMLINSON STOCK PRODUCTION MODEL UNDER NONEQUILIBRIUM CONDITIONS

D. RIVARD AND L. J. BLEDSOE[1]

ABSTRACT

To estimate the parameters of the Pella-Tomlinson model, as restructured by Fletcher in this issue, we suggest a derivative-free version of the Levenberg-Marquardt algorithm, along with an algorithm that locates starting values for the iterative procedure. The iterative method of Levenberg-Marquardt was applied to two versions of the restructured model: five parameters were estimated in the first version and three in the second, the latter preventing degeneracy of the model to exponential form. We discuss in particular the causes of the degeneracies associated with previous applications of the model. Such faults lie, inherently, with the mathematical indeterminacy of the system equations themselves, so that all nonlinear estimation methods will tend to be inefficient in the absence of external constraints. The effectiveness of the Levenberg-Marquardt method was evaluated by Monte-Carlo simulation. As examples, we analyzed catch-effort data from the yellowfin tuna fishery of the eastern Pacific and catch-effort data from the Pacific halibut fishery (Area 2 of the International Pacific Halibut Commission).

Parameter estimation has been the greatest source of difficulty in applying the generalized stock-production model to management schemes, and the problem has attracted considerable attention. Pella and Tomlinson (1969) fitted the model to the catch-effort history of a fishery under nonequilibrium conditions by means of a search algorithm, and although good graphical fits are generally obtained by that procedure, unreasonable parameter estimates are frequently generated owing to the lack of internal constraints on parameter values (see Ricker 1975, example 13.6). Fox (1971) constructed a stochastic representation of the generalized production model and employed simulation to infer the effects of random variability in catch data. Fox suggested that variation in catch increases with the size of the catch (additive proportional error) and he gave a new formulation of the minimization criterion for the Pella-Tomlinson procedure. Walter (1975) suggested a graphical method for calculating the coefficients of the Graham-Schaefer model. Walter's procedure requires the plotting of catch per effort against effort data and then correcting for disequilibrium of the fishery. Fox (1975) also described a procedure for fitting the Pella-Tomlinson model that requires equilibrium approximations. And finally, Schnute (1977) derived linear and nonlinear methods for finding estimates of the coefficients of the Schaefer model; his method also includes a way of measuring the uncertainty of the estimates.

Fletcher (1978b) presented a reparametrization of the generalized production model and explains how the tendency to ill-determined parameter estimates arises from a conflict between variable graph curvature and its coupling with the coefficients of the system. In this paper, we take advantage of that restructuring and examine the use of a derivative-free version of the Levenberg-Marquardt numerical optimization algorithm, together with a Runge-Kutta differential equation solver, to estimate parameters in Fletcher's differential form of the Pella-Tomlinson model. Estimates of the variability in the coefficients are also provided, and the complete estimation procedure is analyzed by a Monte-Carlo simulation. The estimation problem is finally reformulated to prevent ill determination of the parameters and degeneracy of the model to exponential form.

MODEL AND NOTATION

As indicated by Fletcher (1975, 1978b), the generalized production model can be generated by the single differential equation

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$$\dot{B} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right]^n - \dot{Y}, \qquad (1)$$

with the quantity γ wholly a function of n in the relationship

$$\gamma = \frac{n^{n/n-1}}{n-1}. \qquad (2)$$

$B(t)$, the solution of $\dot{B}$, represents the stock size at time t, while $Y(t)$, the solution of $\dot{Y}$, represents the cumulative catch of the stock. Parameter B_∞ is the maximum stock size of the unexploited population, while m is the maximum productivity in the productivity function or the maximum sustainable yield (MSY) in the complete exploitation model. Exponent n controls the location of the inflexion point in the latent productivity function of the stock. Therefore, parameters B_∞, m, and n are nonnegative. With this new formulation of the system equations, the sign reversals of the coefficients at the turning point $n = 1$ are now automatic. Also the parameters are expressed in more meaningful terms for the fishery scientist, and some aspects of parameter estimation are simplified thereby.

By presuming that $f(t)$ units of effort operate on the population over time increment dt, the yield rate is often put into the instantaneous form

$$\dot{Y} = q f(t) B(t) \qquad (3)$$

where q is the catchability coefficient. Equations (1) and (3) constitute a coupled system of nonlinear differential equations. The system, as it is formulated in Equations (1) and (3), represents the continuous-time model. In practice, though, for each finite time interval τ over which yield statistics are integrated, fishing effort is usually assumed to be constant. It follows that $f(t)$ must be a step function that describes the effort as being constant over each time interval τ with abrupt changes at the end of each period. Then the effort required, over one time interval, to maintain maximum productivity is given by

$$f_{MSY} = \frac{\gamma m}{q B_\infty}\left[\frac{n-1}{n}\right], \qquad (4)$$

and at MSY the yield per unit of effort U_{MSY} is obtained by dividing m by f_{MSY}.

DETERMINISTIC MODEL AND STOCHASTIC REPLICATES

The Pella-Tomlinson system has the five parameters m, B_∞, n, q, and B_0. The fifth parameter, initial population size B_0, is needed to specify a particular solution of Equation (1). By taking the following arbitrary values for the parameters,

$$m = 1.36 \times 10^6 \qquad q = 4.60 \times 10^{-6}$$
$$B_\infty = 3.48 \times 10^6 \qquad B_0 = 3.48 \times 10^6$$
$$n = 1.80,$$

we constructed an example of a fishery over the course of 20 yr with $f(t)$ increasing within the first 10 yr and stabilizing thereafter (Table 1).

We also constructed 20 stochastic replicates of the deterministic catch history. In all the stochastic versions we assume additive proportional error terms ϵ_i (with i the annual index), consisting of 20 sets of 20 values each of normally distributed, independent random variables with expected means of zero and standard deviations (σ) of 0.025, 0.050, 0.075, 0.100, 0.125, 0.150, 0.175, 0.200 (12 replicates), and 0.250. Although Fox (1975) takes a similar approach, we recognize the fact that serial correlation of errors is likely to exist in natural data. As put by J. J. Pella in a personal communication, "If yield is above average in one year because the population is above average, it will probably be above average in the following year." But at this stage of the analysis, the explicit consideration of serially correlated errors would only complicate the estimation problem unneces-

TABLE 1.—Simulation of a logistic stock under exploitation (deterministic model).

Time (yr)	Catch	Effort	$U = \frac{\text{Catch}}{\text{Effort}}$
1	79,529	5,000	15.91
2	156,989	10,000	15.70
3	306,812	20,000	15.34
4	516,722	35,000	14.76
5	893,564	65,000	13.75
6	1,129,740	90,000	12.55
7	1,402,830	125,000	11.22
8	1,565,040	160,000	9.78
9	1,631,400	195,000	8.37
10	1,614,130	230,000	7.02
11	1,478,930	250,000	5.92
12	1,434,220	300,000	4.78
13	1,196,850	320,000	3.74
14	988,745	320,000	3.09
15	895,127	350,000	2.56
16	737,908	350,000	2.11
17	607,937	300,000	2.03
18	649,627	300,000	2.17
19	632,633	250,000	2.53
20	773,600	250,000	3.09

sarily; our immediate purposes are better served by the simpler form of the ϵ_i. We want to observe the response of the estimation procedure to realistic levels of stochastic error, but we also want to avoid wrong interpretations in those cases where parameter values might be ill determined because of some inherent fault of the estimation procedure itself and not because of some complication of the error structure. Therefore, the stochastic replicates, as well as the objective function of our estimation procedure, are constructed on the assumption of independence of errors. As we shall see in a subsequent discussion, the following estimation procedure is indeed robust with respect to that assumption.

PARAMETER ESTIMATION PROCEDURE

In its general form, the solution of the nonlinear model described by Equation (3) can be written as

$$\hat{Y}_i = g(f_1, f_2, \ldots, f_i; \boldsymbol{\Theta}) \quad i = 1, 2, \ldots, r \qquad (5)$$

where[2] $\boldsymbol{\Theta} = [m, B_\infty, n, q, B_0]^T$.

Quantity r represents the total number of observations over time, f_i the fishing effort during time interval i, and $\hat{Y}_i$ the predicted yield (biomass or number) over the interval i. Following Fox (1971), we also consider an error term ϵ_i proportional to population size and equivalent in terms of yield to the form

$$Y_i = \hat{Y}_i + \hat{Y}_i \epsilon_i, \qquad (6)$$

where Y_i represents the observed yield over the interval i. Then the error is described by the relationship

$$\epsilon_i = (Y_i - \hat{Y}_i) / \hat{Y}_i. \qquad (7)$$

Least squares estimation of $\boldsymbol{\Theta}$ by a vector $\hat{\boldsymbol{\Theta}}$ requires minimization of the function

$$S(\hat{\boldsymbol{\Theta}}) = \sum_i \epsilon_i^2. \qquad (8)$$

In terms of residuals $(Y_i - \hat{Y}_i)$, this is equivalent to

$$S(\hat{\boldsymbol{\Theta}}) = \sum_i W_i (Y_i - g(f_1, \ldots, f_i; \hat{\boldsymbol{\Theta}}))^2, \qquad (9)$$

where the W_i are statistical weights. That is, from Equation (7),

$$W_i = \hat{Y}_i^{-2}. \qquad (10)$$

If $S(\hat{\boldsymbol{\Theta}})$ were an analytic form, we would find $\hat{\boldsymbol{\Theta}}$ by writing the normal equations

$$\left[\frac{\partial S(\hat{\boldsymbol{\Theta}})}{\partial \Theta_i}\right] = 0.$$

Since S must be calculated via numerical methods, we will instead consider $S(\hat{\boldsymbol{\Theta}})$ as a continuous function that describes a hypersurface in a five-dimensional parameter space; that space must be searched for the appropriate minimum value of $S(\hat{\boldsymbol{\Theta}})$. The iterative process of successive approximations which we employ is an adaptation of the Levenberg-Marquardt technique (Levenberg 1944; Marquardt 1963). Given some initial estimate $\boldsymbol{\Theta}_0$, the method generates a sequence of estimates $\hat{\boldsymbol{\Theta}}_j$ from the inductive relation

$$\hat{\boldsymbol{\Theta}}_{j+1} = \hat{\boldsymbol{\Theta}}_j - \left[\beta_j \mathbf{I}_5 + \mathbf{J}_j^T \mathbf{J}_j\right]^{-1} \mathbf{J}_j^T \boldsymbol{\epsilon}_j. \qquad (11)$$

In Equation (11), β_j is a positive constant, $\mathbf{I}_5$ the identity matrix of order 5, $\mathbf{J}_j$ an r by five matrix having elements $\partial \epsilon_i / \partial \hat{\theta}_k$ $(i = 1, \ldots, r; k = 1, \ldots, 5)$, and $\boldsymbol{\epsilon}_j$ the vector of errors after j iterations. The method combines the best festures of both the gradient and the Taylor series methods and avoids their most serious limitations (Conway et al. 1970). We employ a FORTRAN computer program which incorporates a derivative-free version of the Levenberg-Marquardt method (Brown and Dennis 1972), and we approximate the solution of the model differential equations (1) and (3) by a fourth order Runge-Kutta algorithm for numerical integration. The general structure of the program is shown by the flow diagram of Figure 1. Since all the parameters have to be positive, we also constrain the optimization by transforming each component of $\hat{\boldsymbol{\Theta}}$ by its absolute value before evaluating the model.

ACCURACY OF RESULTS

Since the solution to the least-squares estimation problem is the result of a numerical search along the $S(\hat{\boldsymbol{\Theta}})$ hypersurface, we do not generate

[2]The notation [. . .] indicates that a row vector or matrix is formed of the elements enclosed by brackets.

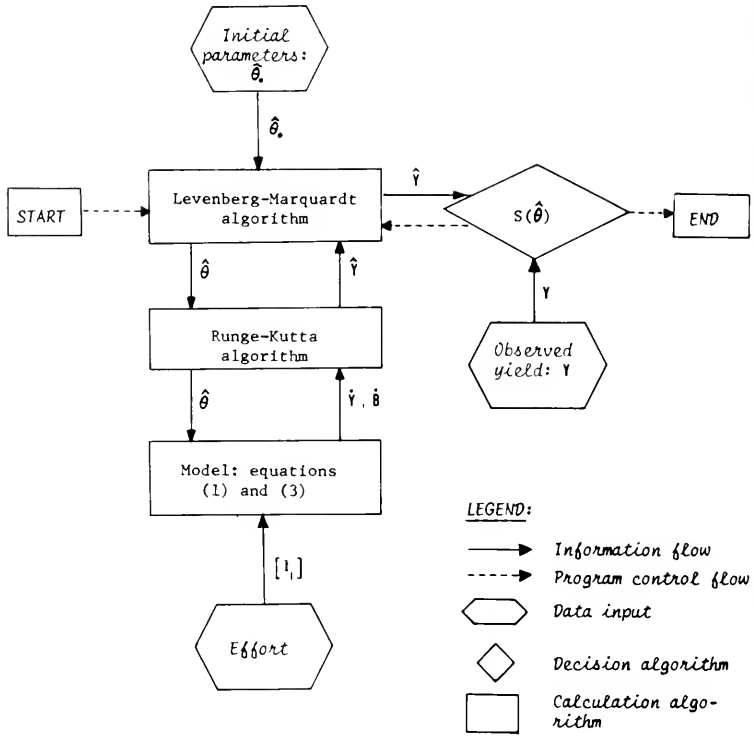

FIGURE 1.—Information flow diagram for the computer program written to estimate the coefficients of the generalized production model.

an analytical form for the uncertainties in the final values of the parameters (Bevington 1969). By letting $S(\hat{\mathbf{O}})$ be the weighted residual sum of squares for the final parameter estimates, however, the variance-covariance matrix of the estimates (Bard 1974) can be approximated by

$$V_{\hat{\mathbf{O}}} = \left[\mathbf{J}^T \mathbf{J}\right]^{-1} S(\hat{\mathbf{O}})/(r-5). \qquad (12)$$

Some idea of the joint variability of the parameters can be obtained by evaluating the ellipsoidal confidence region, based on the assumption that the linearized form has validity around $\hat{\mathbf{O}}$ (Draper and Smith 1966). The confidence region is then given by

$$[\mathbf{O}-\hat{\mathbf{O}}]\ \mathbf{J}^T\ \mathbf{J}[\mathbf{O}-\hat{\mathbf{O}}]^T \leq \frac{5S(\hat{\mathbf{O}})}{r-5}\ F(5, r-5, 1-\alpha), \qquad (13)$$

where $F(5, r\text{-}5, 1\text{-}\alpha)$ is the standard tabulated F-statistic. The ellipsoid is not a true confidence region, of course, since the dependent variable, $\dot{Y}$, is a nonlinear function of $\hat{\mathbf{O}}$. The intervals obtained are valid to the extent that a linear approximation in the neighborhood of $\hat{\mathbf{O}}$ is appropriate. A necessary and sufficient condition for the F-distribution to be appropriate here is that differences in true and estimated parameter values are independent and approximately normally distributed with zero mean and equal variance.

DETERMINATION OF STARTING VALUES

In order to reduce the number of iterations required to minimize Equation (8), reasonably accurate starting values should be employed. Starting values can be calculated from a linearization and simplification of the basic model.

STEP 1. By using $Y_1, Y_2, \ldots, Y_r$ and $f_1, f_2, \ldots f_r$, find an estimate of q from the Delury technique. Note that this procedure generally underestimates q (see Ricker 1975). Correction for q will be provided in step 4.

STEP 2. Find estimates of B_{t+1} from the equation

$$B_{t+1} = (\overline{B}_{t,t+1} + \overline{B}_{t+1,t+2})/2, \qquad (14)$$

where (by assuming $f_{t,t+1}$ constant over the interval $t,t+1$)

$$\bar{B}_{t,t+1} = Y_{t,t+1}/q\, f_{t,t+1}. \tag{15}$$

Note that $Y_{t,t+1}$ and $f_{t,t+1}$ correspond to Y_t and f_t of Equations (6) and (5).

STEP 3. Let $n = 2$, as in the Graham-Schaefer model, and estimate m and B_∞ by fitting the linear model

$$y_t = \alpha_0 + \alpha_1 x_t, \tag{16}$$

where $y_t = \dfrac{dB_t}{B_t\, dt} + qf_t, \quad x_t = B_t^{n-1},$

$$\alpha_0 = \gamma m/B_\infty, \quad \alpha_1 = \gamma m/B_\infty^{n}.$$

Equation (16) is derived from Equations (1) and (3). However, Equation (16) requires an estimate of the relative growth rate $dB_t/B_t dt$, say R_t. As suggested by Causton (1969), the mean value of R between t and $t+2$ is given by

$$\bar{R}_{t,t+2} = (\ln B_{t+2} - \ln B_t)/2. \tag{17}$$

For the purpose of fitting Equation (16), quantity $\bar{R}_{t,t+2}$ may be considered an estimate of R_{t+1}, which corresponds to B_{t+1}. Whence, Equation (16) provides estimates of m and B_∞ as

$$m = \frac{\left[\alpha_1\, \alpha_0{}^{n}\right]^{(1/1-n)}}{\gamma}, \tag{18}$$

$$B_\infty = \left[\frac{\alpha_1}{\alpha_0}\right]^{1/1-n}. \tag{19}$$

STEP 4. Steps 2 and 3 are repeated iteratively for increasing values of q. The value of q which provides the minimum residual sum of squares $[\sum_t (Y_t - \hat{Y}_t)^2]$ is accepted as the appropriate starting value for q.

STEP 5. Step 3 is repeated iteratively for increasing values of n, parameter q being kept constant. The value of n which provides the minimum residual sum of squares $[\sum_t (Y_t - \hat{Y}_t)^2]$ is accepted as the appropriate starting value for n. In the last iteration, Equations (18) and (19) provide estimates of m and B_∞. Finally, B_0 is approximated by

$$B_0 = 2\bar{B}_{0,1} - B_1 \tag{20}$$

where B_1 and $B_{0,1}$ are estimated by Equations (14) and (15), respectively.

Steps 1 through 5 provide a set of starting values for the optimization algorithm (11). Usually the starting values are near the solution and few iterations will be needed. Of course, it would be possible to derive algorithms for more accurate starting values, but our purpose here is to find a rough estimate for each coefficient and to let the iterative procedure (11) converge to the minimum. Sometimes, by experience or by prior information, it is possible to provide starting values as satisfactory as those provided by the algorithm given above.

MONTE-CARLO SIMULATIONS

The parameter values that we chose to generate the data of Table 1 (deterministic model) were recovered exactly by the estimation procedure. Results of fitting 18 stochastic versions of the deterministic model are also included in Table 2. Based on our simulation results, there do not appear to be any serious problems with bias of parameter estimates. The bottom line of Table 2, which gives the coefficients of variation of the parameter estimates, reveals that estimates of the three parameters of principal interest to the manager have the smallest variability. Those parameters are maximum sustainable yield ($\hat{m}$, C.V. = 14%), optimal effort level ($\hat{f}_{MSY}$, C.V. = 6%), and yield per unit of effort at optimum effort ($\hat{U}_{MSY}$, C.V. = 9%). Our results confirm the observations of Fox (1971) and Pella and Tomlinson (1969) on the robustness of m and f_{MSY} with respect to error in the measurement of the yield data. From Table 2, we can also compare variance estimates from Equation (12) with variance of estimates for 10 replicates at $\sigma = 0.200$. Equation (12) appears to give (approximately) unbiased estimates of the variance of the sampling distribution of $\hat{\boldsymbol{\theta}}$. Also, out of the 19 cases considered, the true parameter value lay outside the arbitrary ± 2 (SD) confidence interval twice for $\hat{m}$ and only once each for $\hat{B}_\infty$, $\hat{n}$, and $\hat{B}_0$. Although we did not employ an extensive Monte-Carlo simulation, our results suggest that the normal approximation to the sampling distribution of $\hat{\boldsymbol{\theta}}$ is an acceptable approximation, at least for management purposes.

In a few additional simulations (replicates 13 and 15), parameters obtained by the five-parameter procedure were ill determined. A parameter is considered ill determined if its estimated value responds unreasonably to seemingly insignificant variations in the data (Bard 1974). The basic difficulty is that the model is extremely general and capable of several types of behavior over the space of $\mathbf{\Theta}$. In the Pella-Tomlinson system, ill determination often occurs whenever an iteration of the algorithm (11) gives an estimate of $\mathbf{\Theta}$ such that the point $(\hat{m}, f_{\hat{MSY}})$ of the yield-effort plane lies outside the concentration of data. In such a circumstance the exponent $\hat{n}$ takes on smaller and smaller values in the successive iterations and the solution of system (1) and (3) degenerates to an exponential form for which only four parameters are required for uniqueness. That is, as $n \to 0$, in Equation (1), then $(B/B_\infty)^n \to 1$ and $\gamma \to -1$. The five-parameter procedure then overprescribes the system, which in turn predisposes the coefficient estimates to extremely large variances. The ultimate irony here is the fact that wholly unrealistic parameter estimates still generate good fits to the catch-effort history (i.e. small residuals). For example, in Figure 2 the fitted five-parameter curve predicts f_{MSY} near infinity while in the true model f_{MSY} actually corresponds to 174,000 units of effort. However different the equilibrium curves are, the five-parameter procedure still generates a good fit to the catch history ($S(\hat{\mathbf{\Theta}}) = 1.10$). Incompleteness of information over a wide range of effort values, as well as excessive noise in the catch-effort data, will tend to bring about such pathological conditions.

To overcome these difficulties, reformulation of the estimation problem is necessary. By the following considerations, the five-dimensional parameter space can be reduced to three dimensions. First, we will approximate B_0 by Equation (20). Furthermore, if the data contain information on the yields under low exploitation, we may define B_∞ as

$$B_\infty = \mathrm{MAX}(Y_i/q\, f_i) \quad i = 1, \ldots, r. \tag{21}$$

By using Equations (20) and (21), B_0 and B_∞ can be deleted from $\mathbf{\Theta}$, leaving only m, q, and n as the independent parameters requiring estimation. It is important to understand at this point that B_0 and B_∞ are not fixed; they are reevaluated by Equations (20) and (21) at each iteration, along with the parameters m, q, and n. In fact, the solution of Equations (1) and (3), as well as Equations (20) and (21), specify a new model with unknowns $\mathbf{\Theta} = [m, q, n]^T$. By this restructuring, much of the degeneracy associated with the model can be eliminated. As shown in Figure 2, this procedure also provides a closer correspondence between the "estimated" and the "true" equilibrium model. Furthermore, the three-parameter procedure still generates an adequate nonequilibrium catch history ($S(\hat{\mathbf{\Theta}}) = 1.40$). In a Monte-Carlo simulation study, parameter estimates obtained by using these transformations fell within reasonable

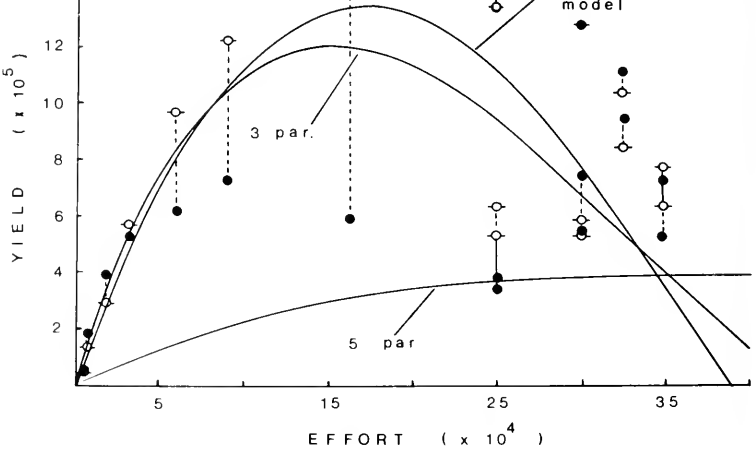

FIGURE 2.—Comparison of the "true" model with the models obtained by using the estimation procedure on three and five parameters respectively. Solid lines show equilibrium yield curves; data points show nonequilibrium simulated (dots) yields and predicted (circles) yield values from the three-parameter approach. Dashed vertical lines indicate the magnitude of residuals.

bounds (Table 3). Out of the 20 cases considered, the true parameter value lay outside the arbitrary ±2 (SD) confidence interval only once for $\hat{m}$ and $\hat{n}$. Also, variance estimates were comparable with the variance estimates of the five-parameter procedure (compare Tables 2 and 3).

TABLE 2.—Estimated parameters for the deterministic model and for 18 stochastic replicates. The Levenberg-Marquardt algorithm is employed in a five-dimensional parameter space (m, B_∞, n, q, B_0). For each parameter and replicate, the parameter estimate ± its estimated standard deviation from Equation (12) are tabulated. Replicates 13 and 15 have been excluded due to degeneracy of the model, as discussed in the text.

Replicate	σ	σ'[1]	m (10^6)	B_∞ (10^6)	n	q (10^{-6})	B_0 (10^6)	f_{MSY} (10^3)	U_{MSY}
1	0 000	0 000	1 34 ± 0 00	3 49 ± 0 00	1 80 ± 0 00	4 60 ± 0 00	3 48 ± 0 00	1 74	7 70
2	0 025	0 014	1 34 ± 0 01	3 56 ± 0 10	1 79 ± 0 03	4 54 ± 0 12	3 44 ± 0 12	1 72	7 75
3	0 050	0 046	1 37 ± 0 04	3 34 ± 0 32	1 88 ± 0 10	4 80 ± 0 42	3 24 ± 0 41	1 76	7 82
4	0 075	0 071	1 49 ± 0 06	2 78 ± 0 36	2 14 ± 0 15	5 68 ± 0 67	2 89 ± 0 63	1 84	8 10
5	0 100	0 111	1 41 ± 0 09	2 62 ± 0 50	2 36 ± 0 28	5 28 ± 0 92	2 86 ± 0 99	1 91	7 36
6	0 125	0 096	1 36 ± 0 09	3 34 ± 0 62	1 81 ± 0 19	4 96 ± 0 87	3 84 ± 0 95	1 72	7 95
7	0 150	0 109	1 55 ± 0 10	2 94 ± 0 59	2 33 ± 0 27	5 23 ± 0 96	5 97 ± 2 60	1 90	8 15
8	0 175	0 159	1 26 ± 0 17	3 92 ± 1 37	1 61 ± 0 35	4 26 ± 1 41	4 13 ± 1 74	1 64	7 66
9	0 200	0 189	1 15 ± 0 24	5 16 ± 2 25	1 56 ± 0 49	2 90 ± 1 36	7 75 ± 3 53	1 69	6 79
10	0 200	0 216	1 75 ± 0 16	1 90 ± 0 53	2 61 ± 0 47	8 34 ± 2 02	0 85 ± 0 66	2 00	8 73
11	0 200	0 159	1 19 ± 0 12	2 91 ± 0 84	1 71 ± 0 28	5 10 ± 1 45	4 89 ± 1 93	1 71	6 97
12	0 200	0 211	1 50 ± 0 23	3 63 ± 1 57	2 06 ± 0 55	4 59 ± 1 79	3 08 ± 1 85	1 78	8 41
14	0 200	0 136	1 24 ± 0 17	4 33 ± 1 55	1 52 ± 0 39	3 85 ± 1 24	3 47 ± 1 43	1 67	7 46
16	0 200	0 187	1 46 ± 0 14	2 45 ± 0 77	2 03 ± 0 38	6 40 ± 1 87	4 34 ± 2 85	1 85	7 88
17	0 200	0 261	1 62 ± 0 20	2 33 ± 0 94	2 28 ± 0 51	7 08 ± 2 55	2 24 ± 2 05	1 87	8 66
18	0 200	0 113	1 37 ± 0 12	3 88 ± 0 91	1 94 ± 0 26	4 10 ± 0 92	5 68 ± 1 59	1 73	7 88
19	0 200	0 185	1 24 ± 0 24	4 50 ± 2 19	1 86 ± 0 57	3 27 ± 1 53	5 32 ± 2 61	1 73	7 15
20	0 200	0 185	1 48 ± 0 16	2 94 ± 1 04	1 98 ± 0 42	5 46 ± 1 77	2 03 ± 1 15	1 85	7 99
21	0 250	0 269	1 38 ± 0 31	4 04 ± 2 46	1 38 ± 0 54	5 25 ± 2 86	2 89 ± 2 25	1 52	9 08
Mean[2]			1 40 ± 0 18	3 40 ± 1 38	1 96 ± 0 44	5 11 ± 1 71	3 97 ± 2 12	1 79	7 79
SD[3]			0 20	1 06	0 33	1 74	2 04	0 10	0 69
Coeff of var			14%	31%	17%	34%	51%	6%	9%

[1] $\sigma = S(\hat{\mathbf{\Theta}})$ (r-5)
[2] For 10 replicates with σ = 0 200
[3] Overall standard deviation of parameter estimates for 10 replicates with σ = 0 200

TABLE 3.—Estimated parameters for 20 stochastic replicates of the deterministic model. The Levenberg-Marquardt algorithm is employed here in a three-dimensional parameter space (m, q, n). For each parameter and replicate, the parameter estimate ± its estimated standard deviation from Equation (12) are tabulated.

Replicate	σ	σ'[1]	m (10^6)	q (10^{-6})	n	f_{MSY} (10^5)	U_{MSY}
2	0 025	0 017	1 35 ± 0 02	4 62 ± 0 15	1 86 ± 0 03	1 75	7 68
3	0 050	0 045	1 38 ± 0 04	4 86 ± 0 40	1 92 ± 0 08	1 78	7 77
4	0 075	0 081	1 46 ± 0 07	5 31 ± 0 74	1 89 ± 0 12	1 73	8 45
5	0 100	0 106	1 40 ± 0 08	5 17 ± 0 86	2 24 ± 0 18	1 87	7 47
6	0 125	0 094	1 35 ± 0 09	4 86 ± 0 85	1 69 ± 0 15	1 66	8 15
7	0 150	0 152	1 48 ± 0 18	4 58 ± 1 34	1 67 ± 0 26	1 63	9 06
8	0 175	0 169	1 25 ± 0 16	4 36 ± 1 26	1 33 ± 0 23	1 49	8 42
9	0 200	0 212	1 19 ± 0 32	3 61 ± 1 96	1 20 ± 0 49	1 51	7 87
10	0 200	0 228	1 72 ± 0 17	7 18 ± 1 92	1 98 ± 0 25	1 75	9 78
11	0 200	0 188	1 17 ± 0 18	5 14 ± 2 01	1 27 ± 0 28	1 48	7 88
12	0 200	0 203	1 44 ± 0 22	4 17 ± 1 48	1 74 ± 0 34	1 66	8 68
13	0 200	0 216	1 39 ± 0 18	3 47 ± 1 06	1 70 ± 0 31	1 66	8 38
14	0 200	0 140	1 06 ± 0 23	2 94 ± 1 18	1 05 ± 0 41	1 53	6 97
15	0 200	0 287	1 19 ± 0 19	4 10 ± 1 50	1 37 ± 0 29	1 48	8 08
16	0 200	0 198	1 42 ± 0 17	5 99 ± 2 07	1 56 ± 0 26	1 64	8 64
17	0 200	0 251	1 60 ± 0 21	6 54 ± 2 38	1 99 ± 0 32	1 74	9 17
18	0 200	0 140	1 31 ± 0 19	3 87 ± 1 22	1 49 ± 0 27	1 53	8 58
19	0 200	0 194	1 24 ± 0 25	3 67 ± 1 72	1 51 ± 0 41	1 60	7 74
20	0 200	0 176	1 46 ± 0 15	5 27 ± 1 63	1 88 ± 0 29	1 82	8 05
21	0 250	0 254	1 38 ± 0 28	5 24 ± 2 65	1 39 ± 0 39	1 53	9 04
Mean[2]			1 35 ± 0 21	4 66 ± 1 72	1 56 ± 0 33	1 62	8 32
SD[3]			0 19	1 34	0 31	0 11	0 73
Coeff of var			14%	29%	20%	7%	9%

[1] $\sigma = S(\hat{\mathbf{\Theta}})$ (r-3)
[2] For 12 replicates with σ = 0 200
[3] Overall standard deviation of parameter estimates for 12 replicates with σ = 0 200

CASE STUDIES

We applied the three-parameter method to the catch-effort data of the yellowfin tuna fishery of the eastern tropical Pacific, 1934 through 1967 [the same data that were analyzed by Pella and Tomlinson (1969) and by Fox (1971)]. Table 4 gives a comparison of results, and our final equilibrium model is shown by Figure 3. As indicated by Table 4, the parameter estimates of the Levenberg-Marquardt method are comparable with the estimates that Fox obtained with his search algorithm. Pella and Tomlinson also employed a searching algorithm but their minimization criterion was an unweighted least-squares function. Our standard deviation estimate is very small for $\hat{m}$ (MSY) but relatively large for $\hat{B}_{\infty}$, $\hat{n}$, $\hat{q}$, and $\hat{B}_0$, which is a consequence of insufficient information in the yellowfin tuna data on yield at high fishing rates. With such limited information, one can anticipate that neither the shape nor the location of the descending portion of the equilibrium curve (dashed in Figure 3) could be determined with much accuracy, and the large variance estimates on the system coefficients reflect this situation. Of course, the variance estimates for $\hat{f}_{MSY}$ and $\hat{U}_{MSY}$ can always be calculated by the delta method, and to avoid the complex derivations that accompany the presence of covariance terms, an alternative would be to define a new parameter space so as to estimate f_{MSY} or U_{MSY} directly. The variance-covariance matrix for the coefficients would then provide the desired information on the variability of those parameters.

Our final example is based on the data from the Pacific halibut fishery in International Pacific Halibut Commission Area 2, as given in Ricker (1975, table 13.1). To analyze these data, Ricker derived an estimate of q from the age composition of the catch. Then he obtained parameter estimates for a Graham-Schaefer model by regressing $Y_E/\bar{B}$ against $\bar{B}$ and Y_E/f against f (Ricker 1975, examples 13.5 and 13.6). In both cases, Ricker employed GM and Nair-Bartlett regression. The results Ricker obtained by fitting the Graham-Schaefer model were compared with the results we obtained from fitting the generalized stock production model by our three-parameter version of the Levenberg-Marquardt method (Table 5). The latter provided estimates of m, q, and n with relatively small variance estimates. Furthermore, the estimate of n appears to be significantly different from 2.00, which validates the use of the Pella-Tomlinson model. Nevertheless, estimates of m are not significantly affected by the choice of the wrong model, while estimates of f_{MSY} are slightly

TABLE 4.—Comparison of parameter estimates obtained by Pella and Tomlinson (1969), by Fox (1971) and by the Levenberg-Marquardt algorithm for the yellowfin tuna in eastern Pacific Ocean. Values that follow the ± signs are the standard-deviation estimates for each parameter.

Reference	p	B_∞ (10^6)	n	q (10^{-5})	B_0 (10^6)	m (10^6)	f_{MSY}	U_{MSY}	Residuals
Pella and Tomlinson (1969, table 5)	—	—	1 40	45 0	—	1 826	35,300	5,173	1 78 · 10^{16}
Fox (1971, table 4)	—	1 427	2 10	8 10	1 206	1 926	32,700	5,890	0 736
Levenberg-Marquardt algorithm	—	1 448	2 08	8 01	1.192	1 924	32,700	5,884	0.735
		±0 890	±0 75	±4 9	±1 24	±0 90			
Levenberg-Marquardt algorithm	0 27	1 274	2 30	9 08	1 079	1 962	32,170	6,097	0 641
(correlated error)	±0 25	±0 653	±0 55	±4 7	±0 553	±0 106			

TABLE 5.—Comparison between the estimates of Ricker (1975) for the Pacific halibut (International Pacific Halibut Commission Area 2) and those obtained by the Levenberg-Marquardt algorithm. Values that follow the ± signs are the standard-deviation estimates for each parameter.

Reference	p	B_∞ (10^6)	n	q (10^{-7})	m (10^5)	f_{MSY}	U_{MSY}
Ricker (1975, example 13 5)							
GM regression	—	204	2 00	9 07	31 2	3 37	92 6
Nair-Bartlett regression	—	195	2 00	9 07	31 0	3 50	88 6
Ricker (1975, example 13 6)							
GM regression	—	256	2 00	9 07	33 0	2 84	116 2
Nair-Bartlett regression	—	239	2 00	9 07	31 8	2 94	108 2
Levenberg-Marquardt algorithm	—	187	1 28	14 45	31 6	2 83	111.7
		±18	±0 09	±1 36	±0 83		
Levenberg-Marquardt algorithm	0 33	188	1 28	14 33	31 8	2 84	112 0
(correlated error)	±0 16	±22	±0 12	±1 67	±1 0		

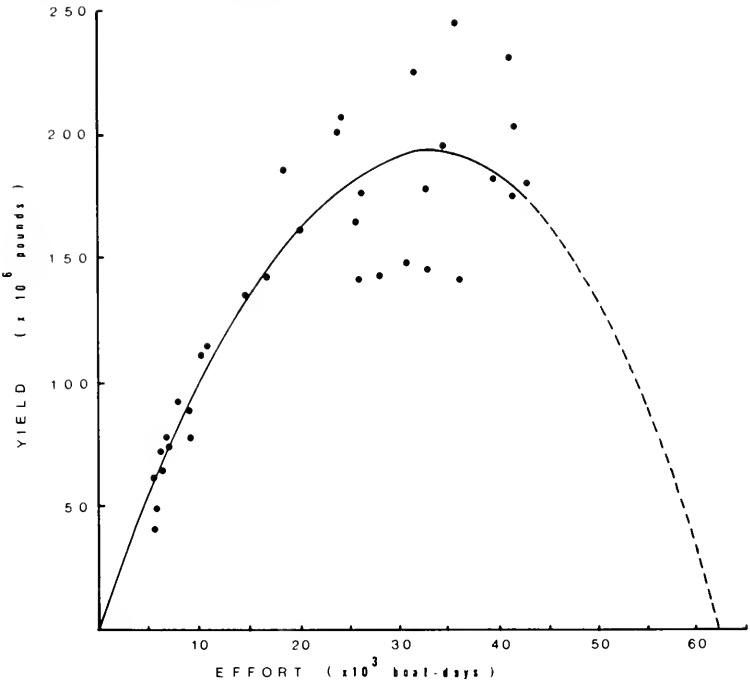

FIGURE 3.—Equilibrium stock production model for yellowfin tuna data, from 1934 through 1967, as determined by the Levenberg-Marquardt algorithm.

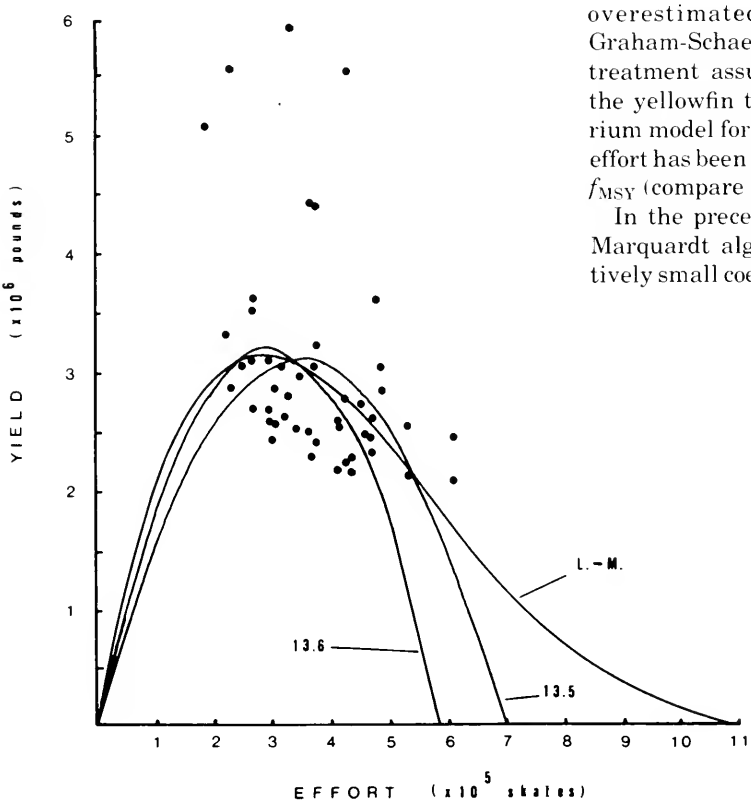

FIGURE 4.—Equilibrium stock production models for Pacific halibut (International Pacific Halibit Commission Area 2), from 1910 through 1957, as determined by Ricker (1975, examples 13.5 and 13.6, Nair-Bartlett regressions) and by the Levenberg-Marquardt algorithm (three-parameter version).

overestimated in most applications of the Graham-Schaefer model (note also that Ricker's treatment assumes equilibrium). In contrast to the yellowfin tuna data, analysis of the equilibrium model for halibut data indicates that fishing effort has been concentrated slightly to the right of f_{MSY} (compare Figures 3 and 4).

In the preceding case studies, the Levenberg-Marquardt algorithm gave estimates with relatively small coefficients of variation. In both cases,

e.g., the coefficients of variation for the estimates of maximum sustainable yield ($\hat{m}$) were below 6%. It is questionable, however, whether the data can justify such precision. Variability of the exploited population due to migration, to changes in fishery regulations over time, and to expansion of the fishing areas, as well as variability of q due to learning by fishermen and to technological developments, are important factors underlying the complexity of events influencing the serial catch-effort information. In future research, alternative forms of the model in which q is a variable parameterized with respect to time will be explored. Furthermore, in a randomly fluctuating environment, equilibrium population levels (and MSY, by extension) are not constant and the equilibrium points are instead described by a probabilistic cloud representing the equilibrium probability distribution (May 1974). The knowledge of this equilibrium probability distribution would give us some idea of the probability of achieving the desired management goal (MSY, for instance).

DISCUSSION ON ERROR STRUCTURE

In the preceding examples, we found runs in the time sequence plot of residuals. Those runs indicate correlations among the residuals. Serial correlation, as we usually find in applying production models to catch data, indicates that the real system is working differently than the presupposed model and that some minor effects have been neglected (such as age composition or environmental factors). But as indicated by Draper and Smith (1966), the effects of correlation can be ignored when the ratio $(r-p)/r$ tends to unity (p being the number of estimated parameters). In certain situations, of course, this ratio is likely to become small (tending to zero as r approaches p) and we may want to consider weights (W_i) which account for both the inequality of variance and the correlations. In our estimation procedure, the assumption of uncorrelated error can be relaxed by writing Equation (9) in the more general form (J. J. Pella, pers. commun.)

$$S(\hat{\boldsymbol{\Theta}},\hat{\rho}) = [\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{W}^{-1}\,[\mathbf{Y}-\hat{\mathbf{Y}}]^{\mathrm{T}}, \qquad (22)$$

where $\mathbf{Y}$ is the row vector of observed yields, $\hat{\mathbf{Y}}$ is the row vector of predicted yields, and $\mathbf{W}$ is the symmetric, positive definite matrix

$$\mathbf{W} = \begin{bmatrix} \hat{Y}_1^2 & \hat{Y}_1\hat{Y}_2\hat{\rho} & \cdots & \hat{Y}_1\hat{Y}_r\hat{\rho}^{(r-1)} \\ \hat{Y}_1\hat{Y}_2\hat{\rho} & \hat{Y}_2^2 & \cdots & \hat{Y}_2\hat{Y}_r\hat{\rho}^{(r-2)} \\ \vdots & \vdots & \ddots & \vdots \\ \hat{Y}_1\hat{Y}_r\hat{\rho}^{(r-1)} & \hat{Y}_2\hat{Y}_r\hat{\rho}^{(r-2)} & \cdots & \hat{Y}_r^2 \end{bmatrix}.$$

Parameter ρ, constrained between 0 and 1, is a measure of the importance of lags and can be estimated along with the parameters of the differential equations (1) and (3). It can be seen that Equation (9) is a particular case of Equation (22), where the off-diagonal elements of $\mathbf{W}$ are null.

The Levenberg-Marquardt algorithm, as formulated in Equation (11), is designed to minimize directly a sum of squares of residuals as given by Equation (9). In order to minimize Equation (22) by using Equation (11), we must scale $\mathbf{W}$ by the transformation

$$\mathbf{X} = \mathbf{D}^{-1}\,\mathbf{W}\,\mathbf{D}^{-1}, \qquad (23)$$

where $\mathbf{D}$ is a diagonal matrix having elements $D_{ii} = \hat{Y}_i$ $(i = 1, \ldots, r)$, and write $\mathbf{W}$ as

$$\mathbf{W} = \mathbf{D}\,\mathbf{U}\,\Lambda\,\mathbf{U}^{\mathrm{T}}\,\mathbf{D}, \qquad (24)$$

where $\mathbf{U}\Lambda\mathbf{U}^{\mathrm{T}}$ is the eigenvalue and eigenvector decomposition of $\mathbf{X}$. Note that $\mathbf{X}$ is actually the correlation matrix of errors. Therefore Equation (22) becomes

$$S(\hat{\boldsymbol{\Theta}},\hat{\rho}) = [\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{D}^{-1}\,\mathbf{U}\,\Lambda^{-1}\,\mathbf{U}^{\mathrm{T}}\,\mathbf{D}^{-1}\,[\mathbf{Y}-\hat{\mathbf{Y}}]^{\mathrm{T}}. \qquad (25)$$

Then Equation (25) has the same form as Equation (9), where the weights (W_i) are the square roots of the eigenvalues of $\mathbf{X}$ and where the residuals are given by $[\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{D}^{-1}\,\mathbf{U}$. Such a procedure requires, however, diagnoalization of an r by r matrix. Moreover, diagonalization must be repeated at least p times for each iteration. This procedure produces a 10-fold increase in computing time.

Although an exhaustive study of all possible stochastic effects on the model was not attempted, some simulations were done to determine the magnitude of error in parameter estimates due to serial correlations of the ϵ_i. Results are given on Tables 4 and 5. For the yellowfin tuna data, $\hat{\rho}$ =

0.27. For the Pacific halibut data, $\hat{\rho} = 0.33$. In either case, $\hat{\rho}$ exhibits a relatively large coefficient of variation when compared with the elements of $\hat{\mathbf{\Theta}}$. One could anticipate such results since ρ reflects the "persistence" of fluctuations in population size, and the estimation of ρ would therefore require a longer catch history in order to achieve a greater precision. But more importantly, the values of $\hat{\mathbf{\Theta}}$ and $\mathrm{Var}[\hat{\mathbf{\Theta}}]$ were not significantly altered by the inclusion of the additional parameter. And while the errors of any particular catch history might indeed by correlated, the minimization criterion (9) will provide satisfactory estimates of $\mathbf{\Theta}$ despite the fact that correlations do not enter into its formulation. The limited results contained herein suggest that serial correlation can be safely ignored when the ratio $(r - p)/r$ is near unity. Under such a condition the estimation procedure is robust with respect to the assumption of independence of errors in actual data.

CONCLUSION

The purpose of this paper has been to examine a version of the Levenberg-Marquardt algorithm as an alternative method for estimating the coefficients of the generalized stock production model. The parameter values obtained by this procedure are close to those obtained by previous studies on yellowfin tuna and Pacific halibut. Obviously, data requirements are such that a full range of effort values (ranging over low and high exploitation rates) are necessary to insure convergence in the estimation procedure and to produce estimates with small variability. Our simulations reveal that with the Levenberg-Marquardt method both the estimates of coefficients and the estimates of variances remain approximately unbiased when white noise is considered. If present, such bias is sufficiently small as to be obscured in the variability associated with catch error. The simulations also showed the range of variability in parameter estimates that might be expected for given levels of normally distributed error in catch data.

Because the parameters of interest appear explicitly in the system equations, the estimation procedure for the parameters also produces the variance estimates directly. Moreover, the method has a reliability and an efficiency of computation somewhat greater than previous methods. And since the estimation procedure relies on a numerically integrated system of differential equations, modifications of the model to incorporate such hypothetical effects as migration or stock interactions can be made easily. Of course, to the extent that the estimation procedure must rely strictly on catch-effort data, it will be subject to the same information uncertainties as any other method. But within the basic estimation procedure, we can combine the catch-effort data with prior information and thereby reduce the uncertainties in our estimates. The prior information can be any information on a state variable, such as $B(t)$, or even any prior knowledge of the coefficients as expressed by $\hat{\mathbf{\Theta}} \pm \mathrm{Var}(\hat{\mathbf{\Theta}})$. Suppose, for example, that we have information from independent surveys on stock density (acoustic surveys, indirect estimation from knowledge of larval densities, or even virtual population analysis from catch records). Such surveys would then provide us with estimates $\hat{B}_t$ each having a variance $V(\hat{B}_t)$, let us say, at various times t. We can easily introduce such information into the estimation procedure by defining the new objective function

$$S(\hat{\mathbf{\Theta}}) = \sum_i W_i(Y_i - \hat{Y}_i)^2 + \sum_j V_{B_j}^{-1}(B_j - \hat{B}_j)^2. \quad (26)$$

Introduction of the second term in the objective function constrains the optimization and thereby improves convergence. If the prior information has extremely large variance, then this information is of no value; the second term of Equation (26) will tend to zero and the objective function then reduces to Equation (9). In general, the alteration permits the simultaneous employment of the two state variables. Therefore, the final coefficients are no longer based solely on catch and effort data; their determination includes our knowledge of previous stock densities.

As observed here in a statistical setting, and by Fletcher (1978a, b) in the exact analysis, the Pella-Tomlinson system exhibits internal instability in its parametric relationships. That behavior arises from the variable nature of the system's nonlinearity, which would not be particularly detrimental if our problems were limited strictly to the geometric syntheses of data by curve fitting. But for the purposes of management and preservation of stocks, the subject is elevated partly at least to the status of parameter estimation "where we look for procedures to obtain values of the parameters that not only fit the data well, but also come on the average fairly close to the true value" (Bard 1974). Although the Pella-

Tomlinson system exhibits a convenient flexibility with a minimum number of coefficients, the peculiar coupling of the coefficients to the nonlinearity of the system often provides more flexibility than we care to have, and a conventional least-squares statistic may not be sufficient to control the system in the estimation procedure. In consequence, many constraints have to be imposed on the system in order to obtain convergence in the estimation procedure and to insure reliability in the coefficient values thus estimated.

ACKNOWLEDGMENTS

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SYSTEMATICS AND ZOOGEOGRAPHY OF THE PORCUPINEFISHES (*DIODON*, DIODONTIDAE, TETRAODONTIFORMES), WITH COMMENTS ON EGG AND LARVAL DEVELOPMENT[1]

JEFFREY M. LEIS[2]

ABSTRACT

The porcupinefish genus *Diodon* is composed of five species: *D. hystrix* Linnaeus and *D. eydouxii* Brissout de Barneville are closely related species, each of which has a relatively elongate body, spines on the caudal peduncle, and high dorsal and anal fin ray counts; *D. holocanthus* Linnaeus and *D. liturosus* Shaw form a second species pair, each of which has a round body, no caudal peduncle spines, and moderate dorsal and anal fin ray counts; *D. nicthemerus* Cuvier is a round-bodied species but differs from *D. holocanthus* and *D. liturosus* in meristic characters and spination.

Diodon hystrix, *D. holocanthus*, and *D. eydouxii* are distributed circumtropically. The Atlantic population of *D. holocanthus* has diverged from the Indo-Pacific (including eastern Pacific) populations. *Diodon eydouxii* is pelagic, and both *D. hystrix* and *D. holocanthus* have pelagic juvenile stages. *Diodon liturosus* is found in the Indo-West Pacific, and *D. nicthemerus* is limited to Tasmania and southern Australia. It is not known whether the latter species have pelagic stages.

The egg and larval stages of *D. hystrix* and *D. holocanthus* (the latter identified by rearing) are similar. The pelagic eggs are 1.6-2.1 mm in diameter and hatch in about 5 days at 25°C. The larvae metamorphose to spiny juveniles at ca. 4 mm in about 3 wk. Both species have pelagic juvenile stages of long duration: *D. hystrix* remains pelagic to ca. 200 mm standard length, thus providing ample time for dispersal. Eggs and larvae of the other species are unknown.

The identities of the species of the genus *Diodon* have been confused since the time of Linnaeus. The most recent description of a valid "new" species was in 1846, but, unfortunately, time has done little to clarify the situation. Twenty-eight nominal species attributable to *Diodon* have been described since 1758, and most contemporary authors recognize two or three species. However, Le Danois (1959), in the only recent review of the genus as a whole, recognized six species.

The present study grew out of attempts to identify juvenile *Diodon* that resulted from rearing of pelagic eggs taken in Kaneohe Bay, Oahu, Hawaii (Watson and Leis 1974). These juveniles could not be identified using existing keys. While current literature recognized only two species of *Diodon* in Hawaiian waters, examination of museum specimens revealed that three were present there. This discovery, together with the encouragement of J. E. Randall of the Bernice P. Bishop Museum, led to the present study clarifying the identities of all of the species of *Diodon* and the description of their development. An attempt was made to obtain information on existing type-specimens and this, along with the examination of a large number of specimens, has led to the conclusion that the genus is composed of five species, three of which are distributed circumtropically. Further, it is shown that the present taxonomic confusion is attributable to inadequate original descriptions, reliance on poor characters for differentiation, the close similarity of several of the species, and unusual aspects of the life histories of the species of *Diodon*. All of the nominal species could be distinguished with some certainty with two exceptions: the type of *Diodon echinus* Rafinesque 1810 could not be located and the original description provides no clue to its identification; the holotype of *Trichocyclus erinaceus* Günther 1870 (BMHN 1976.2.23.1) is a small fish in especially poor condition, giving the appearance of having been obtained from a stomach of some predator, and, while it is certainly a *Diodon*, more specific identification could not be made. *Diodon dussumieri* Bibron (see Le Danois 1959, 1961) is a nomen nudum, but examination of the "type" (MNHN 1306) by J. E. Randall of the Bernice P. Bishop Museum indicates that Le Danois was correct in placing *D. dussumieri* in synonomy with *D. holocanthus*.

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Although basically shorefishes, the diodontids (at least *Diodon* and *Chilomycterus*) are strongly tied to the pelagic environment through pelagic eggs and well-developed pelagic juvenile stages. In *Diodon* these juveniles remain pelagic for weeks or months (judging from size) and are often found far from shore. In fact, juvenile *Diodon* spp. are commonly encountered in the stomachs of such pelagic predators as dolphins (Gibbs and Collette 1959), and one species, *D. eydouxii*, is apparently pelagic throughout its life cycle.

The eggs of diodontids are poorly known. Nichols and Breder (1926) described the unfertilized eggs of *Chilomycterus schoepfi* from New Jersey as demersal, nonadhesive, transparent, and about 1.8 mm in diameter. However, Breder and Clark (1947) suggested that the eggs of *C. schoepfi* may be normally pelagic. The pelagic eggs of *D. holocanthus* and *D. hystrix* from Hawaii were briefly described as *Diodon* sp. and "diodontid II," respectively, by Watson and Leis (1974). Sanzo (1930) described the development of what are apparently the pelagic eggs of *D. hystrix* (identified as *Crayracion* sp.?) from the Red Sea. Wolfsheimer (1957) reported an aquarium spawning of *D. holocanthus* (identified by him as *D. hystrix*), but provided little descriptive information on the eggs. The eggs mentioned by Wolfscheimer sank, but did not adhere, to the bottom of the aquarium. They did not develop, so it is likely that they were not fertilized.

Larval and juvenile *Diodon* are no better known than the eggs. Blanco and Villadolid (1951) illustrated a juvenile "*Diodon bleekeri*," but this fish is clearly a juvenile tetraodontid. Many juvenile tetraodontids have prominent spines, particularly on the ventral surfaces. Fowler (1928) illustrated a juvenile *Diodon*, identified as *D. hystrix*, but the figure does not show spines on the caudal peduncle (see below), so this identification is apparently incorrect (assuming the drawing is accurate). No locality or other descriptive data are given by Fowler, so a specific identification cannot be made. Sanzo (1930) illustrated two larvae that resulted from rearing of his *D. hystrix* eggs and a juvenile *Diodon* captured in a plankton tow. The illustration of this latter fish shows no peduncle spines, but in other respects it resembles *D. hystrix*. Mito (1966) illustrated a larval and a juvenile *Diodon*, both identified as *D. holocanthus*. The pigmentation and the relatively small eye shown in Mito's illustrations more closely resemble the specimens of *D. hystrix* studied here. At least four species of *Diodon* occur in Japanese waters, and Mito's specimens could be any of these, because he gives no information as to how the identifications were made. Nishimura (1960) reported on juvenile *Diodon* cast ashore in the Sea of Japan, but did not provide specific identifications.

MATERIALS AND METHODS

Measurements and counts are as defined by Hubbs and Lagler (1958:19-28) unless otherwise stated. Measurements routinely were made with needle point dividers to the nearest 0.5 mm. Fish <10 mm and all eggs were measured under a dissecting microscope to the nearest division of the ocular micrometer (±0.02 mm at 50×, the power normally used). All measurements are from preserved specimens.

Unspecified lengths are in millimeters standard length. Caudal peduncle length was measured from the posterior base of the dorsal fin to the end of the hypural plate. Head width was measured immediately behind the eyes. Body width was measured at the base of the pectoral fin. Width of the eye was taken horizontally across the clear cornea. Measurements are given as proportions of standard length.

Dorsal and anal fin ray counts included all rays, branched and unbranched. The last two rays were counted separately because they have separate bases. Pectoral fin ray counts excluded the upper ray. This ray, although well developed in small (<30 mm) juveniles, is a rudiment in adults and is often not visible because it is embedded. In large specimens, the fin bases are especially fleshy and accurate fin ray counts are difficult to make without dissection or radiography.

Body measurements are given as range, mean ($\bar{x}$), and standard deviation (SD). The sample size for the measurements is given in parentheses at the beginning of the description of each species. Morphometrics are included only from individuals >50 mm. Fin ray counts are included for all specimens on which counts could be made (Table 1). In most cases, rays in both pectoral fins were counted. Fin rays were not counted on specimens with fin damage or on specimens that had rays obscured due to the thick bases of the dorsal and anal fins. Radiography was tried unsuccessfully to obtain vertebral counts: the dermal spines and their bases obscured the vertebrae, and made accurate counts impossible. The vertebral counts

TABLE 1.—Fin ray counts of *Diodon* species.

Dorsal fin rays	12	13	14	15	16	17	18	$\bar{x}$
D. eydouxii								
Atlantic						3	1	17.25
Indo-Pacific					4	25	6	17.06
D. hystrix								
Atlantic				2	7	1		15.90
Indo-Pacific			2	20	8			15.20
D. holocanthus								
Atlantic			22	4				14.15
Indo-Pacific		9	39	7				13.96
D. liturosus			1	12	15			15.50
D. nicthemerus	1	10						12.91

Anal fin rays	12	13	14	15	16	17	18	$\bar{x}$
D. eydouxii								
Atlantic						3	1	17.25
Indo-Pacific					2	22	11	17.26
D. hystrix								
Atlantic				3	7			15.70
Indo-Pacific			1	15	6			15.23
D. holocanthus								
Atlantic		9	18					13.67
Indo-Pacific		26	27	1				13.54
D. liturosus			10	17	1			14.68
D. nicthemerus	3	5	2					12.80

Pectoral fin rays	19	20	21	22	23	24	25	$\bar{x}$
D. eydouxii								
Atlantic			5	3				21.38
Indo-Pacific	7	58	17					20.12
D. hystrix								
Atlantic				1	10	10	1	23.50
Indo-Pacific			2	16	34	6		22.76
D. holocanthus								
Atlantic			7	31	20			22.22
Indo-Pacific		1	17	57	27	5		22.17
D. liturosus			2	11	24	17	2	23.11
D. nicthemerus	2	9	9					20.35

given for *D. holocanthus* were made on cleared and stained material.

The dermal spines require special terminology and measurements, as given below. Measurements, except for shaft length, were taken on dissected spines (Figure 1).

The spine shaft is that portion bearing the pointed tip, but excluding the shaft extension. The length of the spine (= shaft length) was taken from the lower portion of the lateral arm to the tip of the shaft. The starting point for this measurement can be found most easily by probing around the base of the spine.

The shaft extension is the portion of the shaft extending past the lateral arms of the base, and its length was measured from the lower portion of the lateral arm to the tip of the extension.

The lateral arms of the base are the subdermal portions of the spine upon which the spine pivots during erection. The length of the spine base was the straight line distance from tip to tip of the lateral arms.

The frontal spines are those of the anteriormost row on the head between the eyes. The pectoral axil spines are the spines immediately posterior to the base of the pectoral fin.

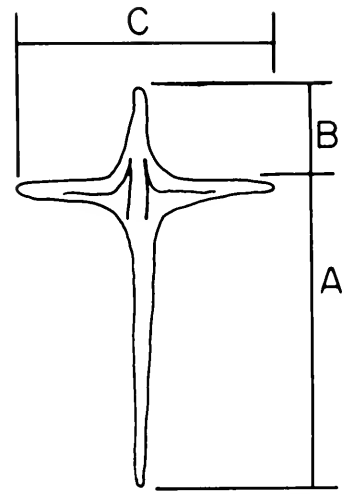

FIGURE 1.—Typical *Diodon* body spine: (A) spine (or shaft) length, (B) length of the shaft extension, (C) length of the spine base. The tip of the spine shaft points caudad.

The number of spines in a longitudinal row over the dorsum from the snout to the dorsal fin base (S-D spines) and the spines in a longitudinal row over the ventrum from the lower jaw to the anus (S-A spines) were counted. These rows of spines are irregular and difficult to follow, so the counts should be considered approximate. With practice, repeated counts of ±1 can be achieved consistently. The numbers of spines between pectoral fins, both over the dorsum (P-D-P spines) and ventrum (P-V-P spines), were also counted, but these counts are even less reproducible than the longitudinal counts.

Repeated reference is made to the spines on the caudal peduncle. In some species the only spines in the region of the caudal peduncle are some rather large spines associated with the dorsal and anal fin bases. Although these spines extend over the peduncle, their subdermal bases (lateral arms and shaft extension) are at least partially anterior to a line between the base of the posteriormost rays of the dorsal and anal fins, and they are considered not to be on the peduncle. In other species, there are relatively small spines which are wholly posterior to the line defined above on the dorsal and dorsolateral surfaces of the peduncle; these spines are considered to be on the peduncle (Figure 2).

Larvae were obtained from plankton samples (field specimens) and rearing experiments using eggs from plankton tows (reared specimens). All eggs and larvae were captured around the Hawaiian island of Oahu. Rearing took place in

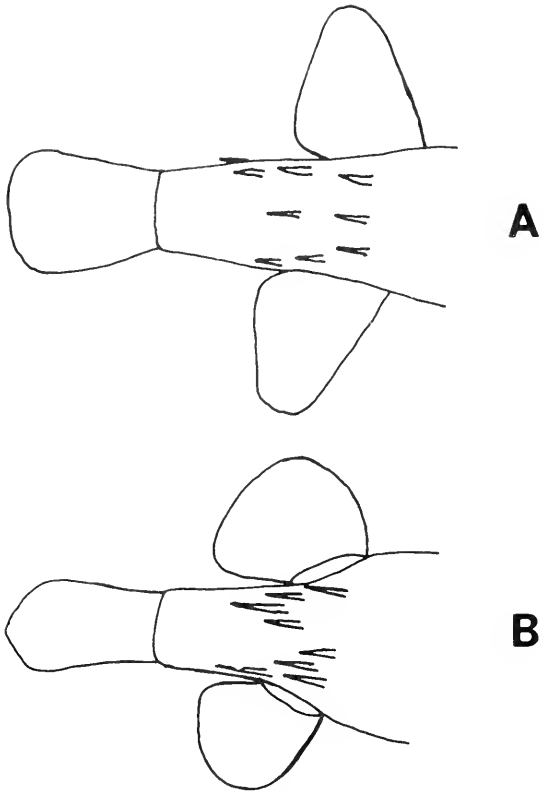

FIGURE 2.—Semidiagrammatic lateral view of the caudal peduncle and posteriormost spines of (A) a slender-bodied, long peduncled species (*Diodon eydouxii*) and (B) a round-bodied, short peduncled species (*D. holocanthus*).

the laboratory under ambient temperature (ca. 25 C) and a variety of conditions. Generally, the eggs were hatched in unaerated 4-l beakers filled with seawater from the collection area. Hatched larvae were transferred to 10-20 l containers and provided with overhead illumination. The containers were wrapped in black plastic. Wild zooplankton (ca. 60-200 μm) from a plankton pump were added on alternate days; this was later supplemented with *Artemia* nauplii. Water was changed twice a week and specimens were removed periodically for preservation. Many rearing attempts were made, but since fewer than 20 eggs usually were available per attempt, few of the attempts were successful.

Some larvae were cleared and stained using the KOH-alizarin red method of Hollister (1934). Measurements and definitions of stages generally follow those of Leis (1977), unless otherwise noted. All drawings of eggs and larvae were made with the aid of a camera lucida.

The institutions housing the examined specimens are as follows: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Gulf Coast Research Laboratory and Museum (GCRL); George Vanderbilt Foundation (GVF), deposited in CAS; Hawaii Institute of Marine Biology (HIMB); Los Angeles County Museum of Natural History (LACM); Museum National d'Histoire Naturelle, Paris (MNHN); National Marine Fisheries Service, Honolulu, Hawaii (NMFS H), La Jolla, Calif. (NMFS LJ), and Miami, Fla. (NMFS M); Naturhistorisches Museum, Vienna (NMV); J. L. B. Smith Institute of Ichthyology at Rhodes University, South Africa (RUSI); Scripps Institution of Oceanography (SIO); Tulane University (TU); National Museum of Natural History, Smithsonian Institution (USNM); University of Arizona (UA). A catalog number is given when available; many GVF specimens were uncataloged and therefore the register or station number is given.

The synonymies include all known original usage of names. In addition, references of systematic or zoogeographic interest are included. If the identification of a nominal species is questionable, it is preceded by a question mark (?). Pre-Linnaean literature is cited in the text if appropriate, but is omitted from the synonymies.

GENUS *DIODON* LINNAEUS

Diodon Linnaeus 1758:334, after Artedi 1738. Type-species *D. hystrix* Linnaeus by subsequent designation of International Commission on Zoological Nomenclature, opinion 77.

Paradiodon Bleeker 1865:49. Type-species *D. hystrix* Linnaeus by original designation.

Trichodiodon Bleeker 1865:49. Type-species *D. pilosus* Mitchill by original designation.

Trichocyclus Günther 1870:316. Type-species *T. erinaceus* Günther by monotypy.

Diagnosis.—Body rotund, width 0.25-0.54, depth varies greatly depending on degree of inflation. Eyes large, 0.05-0.17. Swim bladder bilobed. Teeth in each jaw fused into a single beaklike unit without a median suture dividing upper or lower jaws into right and left halves. Gill opening a short, vertical slit immediately anterior to the

pectoral fin base. Approximately 20 vertebrae. Dorsal and anal fins usually rounded, set far back on body, with 12-18 rays. Caudal rounded, with 9 rays (there are no secondary rays). Pectoral fin slightly emarginate, with 19-25 rays, the uppermost ray (not counted) greatly reduced in adults. No pelvic fins. Body covered with long spines, all but a few (around the gill opening, dorsal fin base, and caudal peduncle) of which are erectile. Erectile spines consisting of a long pointed shaft, two subdermal lateral bases lying in nearly the same plane as the shaft, and usually a shaft extension which is shorter than the shaft. The shaft extension may be greatly reduced. Nasal organs consisting of a short tentacle with a pair of lateral openings near the tip. In larger individuals of some species the tissue closing the end of the tentacle may be absent, giving rise to a bifid nasal tentacle without nostrils. Both species whose reproductive habits are known (*D. hystrix* and *D. holocanthus*) spawn pelagic spherical eggs of 1.6-2.1 mm in diameter.

Remarks.—Only Bleeker's (1865) proposal of *Paradiodon* for the species here considered to belong in *Diodon* (because of page priority, he believed *Diodon* should apply to those species usually referred to *Chilomycterus*) has disturbed the stability of the usage of the name *Diodon*. *Trichodiodon* and *Trichocyclus* are names applied to juvenile stages of *Diodon*.

Although subgeneric status seems unwarranted, *Diodon* can be broken into two groups on the basis of body width, caudal peduncle length, and squamation. The species of the slender-bodied group, *D. eydouxii* and *D. hystrix*, have a rather narrow body (Figure 3, Table 2), long caudal peduncle (Figure 3, Table 2), and several small spines in the dorsal and dorsolateral surfaces of the peduncle. The species of the round-bodied group, *D. holocanthus*, *D. liturosus*, and *D. nicthemerus*, have a wider body, shorter caudal peduncle (Figure 3), and lack spines on the caudal peduncle (although there are strong spines, projecting over the peduncle, at the base of the dorsal and anal fins). Upon inflation, the dorsal and anal fins are engulfed by the expanding skin. In the round-bodied group, the caudal peduncle and fin are also largely obscured in inflated specimens and the large spines mentioned above provide added protection. In the slender-bodied group, the peduncle remains largely uncovered and is protected only by the relatively small spines on its upper surfaces. *Diodon nicthemerus*, although clearly a member of the round-bodied group, appears to have undergone a reduction in spine number and base size, and is thus separable from *D. holocanthus* and *D. liturosus*.

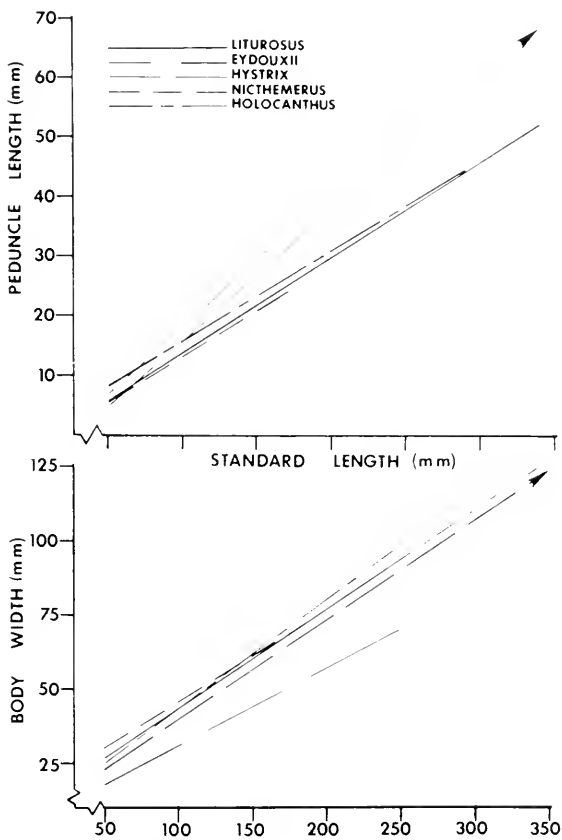

FIGURE 3.—Plotted regression lines of (top) caudal peduncle length vs. standard length and (bottom) body width vs. standard length for the five species of *Diodon*. Lines plotted only over size range of specimens examined. The line with arrow head for *D. hystrix* extends to 571 mm SL. Regression data in Table 2.

TABLE 2.—Regression equations for caudal peduncle length (PL) and body width (BW) vs. standard length (SL) in the five species of *Diodon* (see also Figure 3).

Species	Regression equation	r	t_{slope}	df
D. hystrix	PL = 0.189 SL − 2.79	0.97	21.16	31
D. eydouxii	PL = 0.226 SL − 4.79	0.95	17.44	33
D. liturosus	PL = 0.159 SL − 2.40	0.96	17.88	26
D. nicthemerus	PL = 0.151 SL − 1.38	0.94	7.85	8
D. holocanthus	PL = 0.152 SL + 4.69	0.90	15.86	61
D. hystrix	BW = 0.338 SL + 6.01	0.97	23.41	31
D. eydouxii	BW = 0.262 SL + 5.27	0.88	10.45	33
D. liturosus	BW = 0.333 SL + 10.29	0.90	10.58	26
D. nicthemerus	BW = 0.313 SL + 13.11	0.93	6.44	6
D. holocanthus	BW = 0.368 SL + 6.29	0.96	25.75	62

KEY TO THE SPECIES OF THE GENUS *DIODON*

1a Two or more small spines wholly on the dorsal or dorsolateral surfaces of the caudal peduncle (Figure 2A); color pattern of adults dominated by small (smaller than eye) spots; at least D, P, and C fins of adults with dark spots 2

1b No spines wholly on the caudal peduncle (Figure 2B); color pattern of adults dominated by large dorsal and lateral bars or blotches; fins of adults without spots except in some cases at base 3

2a P 19-22, both D and A 16-18; D and A of adults falcate; S-A spines≤14; head width less than 30% SL ..... *D. eydouxii*
(circumtropical, oceanic)

2b P 22-25 (rarely 21), D 14-17, A 14-16; D and A of adults rounded; S-A spines≥14; head width greater than 30% SL ..... *D. hystrix*
(circumtropical, shore fish but juveniles pelagic)

3a No small, fixed, tribase spine immediately above the gill opening; no small, flat spines on the anterior border of the depression surrounding the gill opening (Figure 4); S-A spines ≤11; adult color pattern dominated by four large lateral bars, dorsum uniformly dark ..... *D. nicthemerus*
(Australia)

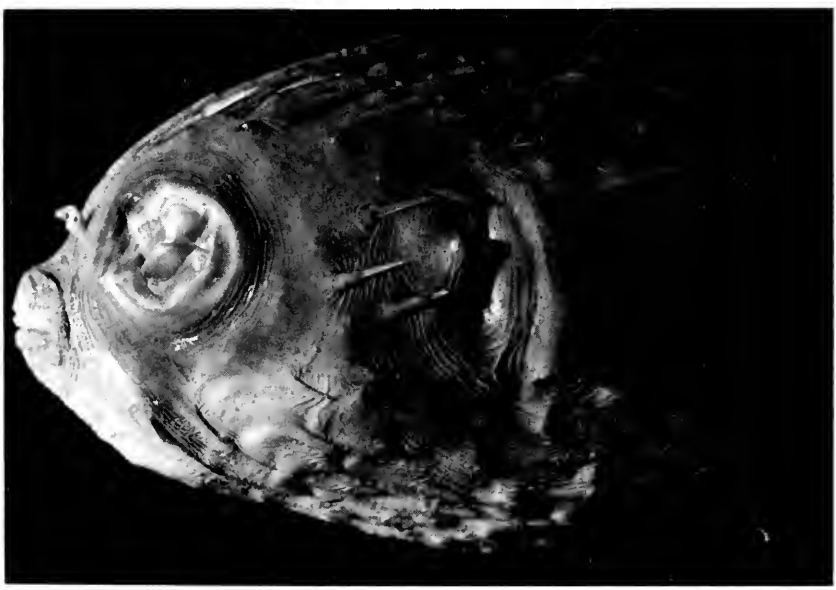

FIGURE 4.—Head of *Diodon nicthemerus* (AMS I.16990-004) showing arrangement of spines in the region of the gill opening. Note that spines anterior to gill opening are not flattened. Also note tubular nostril.

3b One or two small, fixed, tribase spines above the gill opening; three or four small, flat spines forming the anterior border of the depression surrounding the gill opening (Figure 5); S-A spines ≥12; adult color pattern dominated by several dorsal blotches 4

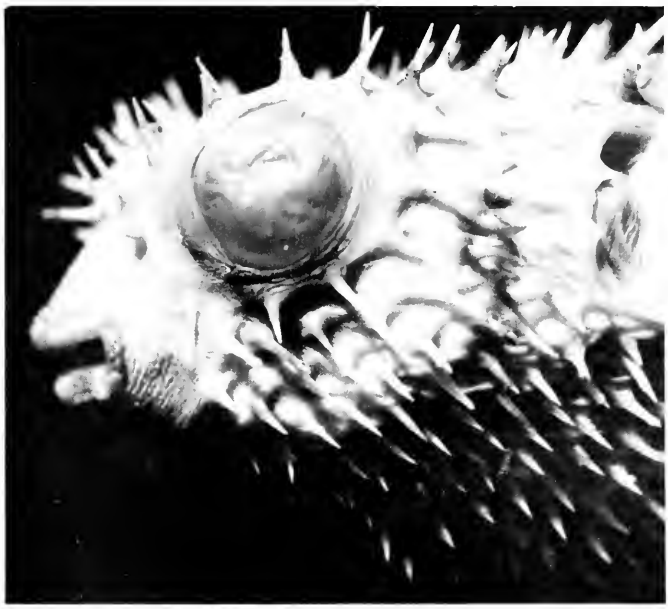

FIGURE 5.—Head of *Diodon liturosus* (CAS 30967) showing arrangement of spines in the region of the gill opening. Note that spines on anterior border of opening are short and flattened. Also note the small downward-pointing spine below the anterior border of the eye.

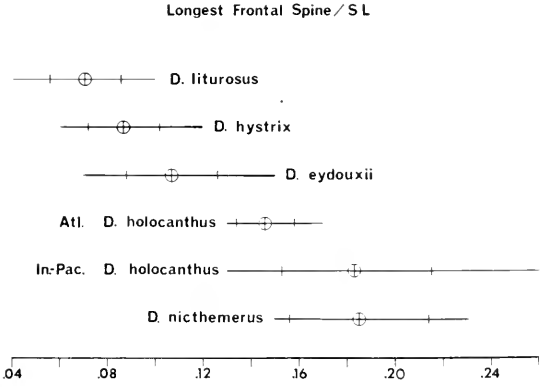

FIGURE 6.—Ratio of frontal spine length to standard length for the five species of *Diodon*. Line indicates range, circle and bar indicate mean, and vertical bars alone denote ±1 SD. Note difference of spine length between Atlantic and Indo-Pacific specimens of *D. holocanthus*. Number of specimens given in description for each species.

4a Frontal spines 0.04-0.10 (Figure 6), much shorter than pectoral axil spines; 17-22 S-A spines; a small downward-pointing spine below the anterior margin of the eye present; dorsal blotches with a distinct light border; a dark gular band from eye to eye under the lower jaw ..... *D. liturosus* (Indo-Pacific)

4b Frontal spines 0.13-0.28 (Figure 6), slightly shorter to much longer than pectoral axil spines; 12-15 S-A spines; a small downward-pointing spine below the anterior margin of the eye absent (Indo-Pacific specimens) or present (most Atlantic specimens); dorsal blotches without a distinct light border; no gular band ..... *D. holocanthus* (circumtropical)

DIODON EYDOUXII BRISSOUT DE BARNEVILLE

Pelagic Porcupinefish (Figure 7)

Diodon eydouxii Brissout de Barneville 1846:142 (eastern Pacific); Troschel 1847:364; Duméril 1855:278.

Diodon melanopsis Kaup 1855:228 (no locality given).

Diodon spinosissimus (not of Cuvier): Günther 1870:307 (Cape of Good Hope, Siam).

Diagnosis.—A slender-bodied *Diodon*, head width 0.25-0.30, peduncle length 0.16-0.22. Caudal peduncle armed dorsally with short spines. Body spines long and slender, moderate in number, S-D spines 13-17, S-A spines 10-14. Pectoral axil spines 0.11-0.16, usually longer than longest frontal spines. A short, fixed tribase spine immediately above gill opening. D 16-18, A 16-18, P 19-22. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles. Dorsal and anal fins falcate (rounded in juveniles). Color pattern dominated by small (ca. = to pupil) dark spots dorsally and laterally. These often associated with the spine axils. A dark gular band starting from below the eyes and continuing under the chin, usually with a branch extending dorsally between eye and gill opening.

Description.—(35 specimens) D 16-18, A 16-18, the first two or three rays unbranched; P 19-22. Head width 0.25-0.30 ($\bar{x}$ = 0.27; SD = 0.01), body width 0.25-0.35 ($\bar{x}$ = 0.30; SD = 0.02), peduncle length 0.16-0.22 ($\bar{x}$ = 0.19; SD = 0.02), eye 0.05-0.10 ($\bar{x}$ = 0.08; SD = 0.01). Dorsal and anal fins falcate, not rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 13-17, S-A spines 10-14, about 12 spine rows over the dorsum between pectoral fin bases, about 21 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.07-0.15 ($\bar{x}$ = 0.11; SD = 0.05), pectoral axil spines 0.11-0.16 ($\bar{x}$ = 0.14; SD = 0.01). Pectoral axil spines usually the longest on the body, 0.61-1.03 ($\bar{x}$ = 0.78; SD = 0.11) in frontal spines. Spines long and slender. Frontal, middorsal, and ventral spines of about the same length. Pectoral axil spines and those dorsolateral spines from over eye to over pectoral fin among the longest on body (ca. 0.8 in frontal spines). Spines on caudal peduncle short (ca. 1.5 in frontal spines) and fixed due to a rather long shaft extension (ca. 2 in shaft). Shaft extension on other spines reduced, never more than 15% of the shaft length. Subdermal bases moderate in extent, and, except for spines around fin bases and caudal peduncle, always shorter than shaft. No spines markedly reduced other than on caudal peduncle; the latter spines generally arranged in one or two bilateral pairs along the dorsolateral edge of the peduncle. Approximately 40% (14 of 36) of the specimens examined also possess a single dorsomedial spine on the caudal peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it above the pectoral base. Three short, flat spines

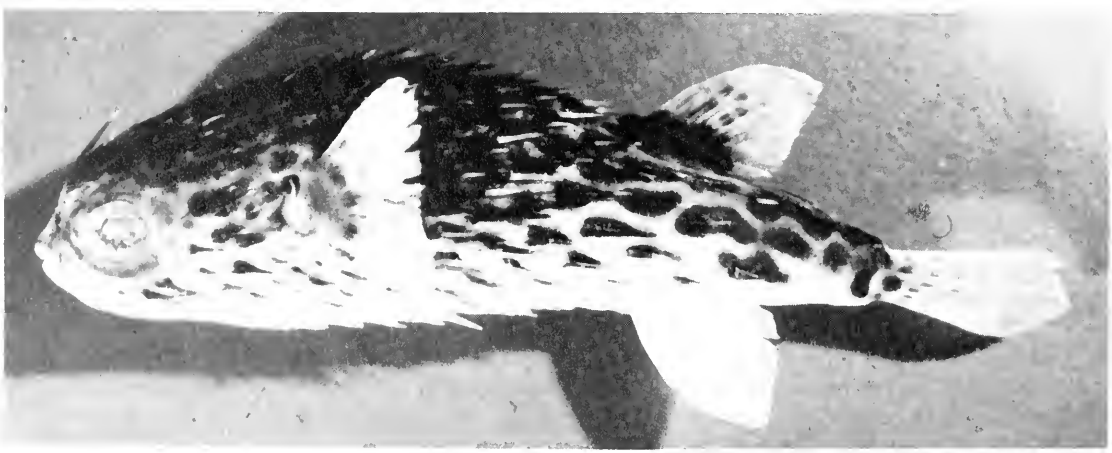

FIGURE 7.—*Diodon eydouxii*, 128 mm SL, central Pacific (NMFS H CHG 55-71).

with broad lateral bases form the anterior border of the gill opening. No spines on the snout.

No barbels or fleshy tentacles.

Dorsally the ground color is light grey to brown grading to white ventrally. Dorsal and lateral surfaces marked with dark ovoid spots (<eye diameter in length) most of which are associated with the spine axils, particularly on the sides posterior to the pectoral fin. Caudal peduncle usually mottled dorsally. Round spots (often diffuse) present on dorsal, pectoral, and caudal fins (caudal spots first seen on 100-mm fish, other fin spots begin to form between 30 and 100 mm). The pectoral spotting is limited to two vertical rows of four to six spots each. The anal fin is often dusky but never spotted. A dark gular band extends from the eye downward and forward, generally paralleling the ventral outline of the head. Usually a branch of this band extends dorsally between the eye and gill opening and is often discontinuous with the gular band. Specimens <100 mm usually have four opposed spots on the iris.

In life the dorsal ground color is medium to dark blue while the dorsal and lateral spots and gular band are dark blue to black. The ventral surfaces are silvery-white and the fins greyish (from a color transparency provided by R. Rosenblatt, SIO).

The largest specimen examined is 252 mm, but the next largest is only 177 mm, apparently a fairly small species. Twelve specimens (125-153 mm) were sexed although none were ripe: 7 males and 5 females.

Eggs, larvae, and pelagic juvenile stages.—No information is available on eggs or larvae. The smallest specimen available is 4.5 mm and is in very poor condition. The fish is almost completely round (inflated?); the spines are short (ca. 0.25 mm) and of uniform length over most of the body. By 13 mm the frontal and pectoral axil spines are ca. 2.5 mm—noticeably longer than the rest of the spines. In the smallest specimen the spines are all erect and the bases resemble small tripods; they may well be fixed at this stage. However, by 8.5 mm the spines are erectile and the fish is definitely capable of inflation. In the 4.5-mm specimen the fin rays are fully formed, as are the nostrils.

The fins remain unpigmented until at least 30 mm except for a small dusky area at the pectoral fin base which forms by 13 mm. In both dorsal and caudal fins, spots gradually spread over the fin from the base. The first row of pectoral fin spots form by 100 mm and the second at about 150 mm. The smallest fish are uniformly dark to medium brown dorsally with a light area at the base of each spine due to the unpigmented spine sheath. Laterally, distinct black spots (0.25-0.50 mm in diameter) are found. These continue across the white ventral surface. By 8.5 mm the white area at the spine bases has disappeared and spots similar to those on the ventral surface have developed on the dorsal surfaces. The spots are now ca. 1 mm in diameter. The ventral spotting is less conspicuous due to the loss of individual spots by 13 mm, and by 20 mm the belly is white and devoid of spots. The dorsal and lateral spots persist and become associated with the spine bases by 100 mm.

Syntypes.—MNHN 2153, two specimens (101 and 108 mm) taken (apparently speared) in the Pacific between Guayaquil and Hawaii.

Distribution.—*Diodon eydouxii* is a pelagic, oceanic species which is found circumtropically (Figure 8) and seems particularly abundant in the eastern Pacific, but this may be an artifact of collecting effort.

Remarks.—In Brissout de Barneville's (1946:142) description, the total mention of *Diodon eydouxii* is as follows: "Mentionnons encore le *Diodon Eydouxii*, Souleyet (Bibron, Coll. Mus. Paris, et Monographie inedite des Diodoniens) remarquable par ses nageoires dorsale et anale subfalciformes." As noted by Brissout de Barneville, Bibron in his unpublished manuscript (MNHN Library MS#867) cited Souleyet as the author of this species. However, Souleyet, insofar as I can determine, never published anything regarding this species. In fact, Bibron's (MS, p. 96) citation refers to the "Voyage de la Bonite. Zool. p . . . . ," i.e., he gave no page number, as if in anticipation of publication by Souleyet. There is no mention of *D. eydouxii* in "Voyage de la Bonite" (Eydoux and Souleyet 1841). Because Brissout de Barneville was the first person to use this name in a published work and because he included descriptive information—albeit limited, *Diodon eydouxii* should be attributed to him.

Kaup's (1855) description of *D. melanopsis* is inadequate, but one of his syntypes (BMNH 1852.3.2.7) is extant. Information provided by A. C. Wheeler (pers. commun., BMNH, 29 October 1975) is sufficient to place *D. melanopsis* in the synonomy of *D. eydouxii*. Günther (1870) incorrectly placed *D. melanopsis* in synonomy with *D.*

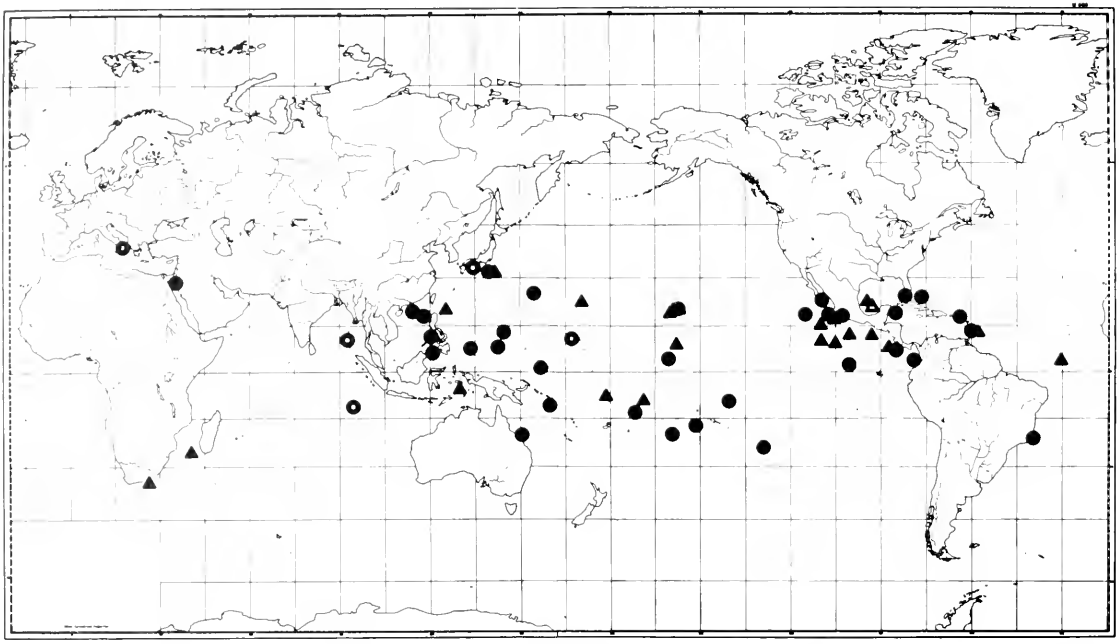

FIGURE 8.—Distribution of *Diodon eydouxii* (triangles) and *Diodon hystrix* (circles). Solid symbols denote specimens examined by me; hollow symbols denote acceptable literature records, photographs, or specimens examined for me by colleagues. Some overlapping records omitted.

spinosissimus Cuvier (see discussion under *D. hystrix*). Le Danois (1959), without comment, incorrectly placed *D. eydouxii* in synonomy with *D. holocanthus*.

The above citations, and those of Troschel (1847) and Duméril (1855) which were essentially reviews of Brissout de Barneville's 1846 paper, constitute the entire literature on *D. eydouxii*.

Diodon eydouxii has undoubtedly been confused in the past with the similar *D. hystrix*. Adaptations to pelagic life by *D. eydouxii* include a lighter, smaller, and more fusiform body compared with *D. hystrix*. The blue color and falcate dorsal and anal fins are also probable adaptations to the pelagic environment. Aside from these characters, *D. eydouxii* differs from *D. hystrix* primarily in its higher dorsal and anal fin ray counts and lower pectoral fin ray counts. *Diodon hystrix* juveniles are pelagic up to a rather large size, and it is tempting to speculate that *D. eydouxii* evolved from this pelagic phase.

All captures of *D. eydouxii* have been at sea (except for one found dead in a South African harbor). Most captures were made under night-lights, and field notes occasionally mention large schools of *Diodon* under the light. Occasional (mostly small) specimens have been taken in plankton, neuston, or midwater trawl hauls.

As a pelagic member of an otherwise slow-swimming, inshore family apparently specialized to feed on heavy-shelled reef animals (e.g., Randall 1967; Hobson 1974), *D. eydouxii* is unusual. However, a well-developed but relatively unspecialized pelagic stage is present at least in *D. hystrix* and *D. holocanthus*. The tetraodontiform fishes, none of which are noted for a combination of rapid and sustained swimming ability and many of which are specialized for feeding on heavy-shelled benthic invertebrates, have a number of pelagic representatives, e.g., *Lagocephalus lagocephalus* (Tetraodontidae) and *Canthidermis maculatus* (Balistidae). In addition, many other species of Tetraodontiformes have pelagic juvenile stages of moderate to long duration. At least 16 of the 22 tetraodontiform genera known to occur in Hawaii, e.g., have an extended pelagic life history stage (no information is available for the other six genera—pers. observ.). The extremely specialized Molidae, a totally pelagic tetraodontiform family, have retained a beaklike jaw structure similar to that of diodontids and tetraodontids. The utility of such jaws in the pelagic environment where the

external shells and exoskeletons of invertebrates are, in general, greatly reduced is difficult to understand.

The stomach contents of three *D. eydouxii* were examined. The two Pacific specimens (BPBM 10551 and NMFS H CHG55-71) examined had fed on a wide variety of large zooplankton: amphipods, crab zoeae, sergestid shrimps, and fish larvae (*Ranzania laevis*, *Acanthocybium solandri*, and a myctophid were identifiable). The Atlantic specimen (ANSP 138122) had eaten approximately 23 small (25-30 mm) fish of the genus *Polydactylus*; these were in a moderately advanced state of digestion.

Material examined.—52 specimens, 4.5-252 mm.

EASTERN PACIFIC: MNHN 2153 (2:101-108), between Guayaquil and Hawaii; SIO 69-394 (1:13) 15°N, 110°W; SIO 69-483 (1:40) 19°36′N, 105°16′W; SIO 64-176 (1:138) 13°30.9′N, 92°02.2′W; SIO H52-346 (1:121) 13°11′N, 102°07′W; SIO 64-174 (1:151) 10°01′N, 115°55′W; SIO 64-213 (1:132) 08°24′N, 87°37′W; SIO 73-348 (1:148) 10°25′N, 108°50′W; SIO H52-422 (3:118-131) 11°00′N, 105°29′W. CENTRAL PACIFIC: NMFS H CHG55-71(7:125-147) 11°11′S, 179°13′E; SIO 68-480 (5:100-115) 22°02.8′N, 171°34.0′E; BPBM 10551 (1:143) 12°20′S, 169°44′W; NMFS H TC32-32,34,36, & 47 (4:14.5-26.0) 21°59′N, 158°29′W; NMFS H TC32-66,70,71,73 (6:4.5-17.0) 19°31′N, 156°06′W; SIO 60-264 (3:33-165) 7°53′N, 157°29′W; SIO uncat. *Climax II* (4:144-177) between 25°S-30°N along 155°W. WESTERN PACIFIC: AMS I.B. 2746-7 (2:156-168) 5°21′S, 131°17′E; SIO 61-551 (1:153) 20°35.6′N, 126°33.2′E; SIO 73-106 (2:10) 33°17′N, 138°08′E. -INDIAN OCEAN: RUSI 3712 (1:252) Pt. Elizabeth, South Africa; LACM 30138-1 (1:145) 27°41′S, 33°22′E. ATLANTIC OCEAN: SIO 63-565 (1:29) 03°21′N, 30°51′W; NMFS M ORII 39-01 (1:ca. 27) 13°00′N, 60°00′W; ANSP 138122 (1:166) 19°28.8′N, 95°27′W; TU 16864 (1:147) 19°35′N, 95°28′W; TU 12766 (1:152) 20°45′N, 93°15′W. NO DATA: SIO uncat. (1:176).

DIODON HYSTRIX LINNAEUS

Porcupinefish (Figure 9)

Diodon hystrix Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Bloch 1785:68-73, pl. 126 (American seas); Günther 1870:306, 1910:474 (worldwide); Klunzinger 1871:647-648 (Red Sea); Day 1878:708, pl. 179 (Andaman Is.); Herre 1924:504-505 (Philippine Is.); Meek and Hildebrand 1928:827-829 (Panama; largest specimen only); Le Danois 1959:229-230 (worldwide); de Beaufort 1962:412-413 (East Indies).

Diodon atinga (not of Linnaeus): Bloch 1785:67-69, pl. 125 (American seas); Lacepède 1798:1, 3, pl. 25 (no locality given); Kaup 1855:227 (East and West Indies).

?*Diodon plumierii*? Lacepède 1798:10, pl. 30 (tropical eastern America).

Diodon brachiatus Bloch and Schneider 1801:513 (no locality given).

Diodon punctatus Cuvier 1818:132-133 (no locality given).

Diodon spinosissimus Cuvier 1818:134-135 (Brazil).

Paradiodon hystrix Bleeker 1865:56-57, pl. 207 (East Indies).

Diodon hystrix var. *hystrix* Eigenmann 1885:298-306 (American seas).

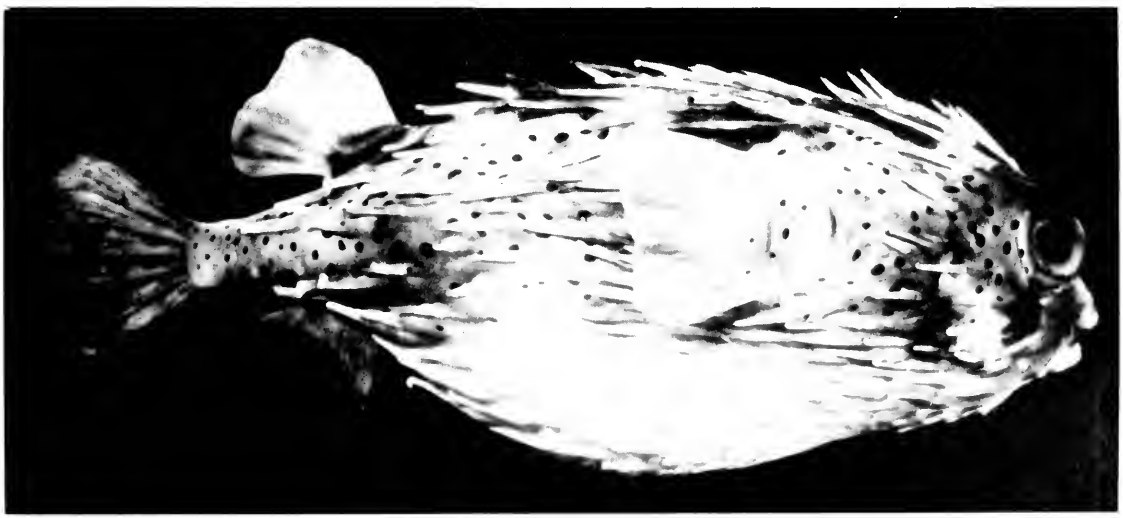

FIGURE 9.—*Diodon hystrix*, 273 mm SL, Oahu, Hawaiian Islands (BPBM 11656). Photo by J. E. Randall.

Diodon nudifrons Jenkins 1904:488-489 (Hawaii).
Diodon armillatus Whitley 1933:107-108, pl. 12, 15 (Australia).
Diodon totara Curtiss 1938:132-133 (Tahiti).

Diagnosis.—A slender-bodied *Diodon*, head width 0.29-0.42, peduncle length 0.14-0.21. Caudal peduncle armed dorsally with short spines. Body spines short to long, slender, and numerous. S-D spines 15-19, S-A spines 14-19. Pectoral axil spines 0.13-0.19, longest on body. A short, fixed tribase spine immediately above gill opening. D 14-17, A 14-16, P 21-25. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles on body. No short, downward-pointing spine below the anterior border of the eye. Dorsal and anal fins rounded. Color pattern dominated by small (<pupil) dark spots dorsally and laterally, these extend onto all fins in adults. A dark gular band starting below the eyes and continuing under the lower jaw, often with a branch extending dorsally between eye and gill opening.

Description.—(34 specimens) D 14-17, A 14-16, the first two rays in each unbranched; P 21-25. Head width 0.29-0.42 ($\bar{x}$ = 0.33; SD = 0.03), body width 0.30-0.51 ($\bar{x}$ = 0.37; SD = 0.04), peduncle length 0.14-0.21 ($\bar{x}$ = 0.17; SD = 0.02), eye 0.05-0.14 ($\bar{x}$ = 0.08; SD = 0.02). Dorsal and anal fins rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 15-19, S-A spines 14-19, about 15 spine rows over the dorsum between pectoral fin bases, about 25 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.06-0.12 ($\bar{x}$ = 0.09; SD = 0.02), pectoral axil spines 0.13-0.19 ($\bar{x}$ = 0.15; SD = 0.02). Pectoral axil spines the longest on the body, 0.45-0.78 ($\bar{x}$ = 0.58; SD = 0.09) in frontal spines. Spines short to long, and slender. Dorsal spines, other than those dorsolateral spines from over the eye to over pectoral fin, are approximately equal and of about the same length as the ventral spines. The dorsolateral spines immediately above the pectoral fin may be nearly as long as pectoral axil spines. Spines on peduncle short (ca. 2 in frontal spine) and shaft extension not very large (ca. 2.5 in shaft). Shaft extension on other spines reduced, never more than 16% of shaft length. Subdermal bases moderate to very long. In ventral and lateral spines the bases may be 1.5× or more the length of the shaft. In an ovoid area extending from the interorbital to the occipit the spines may be greatly reduced or even embedded, particularly in large individuals. Caudal peduncle with one to three dorsolateral pairs of relatively small spines and one or more unpaired spines located either medially or dorsolaterally. Usually one or two ventrolateral spines on peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it (above the pectoral base), both may be embedded. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. No snout spine.

No barbels or fleshy tentacles.

Dorsally in preserved specimens, the ground color is light grey to dark tan grading to white ventrally. Dorsal and lateral surfaces marked with dark brown to black round spots (<pupil). The spots not generally associated with spine axils. Fins unspotted in small specimens (<50 mm), but all fins become covered with spots in adults. The anal fin is not marked except by a dusky area at its base, and in very large individuals by spots.

A dark gular band extends from the eye down and forward generally paralleling the ventral outline of the lower jaw. Often a branch of this band extends dorsally between the eye and gill opening. These bands may be absent in pelagic specimens.

In life the coloration is essentially as described above, but there may be dorsal blotches (similar to those of *D. holocanthus*). These blotches can rapidly appear and disappear. The blotches are particularly evident during feeding but disappear immediately if the fish is disturbed, e.g., by the approach of a diver. I have never seen these blotches retained in a preserved specimen (for examples of these blotches see Clark and Gohar 1953 and Bagnis et al. 1972:225).

The largest specimen examined was 571 mm, but much larger examples have been reported (e.g., 900 mm, de Beaufort 1962).

Eggs, larvae, and pelagic juvenile stages.—The identification of the eggs and larvae described here as *D. hystrix* is tentative because the larvae have not been reared through metamorphosis. Identification is based on the close similarity of these eggs and larvae to those of *D. holocanthus* and the fact that *D. hystrix* and *D. holocanthus* are the only diodontids that commonly occur inshore in Hawaiian waters. *Diodon eydouxii* has not been taken closer than 30 mi from shore around Hawaii, and *Chilomycterus affinis* is very rare

(pers. observ.; J. E. Randall, pers. commun.). The material available for descriptive purposes is limited, 20 eggs (Figure 10) and 7 larvae.

The eggs of *D. hystrix* are similar to those of *D. holocanthus* (see section on the latter species for characters useful in distinguishing the two types of eggs). *Diodon hystrix* eggs are pelagic, spherical, and 1.9-2.1 mm in diameter ($\bar{x}$ = 2.01; SD = 0.06; n = 20) with 30-50 yellowish oil droplets of 0.03-0.15 mm in diameter. The incubation period is about 5 days at 25°C, but hatching occurs at the end of the late stage (i.e., there is no 'final' stage as defined by Leis 1977; see section on development of *D. holocanthus* for comparison and definition of stages); otherwise, these eggs are similar to *D. holocanthus* eggs.

Development is generally similar to *D. holocanthus* and, aside from hatching at the end of the late stage (i.e., before full eye pigmentation), the only substantive difference is the pigment. Early in the late stage, orange and, to a lesser extent, red chromatophores develop on the dermal sac. The oil droplets tend to be more scattered in *D. hystrix* eggs than they are in *D. holocanthus*. Watson and Leis (1974) illustrated a late stage *D. hystrix* egg (figure A21, p. 115) identified as diodontid II.

The newly hatched larvae of *D. hystrix*, ca. 2.6 mm SL (Figure 11), have only slight eye pigment, an open but apparently nonfunctional mouth, and a large amount of yolk. The eyes become fully pigmented by the second day when the mouth apparently becomes functional. The oldest *D. hystrix* larvae available is a 5-day-old individual of 2.60 mm SL. Aside from some shrinkage during the first 2 days after hatching, development is similar to *D. holocanthus*. Table 3 summarizes morphometric data for the larvae.

Melanophores are sparse at hatching, but soon become abundant dorsally and, except for a more caudad extension of melanophores on the caudal peduncle, pigment is essentially the same as that of *D. holocanthus*. The larvae are orange, rather than the yellow background of *D. holocanthus*.

The eggs and larvae described by Sanzo (1930) and tentatively attributed by him to *Crayracion* sp. (Tetraodontidae) closely resemble those here identified as *D. hystrix*. These specimens were clearly not tetraodontids; marine tetraodontids apparently spawn demersal eggs (Breder and Rosen 1966) and their larvae do not resemble those illustrated by Sanzo (pers. observ.). The eggs studied by Sanzo were larger (2.4 mm) and hatched in a shorter period (3 days at 25°C) than *D. hystrix* eggs, but in all other respects they were similar. It is not known how many species of

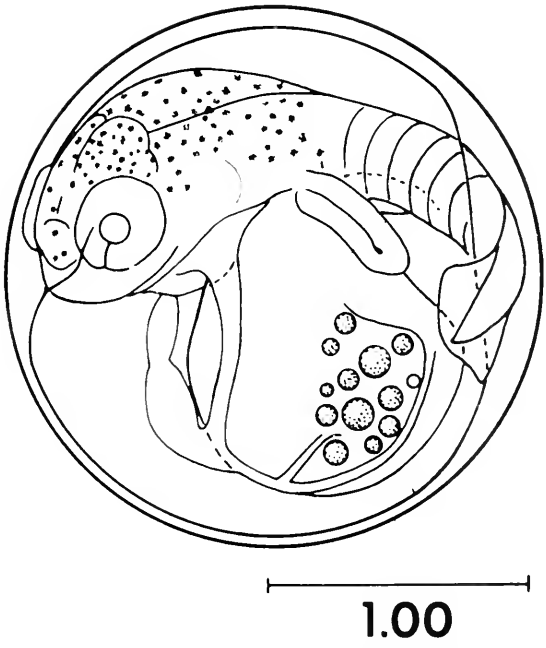

FIGURE 10.—Egg tentatively identified as *Diodon hystrix* just prior to hatching. After Watson and Leis (1974), scale in millimeters.

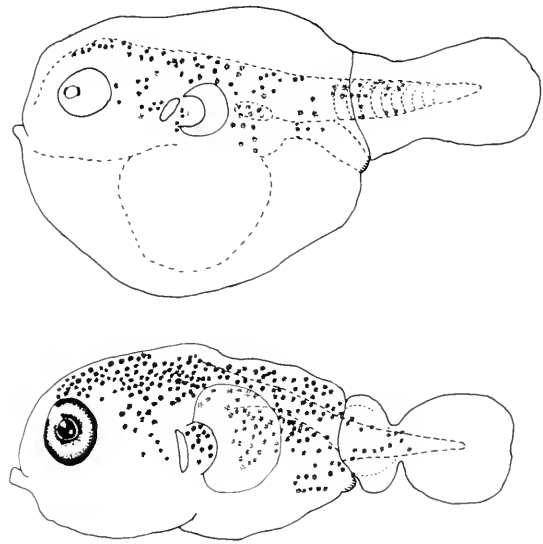

FIGURE 11.—Reared larvae tentatively identified as *Diodon hystrix*: (top) newly hatched larva, 2.57 mm SL, and (bottom) 5-day-old larva, 2.60 mm SL. Hawaiian material.

TABLE 3.—Morphometric and meristic data for larval and juvenile *Diodon hystrix* (measurements in mm). ? indicates individuals of unknown age caught in plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae									
1	2.6	2.0	0.3	0.9	1.0	0.4	0	0	0
3	2.1	1.7	0.3	0.8	1.1	0.7	0	0	0
?	2.4	1.7	0.4	0.9	1.4	0.5	0	0	0
?	2.4	1.9	0.4	1.0	1.5	0.7	0	0	0
?	2.4	1.8	0.3	0.8	1.3	0.5	0	0	0
?	2.4	1.8	0.4	0.8	1.4	0.7	0	0	0
5	2.6	1.8	0.4	0.9	1.2	0.7	0	0	0
Juveniles									
?	5.1	4.5	1.0	1.6	3.2	1.1	×	×	23
?	11.1	9.0	2.1	5.1	7.0	2.5	15	15	22

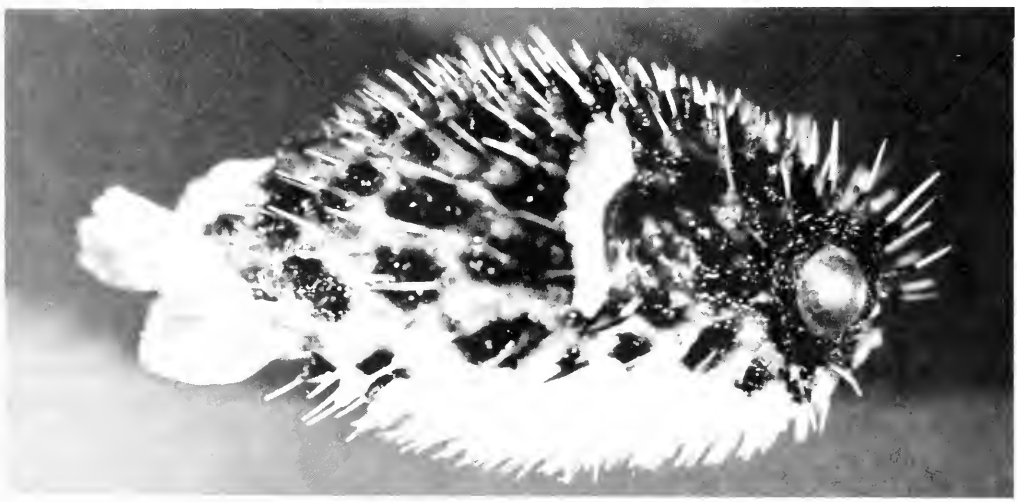

FIGURE 12.—Pelagic juvenile of *Diodon hystrix*, 26 mm SL, western Atlantic (NMFS M *Oregon II* 72-39-36).

Diodon occur in the Red Sea where Sanzo obtained his specimens; only *D. hystrix* is reported to occur there (e.g., Clark and Gohar 1953).

Metamorphosis to the spiny juvenile stage occurs before 5 mm SL. Juveniles of *D. hystrix* are similar in shape, development, and pigmentation to *D. holocanthus* except that the spines of the former are shorter and its snout is more heavily pigmented (Figure 12). *Diodon hystrix* juveniles remain pelagic for an unknown time, but the largest pelagic individual seen was 180 mm while the smallest individual taken inshore was 191 mm.

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon hystrix* is found circumtropically (Figure 8) and often in temperate areas, especially in the western boundary currents. This species apparently is the only member of the genus in the Mediterranean (Torchio 1963).

Remarks.—Linnaeus provided very little diagnostic data in his brief description, the useful information consisting of a mention of long spines, chiefly on the sides. This could apply to *D. hystrix*, as described above, *D. liturosus*, or *D. eydouxii*. Bloch (1785) was the first to use recognizably the name *hystrix*. His illustration of "*D. hystrix*" is clearly of the species here considered as *D. hystrix*.

Several authors have incorrectly applied the name *Diodon atinga* Linnaeus to this species (see synonomy), but it is clear from the original de-

scription that *D. atinga* is a *Chilomycterus* (sensu lato).

Diodon plumierii Lacepède is included in the synonomy of *D. hystrix* with some doubt. The description is not very helpful, but the illustration by Plumier (Lacepède 1790, plate 30), while not immediately recognizable as *D. hystrix*, is probably of that species. The relatively elongate body, short spines, and the three spines on the dorsal surface of the peduncle all indicate *D. hystrix*. The description stated that the fish was blue with white spots; this coloration is not found in any known species of *Diodon*. Lacepède's description was based solely on Plumier's illustration.

Diodon brachiatus Bloch and Schneider is based at least in part on the "Erizo" of Parra (1787) whose illustration is clearly of *D. hystrix*.

Cuvier's *D. punctatus* is attributable to *D. hystrix* on the basis of his description, and examination of the syntypes (MNHN A.8369, A.8373, and A.8367) by M.L. Bauchot (pers. commun. MNHN, 20 May 1975).

Diodon spinosissimus Cuvier has been a source of confusion. This stems at least in part from the presence of two species in Cuvier's syntypic series (M. L. Bauchot, pers. commun., MNHN, 20 May 1975). The larger specimen (MNHN B.1294) is a *D. hystrix* from Brazil, while the smaller syntype (MNHN B.1294) is a *D. liturosus* from Vanikoro, Santa Cruz Islands, in the western Pacific. Le Danois (1961) referred to the above specimen of *D. hystrix* as the holotype, while there is no evidence that Cuvier recognized it as such, I follow Le Danois' lead and designate MNHN B.1294 as the lectotype of *D. spinossisimus*.

Since the publication of Günther (1870), relative unanimity has prevailed, with most authors applying only the name *D. hystrix* to this species. The three exceptions, barring misidentification of *D. holocanthus*, are *D. nudifrons* Jenkins, *D. armillatus* Whitley, and *D. totara* Curtiss. These are easily referred to *D. hystrix* solely on the basis of the published descriptions (S. Karnella, pers. commun., USNM, 28 January 1976, reports that Jenkins' holotype cannot be located at USNM even though it was cataloged as USNM 50854).

The apparent long pelagic stage of *D. hystrix* has undoubtedly contributed to its wide distribution and to the relative uniformity among populations (Table 1).

Little is known of the ecology of *D. hystrix*. Randall (1967) and Hobson (1974) gave information on feeding and diel activity patterns. *Diodon hystrix* is a nocturnal predator on hard-shelled invertebrates such as gastropods, hermit crabs, and sea urchins. Eger (1963) reported toxic dermal secretions in *D. hystrix*. This species is eaten by people in Hawaii (pers. observ.) and Tahiti (Curtiss 1938; Bagnis et al. 1972) without apparent ill effect, although it is frequently classified as poisonous (e.g., Halstead 1967).

Material examined.—43 specimens, 5.5-571 mm. EASTERN PACIFIC: SIO 64-214 (1:128) 7°47'N, 85°45'W; SIO H52-415 (1:180) 2°50.5'N, 101°28'W; UA 73-83-21 (1:236) Cabo San Lucas, Baja California Sur, Mexico; UA 68-59-11 1:199) Punta Mal Paso, Manta, Ecuador; CAS 1244 (1:209) Clarion I., Revillagigedos; CAS H46-241 (2:191-202) Acapulco, Guerrero, Mexico; CAS uncat. (1:215) La Paz, Baja California Sur, Mexico; NMFS LJ N-49, 67-2 (1:5.5) 18°N, 107°W. CENTRAL and WESTERN PACIFIC: HAWAIIAN IS.—HIMB (1:311) Kaneohe Bay, Oahu; NMFS H-243 (1:135) off Kailua, Hawaii; NMFS H-241 (1:142) 10 mi. W. Keahole Pt., Hawaii; BPBM 11656 (1:272.5) Moku Mana, Oahu. LINE IS.—BPBM 9798 (1:338) Washington I. MARQUESAS IS.—BPBM 12139 (1:290) Nuku Hiva. PITCAIRN I.—BPBM 16821 (1:278), 16717 (1:282). SOCIETY IS.—GVF stn 22 (1:211) Maiao I. COOK IS.—GVF M-37 (1:327) Mangaia I. MARCUS I.—BPBM 8403 (1:403). MARIANA IS.—BPBM 5122 (1:200) Guam. SOLOMON IS.—CAS 6003 (1:107) Bellona I. CAROLINE IS.—GVF stn 29 (1:258) Ifaluk Atoll; GVF stn 12 (1:220) Palau Is.; GVF 176 (1:571) Kapingamarangi Atoll. PHILIPPINE IS.: CAS 26419 (1:199) Jolo I.; CAS 26418 (1:286) Culion I. SOUTH CHINA SEA: SIO 70-342 (1:49.5) 18°14.4'N, 119°45.2'E; GVF 1748 (1:196) 20°46'N, 116°53'W. JAPANESE WATERS: SIO 73-106 (1:ca. 10) 33°17'N, 138°08'E. AUSTRALIA: AMS IA.6105 (1:263) Hayman I., Queensland. INDIAN OCEAN: RED SEA—CAS HV-1661 (1:235) Eylath, Gulf of Aqaba. WESTERN ATLANTIC: CAS BMN-7526 (1:465) Vitória, Brazil; CAS 23805 (1:307) Harbour I., Bahamas; GCRL V66:1703 (1:328) St. Thomas, Virgin Is.; CAS 19210 (1:335) Key West, Fla., USA; NMFS M *Bowers* 1-10 (1:29.2) 26°00'N, 70°30'W; NMFS M *Oregon II* 72-39-58 (1:30.0) 21°01'N, 80°14'W; NMFS M *Oregon II* 72-43-146 (2:16.0-18.9) Caribbean; NMFS M *Oregon II* 72-39-36 (1:26.2) 17°08'N, 69°58'W; NMFS M *Oregon II* 72-39-136 (1:25.0) 23°45'N, 84°20'W; NMFS M *Oregon II* 76-66-19791 (1:40.0) 17°50'N, 74°47'W.

In addition, a number of specimens (CAS, NMFS M, material) were identified, but not examined in detail. These fish form the basis for some of the points plotted in Figure 8.

DIODON NICTHEMERUS CUVIER

Globefish (Figures 4, 13)

Diodon nicthemerus Cuvier 1818:135 pl. 2 (Australia).

Diodon nycthemerus: Kaup 1855:228 (no locality given).

Diodon nichtemerus: Duméril 1855:278 (no locality given).

Atopomychterus nychthemerus: Günther 1870:315 (South Australia, Tasmania).
Diodon spinossisimus (not of Cuvier): Castelnau 1872:290 (Australia).
?*Diodon blochii*? Castelnau 1872:210 (Australia).
Atopomychterus nichthemerus: Waite 1923:229 (South Australia, Tasmania).
Dicotylichthys nychthemerus: Fraser-Brunner 1943:17 (Australia).
Atopomycterus nicthemerus: Scott 1957:154 (Tasmania).
Diodon nycthemerus: Le Danois 1959:227 (Australia).
Atopomycterus nicthemerus: Scott 1962:299 (West Australia, South Australia, Tasmania).

Diagnosis.—Round-bodied *Diodon*, head width 0.34-0.43, peduncle length 0.12-0.16. Caudal peduncle without spines. Body spines long and narrow, but relatively few in number, S-D spines 9-12, S-A spines 10-11. Pectoral axil spines shorter than longest frontal spines. No short, fixed tribase spine immediately above gill opening. Fin ray counts low, D 12-13, A 12-14, P 19-21. Nasal tentacle with a pair of lateral openings which are separated by a thin membrane; this is often absent (more often in larger individuals) resulting in the nostrils appearing "confluent, each nasal organ appearing as a bifid tentacle" (Fraser-Bruner 1943:16). Fins without dark spots. Individuals 100 mm and greater with four dark bars on the sides and lacking dark spots on the body.

Description.—(10 specimens) D 12-13, the first unsegmented; A 12-14, the first unsegmented; P 19-21; vertebrae 9 + 12 = 21 (Günther 1870). Head width 0.34-0.43 ($\bar{x}$ = 0.39; SD = 0.03), body width 0.39 - 0.52 ($\bar{x}$ = 0.45; SD = 0.05), peduncle length 0.12-0.16 ($\bar{x}$ = 0.14; SD = 0.01), eye 0.09-0.17 ($\bar{x}$ = 0.12; SD = 0.02) greatest in smaller specimens. Dorsal, anal, and caudal fins all rounded, middle rays longest. Nasal tentacles with a pair of lateral openings which are separated by a thin membrane which is often broken or resorbed, especially in larger individuals, resulting in the nasal organ appearing as a bifid tentacle.

S-D spines 9-12, S-A spines 10-11, about 9 spine rows over dorsum between pectoral fin bases, about 15 spine rows over ventrum between pectoral fin bases. Five frontal spines. Longest frontal spines 0.15-0.23 ($\bar{x}$ = 0.19; SD = 0.03), greatest in smaller specimens, pectoral axil spines 0.11-0.20 ($\bar{x}$ = 0.15; SD = 0.03). Frontal spines longest on body; 1.12-1.35 ($\bar{x}$ = 1.25; SD = 0.08) times pectoral axil spines, although many dorsal spines nearly as long. Ventral spines shorter than dorsal spines (ca. 1.4 in dorsal spines). Lateral spines

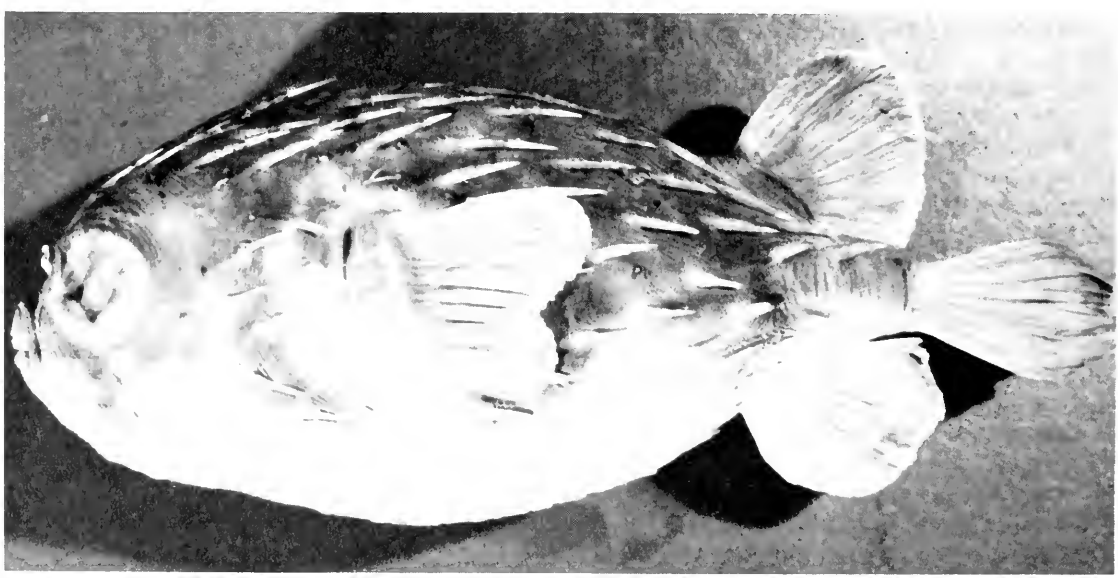

FIGURE 13.—*Diodon nicthemerus*, 110 mm SL, Victoria, Australia (AMS I.16990-004).

nearly as long as dorsal spines (ca. 1.2 in dorsal spines). Spines long and narrow. Subdermal lateral bases short (1.5-5 in shaft length) and the shaft extension reduced or lacking. No spines on caudal peduncle, but along base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. No short fixed spine with three subdermal bases immediately above the gill opening. One or two spines originating between eye and gill opening which extend over the depression surrounding the gill opening. No spines on the snout, but a broad spineless area around the eye. Aside from nasal organs, no barbels or tentacles.

Upper parts in preserved specimens uniformly dark brown to grey with four dark bands descending onto the sides: the first below the eye, the second between the eye and gill opening, the third behind pectoral fin, and the fourth below dorsal fin. The first two bars are swept back and the third swept forward. The second and third bars sometimes meet below the pectoral fin to form a ring about its base and the gill opening. White to light grey below a level even with the mouth (except the bars) with no ventral spotting. Fins somewhat dusky but unspotted. In specimens of about 100 mm the uniformly dark dorsum is broken up into large blotches which appear as continuations of the lateral bars. In smaller fish the dorsal blotches are broken up into small diffuse dark spots (ca. one-half of eye diameter); some of the spots in association with spine bases. Belly is unspotted at all sizes. Le Danois (1959) stated that the bars become lighter in color in large specimens.

Scott (1962:299) gave the following information on live coloration: greenish indigo above, white to silvery below, four dark bars on the sides with several large yellowish spots incorporated in the bars, fins plain yellowish-green and the spines lemon-yellow. An excellent color photograph was provided by Coleman (1974:99).

The largest specimen examined was 158 mm SL. However, both Le Danois (1959) and Scott (1962) reported specimens of 280 mm. A 111-mm specimen was sexable as a male, but may not have been mature.

Eggs, larvae, and pelagic stages.—No information.

Syntypes.—MNHN B.1313 (75 mm) and MNHN 51 (100 mm) taken by Peron and Lesueur in Australia. M.L. Bauchot examined these specimens and provided notes and photographs. Le Danois

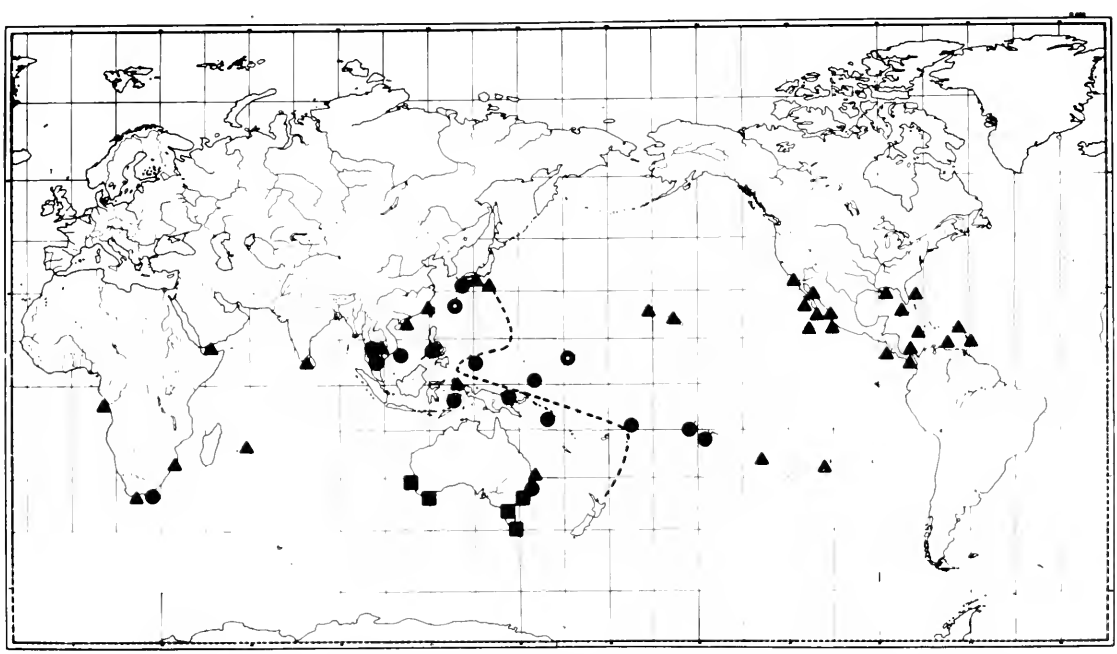

FIGURE 14.—Distribution of *Diodon nicthemerus* (squares), *D. liturosus* (circles), and *D. holocanthus* (triangles). Solid and hollow symbols as in Figure 8. Dashed line indicates position of the Andesite line.

(1961) referred to MNHN B.1313 as the holotype of *D. nichthemerus*. There is no evidence that Cuvier regarded it as such, and I prefer not to regard Le Danois' statement as constituting a lectotype designation.

Distribution.—Apparently confined to the southern half of Australia and Tasmania (Figure 14).

Remarks.—Günther (1870) was the first to place this species in *Atopomycterus*, apparently on the basis of Bleeker's (1865) diagnosis of *A. diversispinus*, the type of the genus, as possessing a bifid nasal tentacle and slender spines with long double roots. However, as indicated above, the double spine roots of *D. nicthemerus* are relatively short and the bifid nasal tentacle is not a consistent character. Bleeker (1865) in the first published usage of the name *Atopomycterus diversispinus*, based his brief description on an unpublished description of a specimen (NMHN 2159) by Verreaux. M. L. Bauchot (pers. commun., MNHN, 23 June 1975) reports that Le Danois (1959) was correct in stating that only the ventral and prepectoral dorsal spines have two bases. The postpectoral dorsal spines are tribased and fixed.

Fraser-Brunner (1943) followed Günther (1870) in placing *D. nicthemerus* in *Atopomycterus* (as a subgenus of *Dictoylichthys*), apparently solely on the basis of the bifid nasal tentacle. Fraser-Brunner and Günther regarded the condition of the nasal tentacle to be of more importance than the character of the spines, but this does not seem tenable to me. Of the 11 specimens of *D. nicthemerus* for which I have data, 6 (41-111 mm) had tubular nostrils on both nasal tentacles, 1 (84 mm) had one tubular and one bifid tentacle, and 4 (100-158 mm) had a pair of bifid nasal tentacles. This indicates that the bifid nasal tentacle is an ontogenetic character that cannot be used in generic classification. The spines of *D. nicthemerus*, aside from their reduced lateral roots and anterior shaft extension, are no different from those of the other species of *Diodon*.

Diodon blochii Castelnau is placed in synonomy with *D. nicthemerus* with some doubt. The type cannot be found in MNHN, AMS or in the National Museum of Victoria, Australia. The description is incomplete and does not fit exactly any of the five species considered here, but of those, it matches *D. nicthemerus* most closely, particularly in meristic characters.

The distribution of *D. nicthemerus* is unusual for a *Diodon* in both its limited range and its location in a temperate rather than tropical area. This limited range might indicate a pelagic stage that is less well developed than that of other members of the genus, but if this species requires a temperate environment it may have colonized all the available habitat within a reasonable dispersal range (although in a personal communication of 4 February 1976, J. Moreland reports that there were no specimens of any *Diodon* sp. in the collections of the National Museum of New Zealand).

Coleman (1974) reported that *D. nicthemerus* inhabits areas of sand or mud bottom and feeds on molluscs, crustaceans, and echinoderms.

Material examined.—Nine specimens, 41-158 mm. All specimens from the Australian Museum: I.13619 (41 mm) Swan R., West Australia; I.12840 (67) Fremantle, West Australia; I.A.629 (78.5) King George's Sound, West Australia; I.16899-003 (84.5) Jervis Bay; I.A.5829 (104) Port Franklin, Victoria; I.16990-004 (110) Port Phillip Bay, Victoria; I.16894-001 (111) Jervis Bay; I.6240 (111) Tamar R., Tasmania; I.17564-001 (158) Snug Beach, Tasmania.

DIODON LITUROSUS SHAW

Short-spine Balloonfish
(Figures 5, 15, 16)

Le Diodon Tacheté Lacepède 1798:13-15 ("New Cythere").

Diodon liturosus Shaw 1804:436 (Indian Seas); Masuda et al. 1975:140, 335 (southern Japan).

Diodon maculatus Duméril 1855:278 (Latinization of Le Diodon Tacheté Lacepède) after Bibron MS.

Paradiodon novemmaculatus (not of Cuvier): Bleeker 1865:57-58, pl. 206 (East Indies).

Diodon maculatus var. B: Günther 1870:308 (East Indies).

Diodon bleekeri Günther 1910:475-476, pl. 179 (Society Is.); Herre 1924:506-507 (Philippine Is.); Orsi 1974:176 (Vietnam).

Diodon holacanthus (not of Linnaeus): de Beaufort 1962:410-412 (Indo-Australian archipelago); Bagnis et al. 1972:227 (French Polynesia).

Dicotylichthys punctulatus (not of Kaup): Grant 1972:472 (Australia).

Diagnosis.—Round-bodied *Diodon*, head width 0.33-0.42, peduncle length 0.12-0.18. Caudal peduncle without spines. Body spines short and

numerous. S-D spines 16-21, S-A spines 17-22. Frontal spines 0.04-0.10, much shorter than pectoral axil spines. A short, fixed tribase spine immediately above gill opening. A short, downward-pointing spine below the front border of eye. Five frontal spines. D 14-16, A 14-16, P 21-25. Nasal tentacle normally with a pair of lateral openings. Usually two small barbels on the chin. A fleshy tentacle may be present over each eye. Color pattern dominated by large, light-edged dorsal, and dorsolateral blotches. The lateral postpectoral surfaces with small spots associated with the spine axils. A dark gular band starting from below the eye and continuing under the chin. Fins without spots except at bases.

Description.—(27 specimens) D 14-16, A 14-16, the first two rays undivided; P 21-25. Head width 0.33-0.42 ($\bar{x}$ = 0.36; SD = 0.03), body width 0.35-0.51 ($\bar{x}$ = 0.41; SD = 0.04); peduncle length 0.12-0.18 ($\bar{x}$ = 0.15; SD = 0.01), eye 0.08-0.15 ($\bar{x}$ = 0.10; SD = 0.02). Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles normally with a pair of lateral openings; occasionally, the end of the tentacle is split, giving rise to a bifid nasal tentacle without nostrils. When split, the bifid arms tend to become thickened and papillose.

S-D spines 16-21, S-A spines 17-22, about 14 spine rows over the dorsum between pectoral fin bases, about 26 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.04-0.10 ($\bar{x}$ = 0.07; SD = 0.02), pectoral axil spines 0.10-0.15 ($\bar{x}$ =0.12; SD = 0.01). Pectoral axil spines longest on body, 0.40-0.78 ($\bar{x}$ = 0.61; SD = 0.09) in frontal spines. Spines generally short. The only markedly elongate dorsal spines are those above the pectoral fin (ca. 0.60 in frontal spines). Frontal, middorsal, and lateral (excluding pectoral axil spines) spines all of about the same length. Ventral spines somewhat shorter (ca. 1.3 in frontal spines). The spines of the interorbital region and nape often reduced or buried, especially in individuals larger than 150 mm, but, in any case, shorter than frontal spines. The shaft extension is variably developed, its size positively correlated with the size of the lateral bases. No spines on caudal peduncle, but along the base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. In two of the specimens examined these spines were on the peduncle, but they were still clearly associated with the fin bases. A short, fixed tribase spine immediately above the pectoral base. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. A short, downward-pointing spine below the anterior border of the eye.

Two small barbels on the chin. A fleshy tentacle above each eye present in about one-third of the specimens. Rarely, a more extensive set of tentacles along the ventrolateral edge of the body similar to that described for *D. holocanthus*.

Background color in preserved specimens varies from dark brown to light buff. The color pattern is dominated by several large dark brown to black blotches on dorsal and lateral surfaces. These blotches edged in a color lighter than background

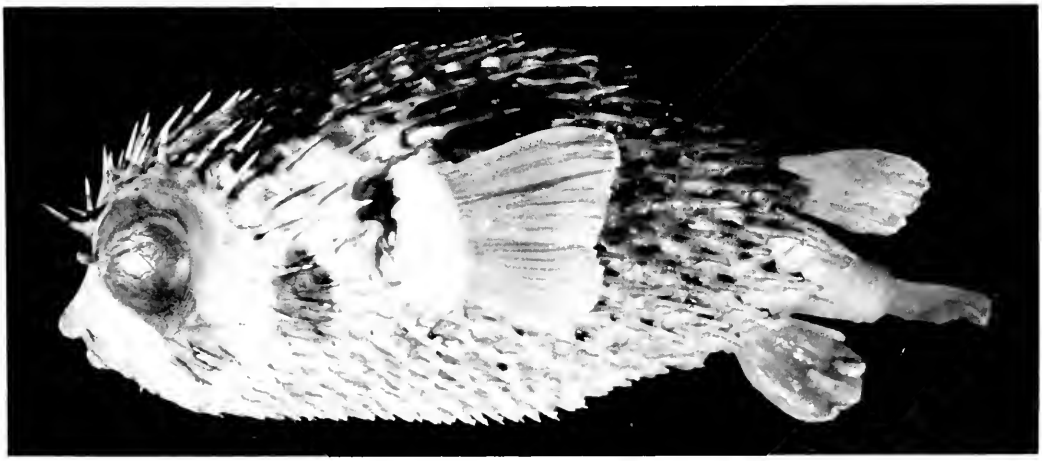

FIGURE 15.—*Diodon liturosus*, 142 mm SL, Ko Samet, Thailand (CAS 30967).

color (usually white). The blotches are located as follows: (Figure 16): 1) one round blotch around the base of the dorsal fin; 2) one round blotch middorsally about midway between the dorsal fin and pectoral base; 3) one round blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base; 4) a broad transverse bar across the occipital region; 5) an irregularly shaped blotch immediately below the occipital blotch, between the eye and pectoral fin; and 6) a bar which crosses each eye downward and usually connects with a broad gular band across the ventral surface just behind the mouth (the bar which crosses the eye does not extend across the interorbital). The chin barbels are located within the gular band, but are light in color. Postpectorally the lateral surfaces are marked with small (<pupil diameter) spots associated with the spine axils. No spots dorsally or ventrally (except in specimens <50 mm). Specimens of 100 mm may be mottled on the caudal peduncle and often have four spots on the iris. Ventrum white and fins unmarked except at bases. A 24.5-mm specimen is light brown dorsally and covered everywhere (except fins) with small (ca. = pupil) dark spots. The spots are less dense on the belly and are not associated with the spine bases. Color in life essentially the same as above but fins yellow.

The largest specimen examined was 349 mm. However, de Beaufort (1962) reported specimens of 500 mm, and Masuda et al. (1975) reported a specimen of 600 mm total length.

Eggs, larvae, and pelagic stages.—No information. However, the 24.5-mm specimen mentioned above which has "pelagic spotting" may be a pelagic juvenile (the collection data are incomplete). The smallest specimen definitely found inshore was 94 mm.

Holotype.—Shaw (1804) based his description on that of Lacepède (1798), who in turn had based his on a manuscript description by Commerson. The fish illustrated by Commerson is apparently lost.

Distribution.—*Diodon liturosus* ranges throughout the Indo-West Pacific (Figure 14) from South Africa to Japan and the Society Islands, but is absent from Hawaii. Areas of overlap with the closely related *D. holocanthus* are along the edges of the Pacific and Indian Oceans.

Remarks.—*Diodon liturosus* usually has been considered a junior synonym of *D. holocanthus* (e.g., Le Danois 1959) but if recognized as a distinct species has generally been called *D. bleekeri*. Shaw's (1804) description is short and based almost totally on color. However, several details clearly indicate which species is involved. The distribution and number of spots, particularly the "two transverse ones, the first situated *beneath* the eye and the second between the eye and pectoral fin" (Shaw 1804:436, emphasis mine), and the "dusky cloud" marking the throat clearly eliminate *D. holocanthus*, and apply only to *D. liturosus* as described above. In addition, Lacepède (1798) gave a pectoral fin ray count of 24 which is rare for *D. holocanthus* (Lacepède did not provide a Latin binomial in his description of Le Diodon Tacheté).

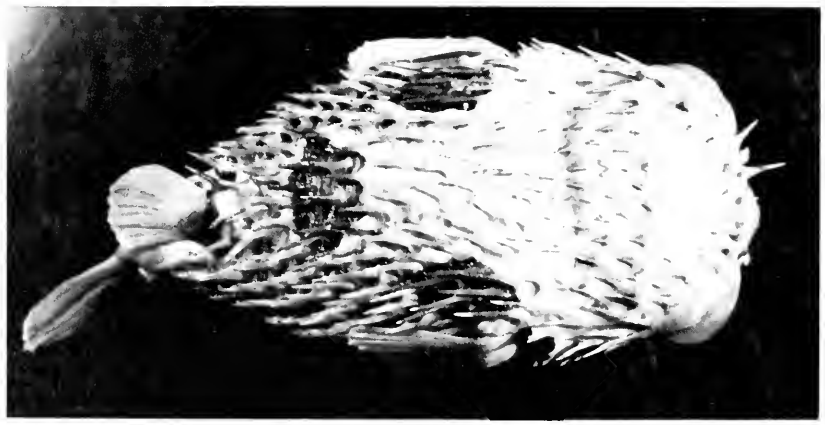

FIGURE 16.—Dorsal view of *Diodon liturosus*, note lack of interorbital bar. Same specimen as in Figure 15.

Günther (1910) did not designate a holotype or syntypic series for *D. bleekeri*, but his description, along with the included plate by Garrett, provide sufficient information to synonymize this nominal species with *D. liturosus*.

In large part the confusion between *D. holocanthus* and *D. liturosus* has resulted from the limited geographical overlap in the distributions of these two species. Because comparative material of both species is rarely available from a given area, it is not surprising that these similar species have been confused, especially considering the less than detailed descriptions available.

Nothing is known of the ecology of this species.

Material examined.—30 specimens, 24.5-340 mm. INDIAN OCEAN: RUSI 3707 (1:124) Port Elizabeth, South Africa. AUSTRALIA: AMS B.1349 (1:128) Port Jackson, New South Wales. EAST INDIES: AMS B.7810 (1:114) Malay Archipelago; CAS 28225 (3:105-116) Madang, New Guinea; BPBM 19239 (1:132) Ambon, Molucca Is. PHILIPPINE IS.: CAS 38383 (1:130) Panay. GULF OF THAILAND: CAS 30967 (4:107-162) Ko Samet, Thailand; GVF stn 135 (1:186) Goh Proet I. Thailand; GVF stn 8 (1:201) Goh Kram I. Thailand; GVF 2646 (1:264) Goh Luem I. Thailand; GVF 2067 (4:94-152) Bangkok. JAPAN: CAS 6987 (1:24.5) Misaki. PALAU IS.: GVF stn 57-45 (1:155); GVF stn 61 (2:133-139); GVF stn 57-43 (1:217). KAPINGAMARINGI: GVF stn 51 (1:125). SOLOMON IS.: CAS 6004 (1:123) Bellona I. AMS B.1350 (1:112) Solomon Is. SOCIETY IS.: GVF (no station data) (1:340) Moorea; GVF stn 39 (1:195) Bora Bora; BPBM 8745 (1:313) Tahiti.

DIODON HOLOCANTHUS LINNAEUS

Balloonfish or Spiny Puffer
(Figures 17, 18)

Diodon holocanthus Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Marshall 1965:500-501, pl. 63 (Queensland, Australia); Orsi 1974:176 (Vietnam).

Diodon pilosus Mitchill 1815:471, pl. 6 (New York); De Kay 1842:326, pl. 55 (New York).

Diodon novemmaculatus Cuvier 1818:136, pl. 6 (no locality given).

Diodon sexmaculatus Cuvier 1818:136-137, pl. 7 (no locality given).

Diodon quadrimaculatus Cuvier 1818:137, pl. 6 (Tahiti? - see text).

Diodon multimaculatus Cuvier 1818:137-138, pl. 7 (no locality given).

?*Diodon maculifer*? Kaup 1855:229 (Cape of Good Hope).

Paradiodon quadrimaculatus: (Bleeker 1865:57-58, pl. 212 (East Indies).

Trichodiodon pilosus: Bleeker 1865:49; Günther 1870:316 (both after Mitchill 1815).

Atopomycterus bocagei Steindachner 1866:447-478, pl. 6 (Port Jackson, Australia).

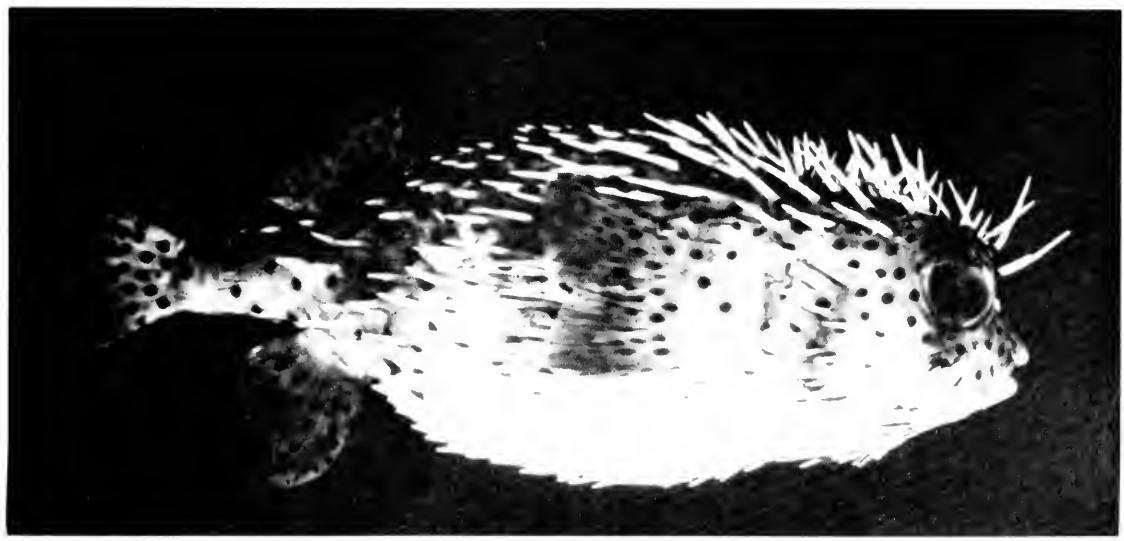

FIGURE 17.—*Diodon holocanthus*, 195 mm SL, Wolmar, Mauritius (BPBM 20255). Photo by J. E. Randall.

Diodon maculatus var. A (not of Lacepède): Günther 1870:307-308, 1910:475 (various localities).

Diodon liturosus (not of Shaw): Jordan and Gilbert 1883:377 (Panama); see Eigenmann (1885) for other references.

Diodon hystrix var. *holocanthus* Eigenmann 1885:298-306 (American seas).

Diodon holacanthus (alternate spelling): Jordan and Evermann 1891:1746 (American seas), 1905:436-437 (Hawaii); Jordan and Snyder 1902:257 (Japan); Herre 1924:505-506 (Philippines); Meek and Hildebrand 1928:829-831 (Panama); Le Danois 1959:231 (in part) (various localities); Randall 1968:282 (Caribbean).

Diodon hystrix (not of Linnaeus): Meek and Hildebrand 1928:827-829 (in part) (Panama); Poll 1959:354-355 (West Africa).

Diagnosis.—Round-bodied *Diodon*, head width 0.26-0.46, peduncle length 0.09-0.20. Caudal peduncle without spines. Body spines rather long, moderate in number. S-D spines 12-16, S-A spines 12-15. Frontal spines 0.13-0.28, from slightly shorter to much longer than pectoral axil spines. A short, fixed tribase spine immediately above the gill opening. A short, downward-pointing spine below the front border of the eye may be present in Atlantic specimens, but is absent in Indo-Pacific specimens. D 13-15, A 13-15, P 21-24. Nasal tentacle with a pair of lateral openings. Two small barbels on chin. On inshore specimens sets of short, fleshy tentacles: one over each eye, a pair in the middle of the back, six along the ventrolateral edge of body, and one on the dorsolateral edge of body posterior to pectoral fin. Some or all of the tentacles often lacking. Color pattern dominated by large dorsal and dorsolateral blotches. Small spots often quite profuse between large blotches. Fins without spots.

Description.—(45 Indo-Pacific and 28 Atlantic specimens) Numbers given are those for Indo-Pacific specimens, those in brackets are for Atlantic specimens. The latter are given separately only if they differ from the former. D 13-15 [14-15], the first two unbranched; A 13-15 [13-14]; P 20-24 [20-23]; vertebrae (2 Pacific, 1 Atlantic specimens) 12 + 9 = 21. Head width 0.26-0.46 ($\bar{x}$ = 0.36; SD = 0.04) [0.33-0.43 ($\bar{x}$ = 0.38; SD = 0.03)], body width 0.33-0.51 ($\bar{x}$ = 0.42; SD = 0.05) [0.38-0.48 ($\bar{x}$ = 0.45; SD = 0.03)], peduncle length 0.09-0.20 ($\bar{x}$ = 0.15; SD = 0.03) [0.12-0.17 ($\bar{x}$ = 0.14; SD = 0.02)], eye 0.07-0.17 ($\bar{x}$ = 0.11; SD = 0.02) [0.08-0.15 ($\bar{x}$ = 0.12; SD = 0.02)]. Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles with a pair of lateral openings.

S-D spines 12-16 [13-15], S-A spines 12-15, about 11 spine rows over the dorsum between pectoral fin bases, about 24 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.13-0.28 ($\bar{x}$ = 0.18; SD = 0.03) [0.13-0.17 ($\bar{x}$ = 0.146; SD = 0.012)], pectoral axil spines 0.11-0.22 ($\bar{x}$ = 0.16; SD = 0.03) [0.11-0.17 ($\bar{x}$ = 0.144; SD = 0.013)]. Frontal spines generally longest on the body. Pectoral axil spines 0.89-1.38 ($\bar{x}$ = 1.12; SD = 0.11) [0.90-1.23 ($\bar{x}$ = 1.00; SD = 0.07)] in frontal spines. Dorsal, dorsolateral, and lateral spines about equal in length (ca. 1.1 in frontal spines). Ventral spines somewhat reduced (ca. 1.5 in frontal spines). Spines at base of dorsal fin moderate (ca. 1.5 in frontal spines) and extend over the peduncle, but no spines wholly on the peduncle. The subdermal lateral bases moderate (1.4-2.3 in shaft length) except in ventral spines where they may equal the shaft length. Shaft extension short, but present on all spines except those on the top of the head. No spines markedly reduced. A short, fixed tribase spine immediately above the gill opening and usually a second slightly posterior to it above the pectoral base. Three or four flat spines with broad lateral bases forming the anterior border of the gill opening. All but one of 86 Indo-Pacific specimens examined without a short, downward-pointing spine below the anterior border of the eye. However, Atlantic specimens usually have this spine on at least one side (52 of 58 examined).

Two small barbels on the chin. Specimens taken pelagically (5-86 mm) lack these as well as the fleshy tentacles described next. A set of fleshy tentacles is variably present; absence may be due to damage or poor preservation. The full set of tentacles consists of the following: 1) one over each eye, 2) one pair middorsally (ca. one-third of the way between pectoral fin base and dorsal fin), 3) two along each postpectoral dorsolateral edge, 4) two along each postpectoral ventrolateral edge, and 5) four along ventrolateral edge of head.

Background color in preserved specimens light tan or grey to medium brown. The color pattern dominated by several large dark brown to black blotches on dorsal and lateral surfaces. Blotches usually lack a distinct light colored border. Blotches arranged as follows (Figure 18): 1) one

round blotch around the base of the dorsal fin, 2) one middorsal blotch of variable shape about midway between the dorsal fin and pectoral base, 3) a round to squarish blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base, 4) a broad transverse bar across the occipital region, 5) a bar beginning below each eye and extending on to the interorbital (in Indo-Pacific specimens this bar is usually continuous across the interorbital, but in Atlantic specimens it is often not), 6) occasionally, a rather diffuse lateral bar between eye and gill opening. The dorsal and lateral surface with scattered small (<pupil diameter) spots the same color as the blotches; these are variable in number and size and rarely may be entirely lacking; they are not associated with the spine axils. Ventral surfaces white, but may be marked with spots which tend to be larger than the dorsal spots. This "pelagic spotting" (Figure 19) of the belly (see section on Eggs, larvae, and pelagic stages) is always found on specimens taken pelagically, but is often retained on specimens collected inshore (60-200 mm); this seems to be the case particularly with eastern Pacific specimens. Pelagic spotting may extend dorsally to the level of the pectoral fin. No dark band on the underside of the head. Fins unspotted, except for some small clusters of melanophores associated with the fin rays. Color in life essentially the same as above, but fins may be yellowish and there may be yellowish areas around the spine bases.

The largest specimen examined was 289 mm. There are literature reports of much larger specimens, but these may be based on misidentifications. However, it is clear that *D. holocanthus* does not reach the size of *D. hystrix*.

Eggs, larvae, and pelagic stages.—The eggs and larvae of *D. holocanthus* were initially identified by rearing eggs from plankton tows. Three larvae were successfully reared through metamorphosis. These fish lived 25-33 days after hatching before being preserved. One was cleared and stained.

The eggs of *D. holocanthus* are spherical, with 10-30 clear, yellowish oil droplets of 0.05-0.25 mm in diameter. The eggs are pelagic, with a narrow perivitelline space, unsegmented yolk, and a

FIGURE 18.—Dorsal view of *Diodon holocanthus*, note interorbital bar. Oahu, Hawaiian Islands, 150 mm SL (HIMB, uncataloged).

FIGURE 19.—Ventral view of pelagic juvenile of *Diodon holocanthus*, 14.5 mm SL, Hawaiian waters (HIMB, uncataloged). Note pelagic spotting.

clear, unornamented chorion. The diameter of the live eggs is 1.7-1.8 mm ($\bar{x}$ = 1.74; SD = 0.03; n = 16) and of preserved eggs is 1.6-1.8 mm ($\bar{x}$ = 1.69; SD = 0.06; n = 191). These means are significantly different at the 5% level (t-test) and a shrinkage of about 4% upon preservation in 5-10% seawater-Formalin[3] is indicated. Rearing experiments indicate that the eggs are spawned in the early evening and hatch in 4-5 days at about 25°C. In rearing containers, the eggs sink to the bottom 12-24 h before hatching.

Embryonic Development: The development of *D. holocanthus* eggs is similar to that of *Ranzania laevis* (see Leis 1977). Development is described here with emphasis on differences between these two species.

Early stage (preclosure of blastopore, Figure 20). The earliest eggs collected were in midgastrulation. The oil droplets are tightly clustered opposite the embryonic axis. These move with the germ ring to the caudal end of the embryo by blastopore closure where they subsequently start to disperse. The elapsed time between midgastrulation and blastopore closure is 3 h. Some segmentation can be perceived on the embryo, but in general little structure is evident. No pigment has formed.

Middle stage (blastopore closure to separation of the tail bud from the yolk, Figure 21). The oil droplets remain scattered over the caudal one-fourth of the yolk sac. The eyes, heart, brain lobes, and otic vesicles are formed within 18 h of blastopore closure. The head is broad and no pigment is visible.

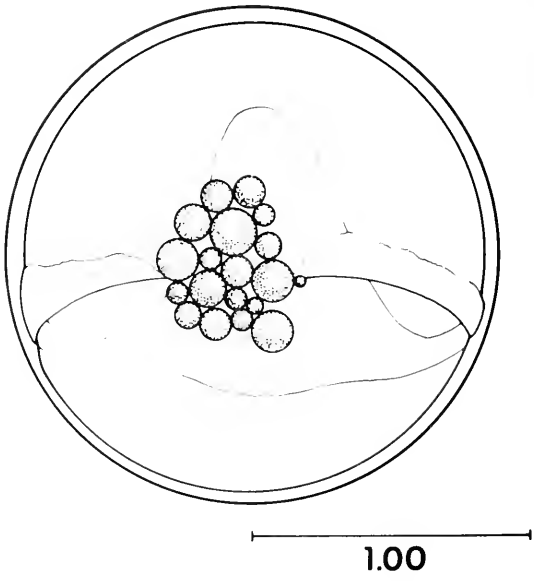

FIGURE 20.—Early stage egg of *Diodon holocanthus*. After Watson and Leis (1974), scale in millimeters.

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

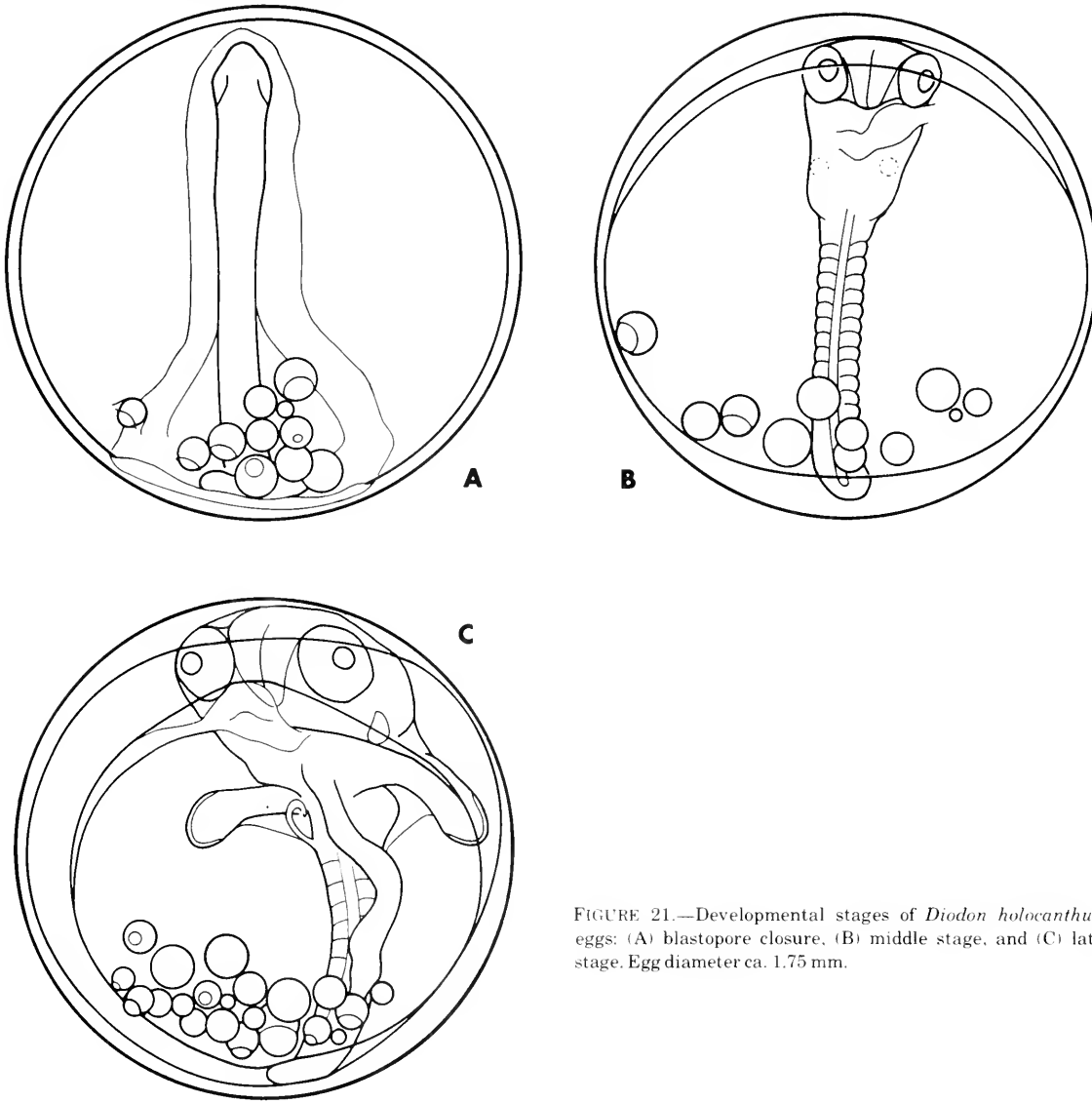

FIGURE 21.—Developmental stages of *Diodon holocanthus* eggs: (A) blastopore closure, (B) middle stage, and (C) late stage. Egg diameter ca. 1.75 mm.

Late stage (tail bud completion to first eye pigmentation and melanophores on body, Figure 21). The oil droplets are on the ventral surface of the yolk sac. The head becomes very broad and enclosed by an inflated vesicular dermal sac which eventually expands to enclose the entire body by the end of this stage. The pectoral fins are well-formed and are occasionally moved by the embryo. An odd hooklike structure which seems to be the incipient pectoral girdle can be seen in live material in the vicinity of the base. The gut forms a long, straight tube. The eyes develop their first pigment during this stage, and a few melanophores appear on the head and dorsal surfaces. At about this time red chromatophores appear, scattered throughout the dermal sac and on the fin buds and folds.

Final stage (acquisition of full eye pigmentation through hatching). The oil droplets are no longer visible, being enclosed with the yolk sac within the abdomen. The mouth apparently becomes functional now, and the exhalant gill openings are visible. The eyes are completely, if lightly, pigmented. Body melanophores have spread over most of the

dorsal surfaces. No melanophores are present on the postanal myomeres or on the dermal sac.

Identification of Eggs: The combination of size (<1.5 mm) and numerous oil droplets serves to distinguish the eggs of *D. holocanthus* from those of all other pelagic eggs except those of other tetraodontiform species. The eggs of the molid *Ranzania laevis* have been described by Leis (1977). *Ranzania laevis* eggs may be distinguished from *D. holocanthus* eggs by the former's smaller size (1.4-1.65 mm) and by the extensive pigment which develops on the ventral surface of the yolk sac of *R. laevis* in the middle stage.

Hawaiian ostraciid eggs (*Ostracion* and *Lactoria*) may be distinguished by their slightly oblong shape, fewer oil droplets (<10), but most reliably by a patch of bumps on the chorion surrounding the micropyle. This "rough patch" is easily overlooked.

Diodon hystrix eggs are the only other *Diodon* eggs known (see section on *D. hystrix*). They can be distinguished from those of *D. holocanthus* by their larger size (>1.9 mm), greater number of oil droplets (>30), and the orange (rather than red) pigment.

Larval Development: Fifteen reared and 12 field-collected larvae in good enough condition for descriptive purposes were available. Morphometric data are summarized in Table 4.

The newly hatched larva has well-developed, apparently functional eyes, jaws, and gas bladder (Figure 22). The pectoral fins are quite large, although no rays are formed. The larvae are 1.9-2.1 mm SL at hatching and the body is rotund. Development in reared larvae is slow. Dorsal and anal fin anlagen form by day 10 (2.4 mm, Figure 22); the olfactory pit also forms by this time and the eyes have become proportionally larger. The oldest reared larva available was 16 days old, but it was smaller than the

TABLE 4.—Morphometric and meristic data for larval and juvenile *Diodon holocanthus* (measurements in mm). ? indicates individuals of unknown age, from plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae									
1	2.0	1.5	0.3	0.9	1.1	0.5	0	0	0
1	2.1	1.5	0.3	0.8	1.2	0.5	0	0	0
1	2.0	1.5	0.3	0.8	1.2	0.4	0	0	0
1	2.0	1.4	0.3	0.8	1.2	0.4	0	0	0
1	1.9	1.4	0.3	0.7	1.2	0.5	0	0	0
?	1.9	1.5	0.3	0.8	1.1	0.6	0	0	0
?	1.9	1.4	0.3	0.9	—	0.4	0	0	0
?	1.9	1.6	0.4	0.9	1.2	0.6	0	0	0
?	1.9	1.0	0.3	0.6	—	—	0	0	0
?	2.0	1.6	0.4	0.8	1.1	0.6	0	0	0
?	2.0	1.6	0.3	0.7	1.1	0.3	0	0	0
5	1.8	1.4	0.3	0.8	1.2	0.6	0	0	0
6	1.8	1.4	0.4	0.8	1.0	0.6	0	0	0
7	1.9	1.4	0.3	0.8	1.0	0.5	0	0	0
8	2.1	1.4	0.4	0.9	1.1	0.6	0	0	0
8	2.2	1.7	0.5	0.9	1.4	0.7	0	0	0
8	2.1	1.5	0.4	0.8	1.1	0.6	0	0	0
9	2.0	1.4	0.4	0.8	1.0	0.5	0	0	0
?	2.2	1.5	0.3	0.8	1.2	0.5	0	0	0
?	2.3	2.0	0.5	0.8	1.5	0.6	0	0	0
?	2.3	1.5	0.3	0.8	1.1	0.5	0	0	0
10	2.4	2.0	0.5	0.9	1.5	0.8	0	0	0
10	2.2	1.7	0.5	0.9	1.3	0.6	0	0	0
?	2.5	2.1	0.5	0.7	—	0.4	0	0	0
?	2.6	2.0	0.5	0.7	0.8	0.4	0	0	0
?	2.7	2.2	0.5	0.7	—	—	0	0	0
16	11.9	1.5	0.5	1.0	1.2	0.7	0	0	0
Juveniles									
?	3.8	3.4	0.8	1.9	2.6	1.0	×	×	22
25	4.8	4.0	1.0	2.3	3.5	1.9	14	14	23
?	5.5	4.8	1.1	2.8	3.3	1.6	—	—	—
?	6.0	5.3	1.2	3.3	3.5	1.8	—	—	—
33	6.7	5.2	1.4	2.9	4.3	1.7	15	×	21
?	7.2	5.5	1.5	3.4	3.7	1.7	14	14	23
ca 30	8.1	6.7	1.8	3.9	4.8	1.8	14	14	21
?	11.0	9.0	2.0	5.5	6.3	2.7	—	—	—
?	14.1	10.9	2.7	6.3	7.6	3.2	15	14	23

[1]Fish in emaciated condition.

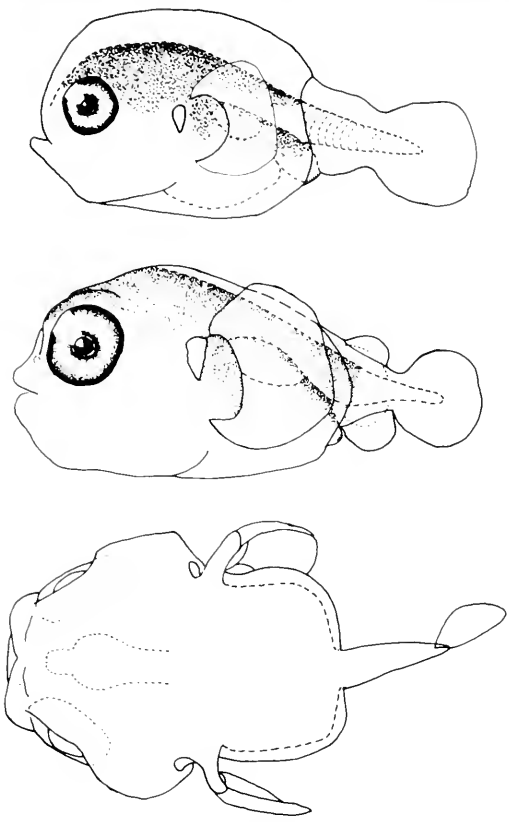

FIGURE 22.—Reared larvae of *Diodon holocanthus*: (top) newly hatched larva 2.0 mm, (middle) 10-day-old larva 2.4 mm, and (bottom) dorsal view of 10-day-old larva with pigment omitted.

day-10 larvae and appeared emaciated. There are incipient fin rays and bases visible in the fins of the 16-day-old larva, but it otherwise is not obviously advanced over the 10-day-old specimen. There is no sign of development of the caudal fin complex. The largest larva available is a 2.7-mm field-collected specimen which is no more advanced than the day-16 larva. The dermal sac is inflated in young larvae (Figure 22), but the subdermal space is virtually gone by day 10 (Figure 22).

The larvae are more or less uniformly pigmented with scattered melanophores on the dorsal surfaces at all stages. The pigment spreads laterally, but there is little below the level of the pectoral fin and the ventral surfaces remain devoid of melanophores until metamorphosis. The newly hatched larvae have no melanophores posterior to the anus (Figure 22), but by day 10 postanal pigment has spread to the middle of the dorsal fin anlage. In life, the newly hatched larva is covered with widely scattered red chromatophores on the dermal sac and fins. The red pigment persists through the larval stage and on about day 2 it is supplemented by a yellow background pigment covering all the body surfaces (not the dermal sac), but being most obvious ventrally due to a lack of melanophores there.

A 2.0-mm field-collected specimen was cleared and stained. The only ossified structures were the cleithrum, coracoid, and six branchiostegals.

Juvenile Development: Metamorphosis apparently occurs at ca. 3 mm at an age of about 3 wk. The smallest juvenile available is 3.8 mm and resembles Mito's (1966) illustration of a 3.7-mm juvenile except that Mito's fish had smaller eyes. The caudal, dorsal, anal, and pectoral fins are all formed as are the teeth, and the body is covered with small spines. The spines do not appear to be erectile, but the fish is capable of inflation. The spines are covered with a sheathlike tissue. They elongate rapidly with growth and by 4.8 mm SL (Figure 23) they are obviously erectile. The nostrils are formed in the 3.8-mm fish, although the nasal tentacle with two lateral openings is not formed until 4.8 mm SL, and in fish as large as 6.0 mm, it may be open at the ends. The 4.8-mm fish is in all respects a miniature adult with all external structures formed and functional. External changes to the adult stage involve only changes in proportion; the spines in particular elongate, the body becomes less rotund and the eye relatively smaller. Morphometric and meristic data are summarized in Table 3.

A 33-day-old juvenile of 6.7 mm was cleared and stained. The vertebral column and skull are incompletely ossified but all other structures are ossified. The vertebral formula is $12 + 9 = 21$ and the vertebral column is strongly arched. There are 11 dorsal and 11 anal pterygiophores which are associated with vertebrae 12-16 and 13-17, respectively.

At metamorphosis, pigment changes radically. The background color in live material is still predominantly yellow with scattered red chromatophores but this does not persist. Dorsally, the melanophores are scattered fairly uniformly, with a concentration at the pectoral base and very little pigment on the caudal peduncle.

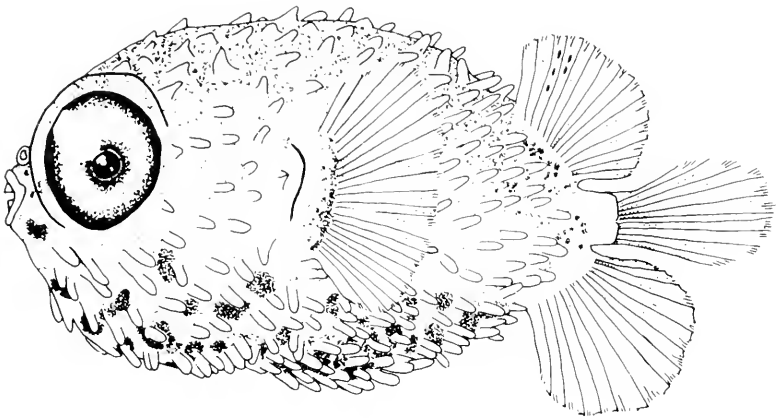

FIGURE 23.—Reared juvenile of *Diodon holocanthus*, 4.8 mm SL, 25 days old. Note pelagic spotting. Hawaiian material.

Ventrally, however, a number of distinct spots have formed that cover the belly (Figure 23). The spots (pelagic spotting) are at first close together but become less numerous and proportionately larger, aligning in rows with growth (Figure 19). Dorsal spotting (always more diffuse than ventral spotting) begins to form at around 10 mm and the characteristic dorsal blotch pattern is generally visible by 30 mm, although in pelagic specimens the contrast with the background color is not great. The pelagic spotting is retained in all pelagic individuals examined (to 86 mm) and in some specimens collected inshore. The fins remain unpigmented except for a few melanophores along the fin rays of the dorsal fin.

Identification of Larvae and Juveniles: Diodontid larvae are likely to be confused only with the rotund, heavily pigmented, sac enclosed ceratioid larvae and other tetraodontiform larvae. Reference to Bertelsen's (1951) work should allow ceratioid larvae to be distinguished as such. Rotund tetraodontiform larvae may be distinguished from diodontid larvae as follows: molids by their body spination and early forming pectoral rays; ostraciids by their pigmentation and early forming pectoral rays; tetraodontids by their relatively more elongate body shape and early forming fin rays. *Diodon* larvae are heavily pigmented only on dorsal surfaces, do not develop fin rays until near or at metamorphosis, have very wide heads and bodies (>body depth), and have very wide mouths.

The larvae of *D. holocanthus* can be distinguished from the putative *D. hystrix* larvae, the only other larval diodontid known, by the less well-developed condition at hatching of the latter (see section on *D. hystrix*). In addition, *D. hystrix* larvae are predominantly orange upon hatching while those of *D. holocanthus* are yellow. Melanophores of *D. holocanthus* do not extend onto the postanal myomeres past the middle of the dorsal and anal fin anlagen; the postanal myomeres of *D. hystrix* are moderately pigmented. Lastly, the eyes of *D. hystrix* larvae are smaller than those of *D. holocanthus* larvae (Tables 2,3).

Once the spines form, the lack of caudal peduncle spination, fin ray counts and spine placement serve to distinguish *D. holocanthus* from all other *Diodon* species (see Key).

The duration of the pelagic stage is unknown, but judging from reared specimens, metamorphosis occurs about 3 wk after hatching at about 4 mm SL. The largest individual captured pelagically was 86 mm while the smallest captured inshore was 60 mm. A certain amount of plasticity in the duration of the pelagic stage is indicated, but its length clearly must be measured in terms of months. No special adaptations for pelagic life are evident in these juvenile stages except, perhaps, in color. In the tetraodontiform fishes (except the molids) the larval stage is short and relatively unspecialized, while a relatively unmodified pelagic juvenile stage may be quite long (see Remarks under *D. eydouxii*). This strategy (for dispersal?) is in marked contrast to that in many advanced perciform shorefishes (e.g., Acanthuridae, Chaetodontidae) where bizarrely modified and long-lived larval and pelagic prejuvenile stages are developed which subsequently undergo marked (and rapid) metamorphosis upon becoming benthic.

Diodon holocanthus eggs and larvae have been found in Hawaiian waters from February through September, with an apparent peak in abundance in May-June, although they are never common. Larvae usually occurred singly in plankton tows (volume filtered 200-1,000 m^3). Although as many as 30 eggs/1,000 m^3 have been taken, 1-5 eggs/1,000 m^3 were more usual, and most tows contained none. Eggs were usually found close to shore, but larvae rarely were found closer than 1 km from shore (pers. observ.).

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon holocanthus* is circumtropical in distribution, but is seemingly absent in the southwest and central Pacific east of the andesite line (the separation of continental from oceanic rocks, Figure 14). However, it reappears in Hawaii, Pitcairn, and Easter Islands. Cuvier's holotype of *D. quadrimaculatus* was allegedly collected by Peron in Tahiti (see Le Danois 1961). Inasmuch as it is known that much of the locality data accompanying Peron's specimens are incorrect (associated with a shipwreck, see Whitley 1931:25) this record is questionable. There is evidence of divergence of the Atlantic population(s) from those of the Indo-Pacific (see Remarks).

Remarks.—I follow the spelling *holocanthus* (rather than *holacanthus* of many authors) which was used consistently by both Linnaeus and Artedi (see also Bailey et al. 1970), and is thus not considered to be a misprint as maintained by Jordan and Evermann (1891). Linnaeus' description is brief; the only useful information being the statement that the spines are terete and extremely long on the head and nape. However, this can apply only to *D. nicthemerus* or *D. holocanthus*. Assuming that "Habitat in India" means India as understood today, and not the entire Indo-Pacific, *D. nicthemerus* is eliminated. However, even if "Habitat in India" means the entire Indo-Pacific, it is unlikely that specimens of *D. nicthemerus*, a species apparently confined to southern Australia, could have reached Artedi by 1738. In any case, subsequent usage and stability demand that the name *D. holocanthus* apply to the species described above.

Diodon pilosus is synonymized with *D. holocanthus* on the basis of Mitchill's observation that no spines were present between the dorsal and caudal fins of his small (ca. 38 mm) New York specimen. *Diodon holocanthus* is the only Atlantic species that lacks peduncle spines. Mitchill distinguished *D. pilosus* on the basis of its flxible spines, but this is the usual condition in small specimens. No holotype is known to exist.

Cuvier's types are extant. Information and photographs of these specimens (catalog numbers and other information are given by Le Danois 1961) provided by M. L. Bauchot (pers. commun., MNHN, 20 May 1975) clearly establish *D. novemmaculatus*, *sexmaculatus*, *quadrimaculatus*, and *multimaculatus* (all of Cuvier) as junior synonyms of *D. holocanthus*. Inasmuch as Cuvier's (1818) descriptions are relatively clear, only his *D. novemmaculatus* requires comment. The holotype of *D. novemmaculatus* (MNHN A.9928, 107 mm) is *D. holocanthus*, apparently from the Atlantic (no locality data are available for this specimen). A spine is present below the anterior margin of the eye and the eye bar is discontinuous over the interorbital. Unfortunately, Cuvier's figure resembles *D. liturosus* as much as *D. holocanthus* (the figure shows the frontal spines shorter than they actually are). This probably led Bleeker (1865) to apply the name *D. novemmaculatus* to *D. liturosus*.

Diodon maculifer Kaup (1855) is included here with some questions. Kaup's description is of little help, and no type material can be found in the British Museum where it would be expected to reside. The holotype may have been part of Kaup's lost personal collection (A. C. Wheeler, pers. commun.). Examination of one of the South African (Kaup's type-locality) specimens of *"Diodon maculifer"* listed by Günther (1870) (BMNH 1845.7.3.103, 100 mm, loaned by A. C. Wheeler) reveals it to be an inflated, dried *D. holocanthus*. In this specimen, inflation is so great (an artifact of stuffing and drying?) that the subdermal spine bases project through the dried skin. Thus, the base of the spines appear to be expanded and transversely compressed. The only characteristic feature of Kaup's description is the compressed nature of the spines, and it seems likely that his description was based on a dried, inflated *D. holocanthus*.

Steindachner's *Atopomycterus bocagei* can be placed in the synonomy of *D. holocanthus* on the basis of information on the holotype (NMV 63848)

provided by P. Kähsbauer (pers. commun., NMV, 1975). Steindachner's (1866) description is essentially correct and unquestionably refers to *D. holocanthus*. The placement of this specimen in *Atopomycterus* was apparently based on the split nasal tentacle (see section on *D. nicthemerus*). A single split nasal tentacle was present on only 3 of the more than 100 specimens of *D. holocanthus* examined, so this condition is rare but not unprecedented.

Both *D. liturosus* Shaw and *D. maculatus* Lacepède (the Latinized version of Le Diodon Tacheté) have been incorrectly applied to *D. holocanthus* by various authors (see section on *D. liturosus*).

For about the past 50 yr the chief sources of confusion on the identity of *D. holocanthus* have been confusion with *D. histrix* by some (mostly American) authors and the lumping of *D. liturosus* under *D. holocanthus* by nearly all authors. The latter problem is discussed under *D. liturosus*.

The confusion between *D. hystrix* and *D. holocanthus* stems primarily from three sources. Many authors (e.g., Gosline and Brock 1960) have conjectured that *D. holocanthus* is the young of *D. hystrix* because the former does not reach a large size, and few, if any, small specimens of the latter were available. However, as discussed under *D. hystrix*, this species is pelagic to ca. 200 mm and is thus unavailable to inshore collecting. Inasmuch as *D. holocanthus* does not commonly exceed 200 mm, the confusion was perhaps understandable.

Second, many early descriptions are poor and keys often rely solely on the size of frontal spines relative to the pectoral axil spines to distinguish the two species. Especially in Atlantic specimens of *D. holocanthus*, the frontal spines are likely to be approximately the same size or even shorter than the pectoral axil spines.

Finally, as noted by Clark and Gohar (1953) (see also Bagnis et al. 1972:225), living *D. hystrix* often display a dorsal blotch pattern not unlike that of *D. holocanthus*. I have not observed this color pattern in preserved *D. hystrix*.

The apparent divergence of the Atlantic and Indo-Pacific populations of *D. holocanthus* mentioned above is of interest. At present, since *D. holocanthus* is apparently absent from the Red Sea and the Mediterranean, gene flow could occur only around southern Africa. Evidence that this is apparently not happening comes from the Indian Ocean specimens which lack a snout spine and have very long frontal spines in contrast to the Atlantic specimens (Table 5). In addition, Poll's (1959) description (as *D. hystrix*) of a west African specimen is typical of the specimens from the western Atlantic examined by me. The apparent increase in frontal spine length from the Atlantic to the Pacific to the Indian Oceans is curious. Based on studies of other groups (Ekman 1967) affinities might be expected between the Atlantic and eastern Pacific populations, but no extension to Hawaii and Easter and Pitcairn Islands would be expected. The lack of the snout spine in all but the Atlantic population and one Hawaiian specimen may indicate that the Atlantic population is distinct. Fin ray counts are of little help in resolving this question. Because all the characters which appear to differ between the Atlantic specimens and those from other areas are rather variable (although some are significantly different in a statistical sense), I choose not to distinguish formally the populations nomenclaturally at the subspecific level. If future study shows this split to be desirable, the proper name for the Atlantic specimens would be *Diodon holocanthus pilosus* Mitchill.

Le Danois (1954) reported sexual dimorphism in *D. holocanthus*, but her illustration of a female *D. holocanthus* (p. 2355:fig. 3) appears to be *D. liturosus*.

Material examined.—141 specimens, 5-289 mm.

EASTERN PACIFIC: NMFS LJ (1:18.5) 18°56'N, 104°10'W; NMFS LJ D31-133.25 (1:64.5) 26°04.5'N, 112°48.0'W; NMFS LJ TO-5801 (1:85.5) 5°29.5'N, 77°57'W; NMFS LJ (1:73.5) "350 mi. west of Costa Rica"; NMFS LJ B-5011 157.40 (2:41-41.5) 21°32.5'N, 111°14.5'W; UA 66-39-18 (1:242) San Agustin Bay, Sonora, Mexico; UA 69-35-25 (1:245) Guaymas, Sonora, Mexico;

TABLE 5.—Comparison of selected characters of *Diodon holocanthus* from five regions (see also Figure 6). n = number of individuals examined for snout spine.

Area	n	No. with snout spine	Frontal spine/SL	Fin rays ($\bar{x}$) D	Fin rays ($\bar{x}$) P	Interorbital bar
Atlantic	58	52	0.146	14 15	22.15	Usually discontinuous
E. Pacific	11	0	0.154	13.80	22.10	Usually continuous
Hawaii, Pitcairn, and Easter Is.	24	1	0.174	14 44	22.57	Usually continuous
W. Pacific	29	0	0.205	14 11	22.17	Usually continuous
Indian	6	0	0.200	13.80	21.92	Usually continuous

UA 71-63-8 (1:145) Puerto Vallarta, Jalisco, Mexico; UA 71-65-9 (1:126) Isla Jaltemba, Jalisco, Mexico; SIO 59-373 (1:ca. 200) La Jolla, Calif.; SIO 63-82 (1:ca. 90) Cape Marco, Columbia. HAWAIIAN IS.: HIMB (3:135-289), HIMB 67-58 (1:67) Kaneohe Bay, Oahu; HIMB (1:181) Punaluu, Oahu; BPBM 10635 (1:63), BPBM 6977 (1:167) Diamond Head, Oahu; BPBM 5124 (1:129) French Frigate Shoals; NMFS H TC32-6,9,11,14 (6:12.5-30) 21°22′N, 158°14′W; NMFS H TC32-23 (1:14) 21°00′N, 158°30′W; NMFS H TC32-73 (1:7.0) 19°31′N, 156°06′W. SOUTHEAST PACIFIC: (all BPBM) 16459 (2:144-168), 13251 (1:135), 16455 (1:122) Pitcairn I.; 6797 (1:150.5), 6798 (1:185), 6799 (1:158), 6800 (1:156.5) Easter I. WESTERN PACIFIC: GVF stn HK91 (2:85-109) 19°38′N, 111°30′E; GVF 2269 (1:128) Gulf of Thailand; CAS 29126 (1:32) Ternate, Moluccas; CAS 6987 (1:41) Misaki, Japan; CAS 6752 (3:100-114) Wakanoura Kii, Japan; CAS 53402 (1:225) Hachijo I., Japan; CAS 15849 (10:90-125) Taiwan Strait. AUSTRALIA: AMS I.17228-001 (10:67-91) New South Wales. INDIAN OCEAN: RUSI 2782 (1:47.5) Knysna, South Africa; RUSI 3709 (1:60.5) East Cape, South Africa; RUSI 3710 (1:65) Inhaca, Mozambique; BPBM 19022 (2:173-188) Negombo, Ceylon; BPBM 20255 (1:195) Wolmar, Mauritius. WESTERN ATLANTIC OCEAN: CAS 4761 (1:150) Jamaica; CAS 54039 (1:94) Havana, Cuba; CAS 18182 (2:50.5-57.5) 29°14′N, 88°19′W; CAS 17184 (1:91) Pine I., Fla.; GCRL VTS:11184 (1:113) San Blas, Panama; LACM 1463 (1:84.5) Key Biscayne, Fla.; LACM 6281, 6282, 6283, 6284, 5781, 5872 (23:64-159) southern Jamaica; NMFS LJ *Gill* 3-64 (1:59) 33°29′N, 76°40′W; NMFS LJ *Silver Bay* 3458 (1:60) 29°03′N, 78°04′W; NMFS M *Oregon II*-72-39-144 (1:12.5) 23°34′N, 82°22′W, 39-73 (1:13) 21°31′N, 86°14′W, 39-50 (1:24) 16°50′N, 80°13′W, 39-48 (1:24.5) 17°26′N, 79°26′W, 39-58 (1:30) 21°01′N, 80°14′W, 39-63 (2:10-40) 19°41′N, 84°13′W, 39-01 (1:23) 13°00′N, 60°00′W, 39-39 (1:45) 18°00′N, 73°00′W, 39-11 (1:56.5) 17°25′N, 63°00′W; NMFS M *Bowers* 75-126-8 (1:28) 26°00′N, 79°30′W; NMFS M *Oregon II*-76-66-19786 (2:23-32) 18°18′N, 75°22′W, 66-19789 (2:20-30) 18°49′N, 74°44′W, 66-19790 (6:27-34) 19°22′N, 75°44′W, 66-19791 (18:19-33) 17°50′N, 74°47′W.

Note.—Since this paper was accepted for publication, NMFS H and most HIMB specimens were transferrred to BPBM.

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PROBABLE CASE OF STREAMBED OVERSEEDING—1967 PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, SPAWNERS AND SURVIVAL OF THEIR PROGENY IN SASHIN CREEK, SOUTHEASTERN ALASKA

WILLIAM R. HEARD[1]

ABSTRACT

The 1967 escapement of 38,067 pink salmon, *Oncorhynchus gorbuscha*, to Sashin Creek, southeastern Alaska, was the largest since 1942. Studies on distribution and density of spawners and freshwater survival of their progeny indicated that deposition of excessive numbers of eggs caused a severe compensatory mortality of alevins during winter. Spawner density was 1.7, 1.6, and 1.2 females/m^2 in upper, middle, and lower study areas respectively. The greater density of spawners in the upper area in the odd-numbered years may be determined by genetic factors like timing of escapements and by greater marine survival of fry from the upper area. Based on the previously consistent relation between timing of adult entry and resulting freshwater survival, 1967 spawners should have produced 8 million fry rather than the 3 million that were produced.

Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins, 10.7 million of which were alive on 1 December, disappeared within the streambed. Initial mortality of these progeny probably occurred in the early alevin stage from oxygen privation, whereas disappearance was probably related to rapid decomposition and invertebrate scavenging. A "snowball effect" is postulated whereby alevins that die shortly after hatching place increasing demands on available oxygen, causing accelerated mortality. A review of historical patterns of fry production in Sashin Creek indicates that streambed overseeding occurred in 1967.

Studies of pink salmon, *Oncorhynchus gorbuscha*, in Sashin Creek, Baranof Island, southeastern Alaska, have shown that certain factors markedly affect freshwater survival. These factors include: 1) seasonal timing of spawning (Skud 1958); 2) density and distribution of adults on the spawning grounds relative to ecological characteristics of the stream, especially gradient (Merrell 1962); and 3) quality of the intragravel environment, including oxygen content of intragravel water and amount of silt and fine particulate material in streambed gravels (McNeil 1966, 1968). Other factors of significance, but believed to be of less influence on freshwater survival in Sashin Creek, include predation on eggs and alevins (McLarney 1967), stream discharge during spawning (Ellis 1969), and incubation (McNeil 1968).

The spawning ground of Sashin Creek extends from the head of tidewater to an impassable falls 1,200 m upstream and includes 13,629 m^2 of streambed. Ninety-six percent (13,084 m^2) of this ground comprises three distinct ecological areas that differ in gradient and size of particles in the substrate. McNeil (1966) called the areas upper, middle, and lower and described them briefly as follows: upper (2,945 m^2)—relatively steep gradient (0.7%) and coarse streambed gravel; middle (4,067 m^2)—intermediate gradient (0.3%) and medium-sized streambed gravel; and lower (6,072 m^2)—low gradient (0.1%) and relatively fine streambed gravel. The remaining 4% (545 m^2) of spawning ground is located in a short section of stream between the counting weir and the lower area and is not treated in this paper.

Pink salmon spawners entering Sashin Creek (the escapement) have been counted at a weir at the mouth of the creek since 1934, and the resulting numbers of fry from these escapements have been determined since 1940. During this time, the number of spawners varied from as few as 8 to more than 90,000 and the number of fry produced varied from 50 to almost 6 million. The percentage of freshwater survival, based on the estimated potential egg deposition, ranged from 0.06 to 21.75% (Table 1).

The high escapement of 38,067 pink salmon spawners in 1967, following a long series of relatively low escapements, gave me an opportunity to

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TABLE 1.—Number of adult pink salmon, potential egg deposition, number of fry produced, and freshwater survival in Sashin Creek, 1934-67. (Modified from McNeil 1968.)

Brood year	Number of adults	Potential egg deposition[1]	Number of fry produced	Percentage freshwater survival
1934	7,917	—	—	—
1935	6,323	—	—	—
1936	5,364	—	—	—
1937	9,085	—	—	—
1938	6,467	—	—	—
1939	16,830	—	—	—
1940	53,594	52,858,000	3,399,900	6 43
1941	84,303	88,678,000	1,024,300	1 16
1942	92,085	78,894,000	674,000	0 85
1943	14,883	14,980,000	227,800	1 52
1944	4,050	3,904,000	105,600	2 71
1945	5,465	5,062,000	43,100	0 85
1946	933	736,000	1,200	0 16
1947	1,486	1,330,000	27,600	2 07
1948	597	516,000	9,100	1 76
1949	4,902	4,800,000	176,200	3 67
1950	112	86,000	50	0 06
1951	4,366	4,062,000	412,500	10 15
1952[2]	45	—	740	—
1953	1,164	1,284,000	95,400	7 43
1954	21	12,000	660	5 48
1955	9,267	10,286,000	266,200	12 31
1956	933	1,018,000	5,040	0 50
1957	2,834	2,588,000	562,900	21 75
1958	217	174,000	10,700	6 13
1959	35,391	40,379,000	5,332,400	13 21
1960[2]	162	—	480	—
1961	28,759	29,425,000	5,940,300	20 19
1962[2]	8	8,000	100	1 20
1963	16,757	16,640,000	3,256,300	19 57
1964	[3]2,193	2,230,000	[4]310,000	13 91
1965	14,833	12,668,000	[4]2,235,000	17 92
1966	5,761	6,255,000	[4]744,000	11 99
1967	38,067	44,384,000	3,007,200	6 78

[1]Based on 2,000 eggs female except when actual fecundity was calculated
[2]An attempt was made to destroy the spawners or their progeny
[3]Natural returning adults (327) were supplemented by the introduction of 1,866 adults taken from Bear Harbor, Kuiu Island
[4]Fry weir not operated; figures are estimates of live alevins in the gravel just before start of emergence

study the effects of a large spawning population on freshwater survival. For the 1967 escapement I studied 1) timing of entry into the stream and the distribution and density of pink salmon on the spawning grounds, and 2) survival of progeny by time periods in the three ecological areas of the stream and the overwinter disappearance of eggs and alevins from streambed gravels. In this paper I present all the available data on escapament size and production of fry in Sashin Creek and develop the hypothesis that streambed overseeding occurred in 1967. As Ricker (1962:186) pointed out, detailed knowledge on the effects of overseeding is important in understanding why pink salmon populations fluctuate. He stated, "Because it [overseeding] happens rarely nowadays, no chance should be lost to make such a study if one occurs." Simply stated, overseeding can be defined as an egg density in spawning bed gravels that leads to a significantly greater freshwater mortality than a lesser density would cause. As discussed more fully later, it is a complex and dynamic interaction between egg density, streambed ecology, and specific climatic conditions.

TIMING OF ENTRY AND DISTRIBUTION AND DENSITY OF SPAWNERS

The timing of stream entry was determined from daily counts of the adults at the Sashin Creek weir. This timing apparently influences the freshwater survival of the progeny. An inverse relation between time of stream entry of spawners and survival of progeny is usual in Sashin Creek (Skud 1958; Merrell 1962; McNeil 1968; Ellis 1969): high survival has been associated with early spawning and low survival with late spawning. Merrell (1962) further pointed out that pink salmon spawn in Sashin Creek an average of 12 days earlier during odd years than even years.[2] As a result, freshwater survival is usually higher among progeny of spawners from odd years than among those from even years (Table 1).

In 1967, 50% of the spawners had entered Sashin Creek by 20 August, the second earliest date on record. The early entry indicated that survival of eggs and alevins would be high, but this did not prove to be the case.

Throughout the run, random lots of females were tagged at the weir, and the distribution and density of spawners were determined from daily counts of both tagged and untagged females on the spawning grounds. This technique, described by McNeil (1968) and used by Ellis (1969), provides two methods of estimating the numbers of females spawning in the upper, middle, and lower areas. One method assumes that tagged females distribute themselves among the three sections the same as untagged females. In the other method, the summed daily count of all females in each area is divided by the average longevity on the spawning grounds. The results from the two methods were generally in agreement, except for the upper area where estimates based on distribution of tagged females were considerably higher than those based on total females. The difference may reflect the difficulty in making accurate counts on spawning riffles where densities of spawners are high; in such a situation an observer might count small

[2]The date when 50% of the escapement to Sashin Creek had entered the stream has been commonly used as an index of time of spawning.

numbers of tagged females more accurately than large numbers of untagged females. Because the relative accuracy of the two methods is unknown, I averaged them to arrive at mean estimates of densities of females in the three areas (Table 2).

Spawner density in Sashin Creek is usually unequal in the three study areas, depending in part on the total number of spawners. Densities in 1967 were the highest recorded for specific areas[3] of the stream (Table 3). Merrell (1962) noted that in years when many spawners were present, they utilized all of the available spawning grounds, and in years when few were present, they spawned mostly in the lower portion of the stream. When the upper area was used, survival of eggs and alevins in that area was higher and the number of fry produced was proportionally much greater than in the middle and lower areas (Merrell 1962). In addition, the sediment content and water quality of the stream in the upper area were better than in the other two areas (McNeil 1966, 1968). Sashin Creek thus presents an apparent paradox—the least favorable areas are used in years of relatively few spawners, and the best areas are used only during years of great numbers of spawners.

Merrell (1962) thought that the greater use of the upper area was related primarily to density-dependent spawner interactions. In 1967, however, the heavy use of the upper area was apparently not the result of high densities downstream forcing spawners into upstream areas: spawner densities in the upper area built up rapidly before spawning reached significant levels in the middle and lower areas. Although the upper area contains only 22% of the combined spawning grounds of the three areas, in 1967, 62% of the first group of female pink salmon tagged at the weir spawned in the upper area (Table 4). In general, the intensity of spawning in 1967 progressed to downstream areas from the upper area rather than the reverse. McNeil (1966, 1968) noted similar downstream shifts in spawning in Sashin Creek in 1963 and 1965. Although McNeil (1966) felt that the shift occurred because of heavy rainfall during the spawning period, he later noted (McNeil 1968) the same phenomenon during an unusually dry year.

It appears that the upper area in Sashin Creek is not necessarily used because of spawner overflow but because of more complex factors. Two interrelated factors could account for the spawner distributions observed in recent years: 1) migratory behavior associated with timing of the escapement, and 2) a genetic tendency for odd-year spawners to use upstream areas. Odd-year spawners enter the stream earlier than even-year spawners. A characteristic of early stream entry in anadromous fishes may be a tendency to migrate farther upstream than spawners associated with late stream entry (Briggs 1955). In addition to early entry and use of the upper area, odd-year spawners for the past 9 or 10 generations have consistently had higher escapements and, except for 1967, higher freshwater survival of progeny than even-year spawners (Table 1). Natural selection may be operating, in recent odd-year generations, to encourage progeny produced in the upper area to spawn in that area. Wells and McNeil (1970) showed that fry produced in the upper area of Sashin Creek were larger and presumably of better quality than those produced in the downstream areas. Differential marine survival

[3]Although the total number of spawners entering the stream has been recorded since 1934 (Table 1), detailed studies on the distribution of spawners in the upper, middle, and lower areas of the stream have been available only since 1961.

TABLE 2.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1967.

Area	Females per square meter: Based on counts of tagged females only	Based on counts of tagged and untagged females	Mean
Upper	1.90	1.59	1.74
Middle	1.49	1.76	1.62
Lower	1.19	1.15	1.17

TABLE 3.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1961-67.

Area	Females per square meter: 1961[1]	1963[2]	1964[3]	1965[4]	1966[5]	1967
Upper	1.00	0.59	0.01	0.58	0.04	1.74
Middle	1.00	0.89	0.09	0.62	0.27	1.62
Lower	1.00	0.59	0.13	0.44	0.28	1.17

[1]Extrapolated from subjective estimate (McNeil et al. 1964)
[2]Adjusted from McNeil (1966).
[3]McNeil et al. (1969).
[4]McNeil (1968).
[5]Ellis (1969).

TABLE 4.—Dates of tagging and percentage of total escapement counted through weir, numbers of female pink salmon tagged, and spawning distribution of tagged females in three areas of Sashin Creek, 1967.

Date of tagging[1]	Percentage of total escapement counted through weir	Females tagged	Tagged females observed spawning	Percentage of tagged fish accounted for: Upper area	Middle area	Lower area
10 Aug.	3	49	40	62	25	12
12 Aug.	13	50	40	22	37	40
17 Aug.	26	50	42	21	23	55
20 Aug.	54	50	50	22	42	36
5 Sept.	98	50	40	22	30	48

[1]Females tagged on each date received color-coded tags that differentiated them from females tagged on other dates.

that favored fry produced in the upper area over those produced in the downstream areas could account for the greater escapements of odd-year spawners in recent years.

SURVIVAL OF EGGS AND ALEVINS

Survival of eggs and alevins from the 1967 brood year was estimated in Sashin Creek for four time periods: 1) from stream entry to end of spawning, 2) from end of spawning to hatching, 3) from hatching to shortly before fry emergence, and 4) from shortly before emergence to emergence and downstream migration of fry.

The estimates of survival were based on estimates of the potential egg deposition of female spawners and estimates of the surviving eggs and alevins in the three study areas. Potential egg deposition was estimated by multiplying the number of females by average fecundity. Densities of eggs and alevins were determined after spawning, during hatching, and before fry emergence by sampling randomly selected 0.1-m^2 points in the streambed with a hydraulic sampling technique described by McNeil (1964a). The number of fry migrating from the stream were estimated on the basis of daily counts of fry migrating through a weir at the stream mouth.

Numbers of females entering the stream and average fecundity were derived from counts and samples taken at the weir. Of the 38,067 pink salmon spawners entering Sashin Creek in 1967, 19,639 (52%) were females. Total counts of mature eggs from each of 35 females selected at random from the run ranged from 810 to 2,954 (average 2,260) eggs/female (90% confidence limit of mean fecundity was ±115 eggs).

The percentage of eggs available for deposition that are actually buried in the streambed is partly dependent on the density of spawners. McNeil (1964b) discussed the role of redd superimposition and showed that at spawner densities approaching 3 to 4 females/m^2 of spawning ground, an upper asymptotic limit on the density of eggs in the streambed is reached. Factors other than spawner density that may influence egg deposition include loss of adults in the stream before spawning and retention of eggs in the female's body (Neave 1953), type and characteristics of the spawning substrate (McNeil 1966), streamflow during spawning (Ellis 1969), and loss of eggs to vertebrate predators during the spawning process (Moyle 1966; McLarney 1967; Reed 1967).

The efficiency of egg deposition of pink salmon spawners in Sashin Creek is highly variable, from 37 to 82% of the potential egg deposition (Ellis 1969). In 1967 the number of pink salmon eggs potentially available for deposition was 44.4 million, with 19.9 million of these (45% of the potential) estimated to be in the streambed after spawning. The efficiency of egg deposition was 47% in the upper area, 50% in the middle area, and 38% in the lower area.

Although spawner densities were high in 1967 (Table 3), the ability of pink salmon to void most of their eggs during spawning did not seem to be affected. Egg retention is characteristically low in Sashin Creek, usually less than 5% of fecundity (McNeil 1966; Ellis 1969). In 1967, I examined the body cavities of 402 spent female pink salmon (about 2% of the total) and found that average egg retention was 1.5% of average fecundity.

The proportion of eggs actually deposited that were alive at the end of the spawning period in 1967 was highest (93%) in the upper area, intermediate (83%) in the middle area, and lowest (74%) in the lower area (Table 5). This high survival in the upper area is consistent with that of previous years. The ratio of live to combined live and dead eggs and alevins was usually higher in the upper and middle areas than in the lower area through hatching to the beginning of fry emergence (Table 5).

Survival of eggs and alevins varied among the three time periods (during spawning, between end of spawning and hatching, and between end of hatching and emergence). Survival within each time period for each area was higher between spawning and hatching than during spawning or between hatching and emergence (Table 6). As previously discussed, survival during spawning was related primarily to the ability of females to successfully deposit their eggs because a high percentage of the eggs buried were alive shortly after spawning. Survival between spawning and hatching and between hatching and emergence pertains to survival of eggs and alevins within the streambed.

The densities of live preemerged fry in the streambed of Sashin Creek in late March 1968 were 382, 260, and 108/m^2 in the upper, middle, and lower areas, respectively. From these densities I estimated a population of 2.9 million fry in the entire stream. Operation of the fry weir began just after the late March streambed sampling was

TABLE 5.—Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and estimated survival of 1967 brood year pink salmon in three areas of Sashin Creek.

Area	Potential egg deposition per square meter: Mean	Potential egg deposition per square meter: 90% confidence limits of mean	Period beginning 10 Aug and ending	Combined live and dead eggs and alevins per square meter: Mean	Combined live and dead eggs and alevins per square meter: 90% confidence limits of mean	Percentage of live to combined live and dead eggs and alevins: Mean	Percentage of live to combined live and dead eggs and alevins: 90% confidence limits of mean	Percentage calculated survival
Upper	3,947	±201	1 Oct	1,863	±254	93	± 1	43
			1 Dec.	1,714	±295	86	± 4	37
			25 Mar	647	±138	59	±13	10
Middle	3,672	±187	1 Oct	1,826	±218	83	±12	41
			1 Dec	1,591	±226	70	± 7	30
			25 Mar	702	±147	37	± 2	7
Lower	2,644	±136	1 Oct	1,015	±120	74	±17	28
			1 Dec	989	±116	72	± 2	27
			25 Mar	350	±70	31	±10	4

TABLE 6.—Percentage of estimated survival of 1967 brood year pink salmon eggs and alevins for three time periods in three areas of Sashin Creek and for the entire stream, 1967.

Area	Percentage survival: During spawning	Between end of spawning and hatching	Between end of hatching and emergence	Total
Upper	43	85	26	10
Middle	41	73	23	7
Lower	28	95	15	4
Entire stream[1]	37	83	22	6 8

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas

completed. Relatively few fry migrated downstream through the weir until mid-April; the daily fry migrations increased steadily through late April, reached a peak in early May, then declined rapidly, and were essentially completed by early June (Figure 1). The total number of pink salmon fry estimated to migrate from Sashin Creek from the 1967 brood year spawners was 3 million. Similar close agreements between estimates based on densities of preemerged fry and those based on number of fry counted at the weir have occurred in previous years (McNeil 1968).

The 3 million fry migrating from Sashin Creek in the spring of 1968 represent a total freshwater survival of 6.8% of the 44.4 million potential egg deposition. This is the lowest freshwater survival in the odd-year line of pink salmon spawners in Sashin Creek since 1949 (Table 1). I will subsequently attempt to show that this reduced survival was primarily due to excessive seeding of the streambed during spawning.

DISAPPEARANCE OF EGGS AND ALEVINS

To determine the number of eggs and alevins that disappeared from the streambed, I compared the potential egg deposition with the numbers of live and dead eggs at the end of spawning and the number of eggs and alevins at the time of hatching and just before emergence. In 1967, 55% of the potential egg deposition disappeared during spawning. The fate of these eggs is unknown, but they were probably removed from the stream during the spawning period by predators, scavengers, or turbulent streamflow. McLarney (1967) and McNeil (1968) discussed the roles of fish predators (especially sculpins) and water turbulence in removing eggs from Sashin Creek during spawning and between spawning and hatching.

McNeil (1968) found that eggs and alevins of the 1963 and 1965 brood years disappeared at different rates in the upper, middle, and lower study areas of Sashin Creek. Most of the 1963 brood year progeny disappeared during spawning, and most of the 1965 brood year progeny disappeared between hatching and emergence (over the winter). I will examine closely the possible fate of eggs and alevins during this period (December to March) because the factors that caused a reduced freshwater survival of 1967 brood year progeny prevailed during this period.

The estimated percentages of the potential egg deposition that disappeared in the upper, middle, and lower areas of Sashin Creek were similar within each of the three periods. This disappearance varied greatly between periods: 55% of the progeny (eggs or alevins) had disappeared by 1 October, 4% between October and December, and 25% between December and March (Table 7). The disappearance between hatching and emergence (December and March) appears more significant when expressed in terms of numbers present in December; 56-65% of the eggs and alevins in the upper, middle, and lower areas of Sashin Creek on 1 December had disappeared by 25 March (Table 8).

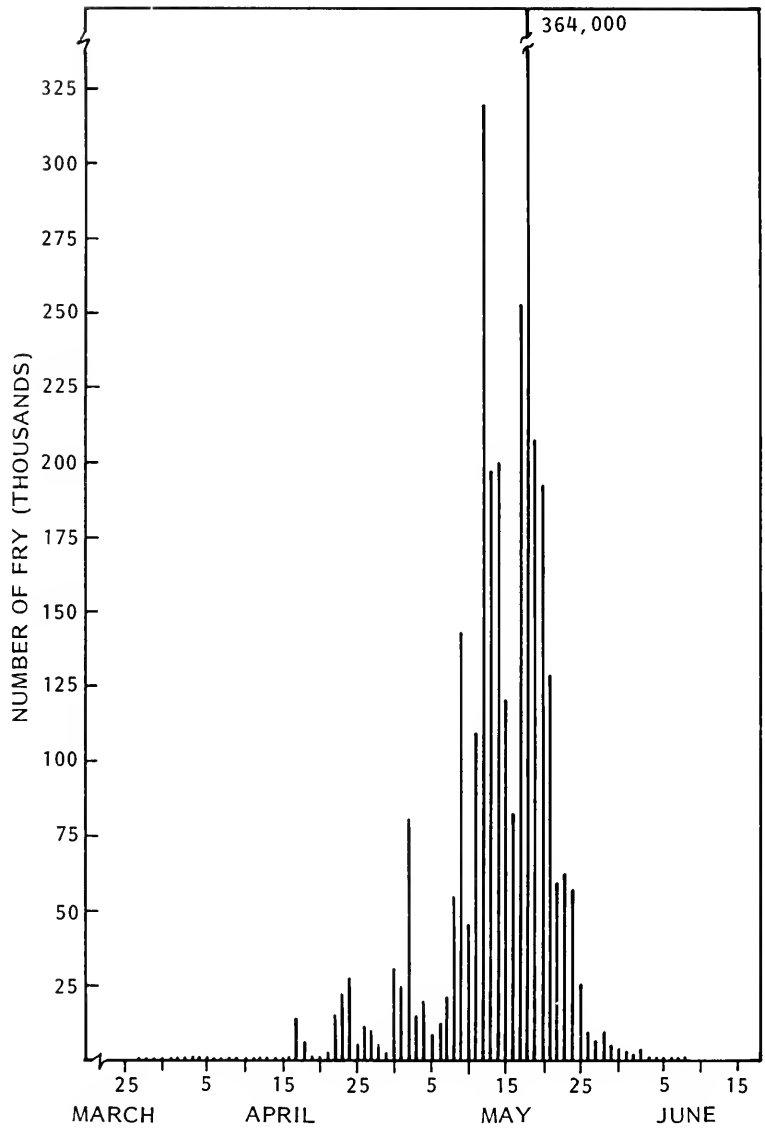

FIGURE 1.—Daily number of 1967 brood year pink salmon fry counted through Sashin Creek weir in spring 1968.

Mortality Patterns in the Streambed

Mortality of eggs and alevins within the streambed at Sashin Creek is evident in two ways: 1) as a reduction in the total population of eggs and alevins within the streambed, i.e., they disappear, and 2) as an increase in the number of dead eggs and alevins in the streambed and a decrease in the number of live eggs and alevins. In the first instance, some factors that can cause eggs and alevins to disappear are turbulent streamflow, streambed scouring, predation, and scavenging. Excluding predation, these same factors can also cause dead eggs and alevins that may have died for other reasons to disappear from the streambed. In the second instance, factors causing an increase in the number of dead eggs and alevins within the streambed are generally relatable to desiccation, freezing, and the quality of intragravel water.

In addition, dead eggs and alevins may disappear because of at least two factors that do not affect live eggs and alevins: biochemical decomposition and consumption by intragravel invertebrate scavengers. Thus, factors that cause eggs

TABLE 7.—Percentage of potential egg deposition of 1967 brood year pink salmon that disappeared from three areas of Sashin Creek and from the entire stream by 1 October 1967, 1 December 1967, and 25 March 1968.

Area	Estimated percentage of potential egg deposition disappearing		
	By 1 Oct.	1 Oct. to 1 Dec.	1 Dec. to 25 Mar.
Upper	53	4	27
Middle	50	6	24
Lower	62	1	24
Entire stream[1]	55	4	25

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas

TABLE 8.—Estimated densities of all eggs and alevins (live and dead) in three areas of Sashin Creek on 1 December 1967 and 25 March 1968, and percentage that disappeared between the two dates.

Area	Number of eggs and alevins per square meter on		Percentage that disappeared between dates
	1 Dec	25 Mar	
Upper	1,714	647	62
Middle	1,591	702	56
Lower	989	350	65

or alevins to disappear from streambed gravels may or may not have been the initial cause of death.

It is unlikely that turbulent streamflow, streambed shifting, or predation were the reasons that 1967 brood year eggs or alevins disappeared between early December and late March. Streamflows were generally low, and although an intermittent ice cover was present on Sashin Creek during January, February, and March, there was no indication of streambed shifting because of ice scouring. A series of short metal stakes driven into the streambed throughout the stream in November to mark coho salmon, *O. kisutch*, redds was still in place in March, indicating that no streambed shifting had occurred.

Most fish in Sashin Creek that could eat pink salmon eggs and alevins (juvenile coho salmon; rainbow trout, *Salmo gairdneri*; Dolly Varden, *Salvelinus malma*; and coastrange sculpin, *Cottus aleuticus*) are essentially dormant during the winter when water temperatures are low. Chapman and Bjornn (1969) have shown that resident stream salmonids may disappear into the substrate when water temperatures fall below 4.4 °-5.5 °C. I have observed similar behavior in Sashin Creek. Stream temperatures in Sashin Creek were below 4.4 °C from 13 December 1967 to 20 April 1968.

Water ouzels, *Cinclus mexicanus*, and mergansers, *Mergus merganser*, are occasionally present on Sashin Creek during the winter and could account for the disappearance of some eggs and alevins during open water periods. In considering the magnitude of the disappearance of 1967 brood year eggs and alevins in Sashin Creek between December and March, it is unlikely that the maximum possible loss to these sources is significant. This conclusion is based on the small numbers of mergansers and ouzels present, the amount of time the stream was covered with ice, and the large number of eggs or alevins that disappeared. Between two and five mergansers were noted in the vicinity periodically. When present, these birds spent much of their time in the intertidal portion of Sashin Creek or in the adjacent estuary. Only four of the smaller and territorial ouzels normally occur along the upper, middle, and lower areas of Sashin Creek in winter, and during periods of ice cover these birds go elsewhere. Based on periodic observations and temperature records, I estimate the stream was covered with ice approximately half the 1967-68 winter.

The estimated population of live and dead pink salmon eggs and alevins in Sashin Creek was 18.3 million on 1 December 1967 and 7.2 million on 25 March 1968 (Table 9), making a loss of 11.1 million eggs and alevins between the two dates. Because there is little evidence that the loss was caused by external factors that physically removed eggs or alevins from the streambed, the loss was likely due to factors within the intragravel environment.

The disappearance of 11.1 million eggs and alevins from the streambed between hatching and emergence led me to examine the relation between live eggs and alevins and dead eggs and alevins in the streambed. The densities of dead eggs and alevins in the upper, middle, and lower areas (Table 10) indicated that the numbers of dead eggs and alevins remained relatively stable between the time periods. This does not necessarily indicate that dead eggs in the streambed during one sampling period were still there during a later sampling period. Dead eggs can disappear at any time for many reasons, but can persist in a

TABLE 9.—Estimated population of live and dead pink salmon eggs and alevins in Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

Sample date	Millions of eggs and alevins in streambed		
	Live	Dead	Total
1 Oct. 1967	16.5	3.4	19.9
1 Dec. 1967	13.7	4.6	18.3
25 Mar. 1968	3.0	4.2	7.2

streambed for as long as 18 mo (McNeil et al. 1964). Once hatching is completed, no new dead eggs can be added to the streambed. Because hatching of live eggs was well underway on 1 December (about 35% completed), many of the dead eggs present in March had already died by 1 December (Table 10).

Most of the eggs and alevins that disappeared over the winter (about 11 million; Tables 7, 8, 9) were individuals that had been alive on 1 December because the number of dead eggs and alevins was essentially unchanged from December (4.6 million) to March (4.2 million) (Table 9). Mortality (in the form of disappearance) of live eggs and alevins in the streambed between 1 December and 25 March was 74% in the upper area, 77% in the middle area, and 85% in the lower area (Table 11). Of the 11.1 million pink salmon eggs and alevins that disappeared within the streambed between 1 December and 25 March, 10.7 million were alive on 1 December.

As previously mentioned, the cause of the disappearance of dead eggs and alevins in the streambed may differ from the cause of their deaths. This apparently occurred with the 1967 brood year pink salmon progeny in Sashin Creek, and I offer the following theoretical sequence to explain the major overwinter disappearance of eggs and alevins.

The greatest number of fry produced in Sashin Creek since 1940 was 5.9 million (Table 1). On 1 December 1967, 13.7 million live pink salmon eggs and alevins were in the Sashin Creek streambed (Table 9), a number that appears to exceed the capacity of the streambed for pink salmon fry production. I postulate that the high initial density of eggs led to a severe mortality of embryos in the early alevin stage, probably because of widespread oxygen privation or a combination of oxygen privation and a buildup of toxic metabolites. The rate of oxygen consumption by embryos increases steadily with development (Wickett 1954, 1962) and coincides with the general lowering of streamflows during the late fall, followed by stabilization of streamflows at near the normal winter levels.[4] This combination of conditions permitted the embryo population to survive up to, but not much beyond, the hatching period. These recently hatched dead alevins then apparently disappeared rapidly within the streambed through the combined action of biochemical decomposition and intragravel invertebrate scavenging. As I will show later, the rapid disappearance of recently hatched dead alevins in the streambed seems consistent with this hypothesis.

Although no intragravel water quality data are available from Sashin Creek during or shortly after hatching to support the above theory, a comparison of the rates of oxygen consumption by pink salmon embryos of various ages indicates that oxygen requirements do steadily increase during the hatching period. The rates of oxygen consumption reported for early stage eggs (7-26 days old) have ranged from 0.0003 mg O_2/egg per h (Wickett 1954) to 0.0005 mg O_2/egg per h (Brickell 1971). Brickell found that the rate of oxygen consumption by 35-day-old pink salmon eggs was 0.0018 mg O_2/egg per h, almost four times the rate he measured for 7-day-old eggs. Faintly eyed 38-day-old eggs had an oxygen consumption rate of 0.002 mg O_2/egg per h (Wickett 1962) while 7-day-old alevins had a consumption rate of 0.01 mg O_2/alevin per h (Wickett 1954).

TABLE 10.—Estimated densities of dead pink salmon eggs and alevins in three areas of Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

	Dead eggs and alevins per square meter					
	Upper area		Middle area		Lower area	
Date	Eggs	Alevins	Eggs	Alevins	Eggs	Alevins
1 Oct. 1967	129	0	310	0	264	0
1 Dec. 1967	223	7	459	18	266	11
25 Mar. 1968	196	69	334	108	199	43

TABLE 11.—Estimated densities of live pink salmon eggs and alevins in three areas of Sashin Creek on 1 December 1967 and 25 March 1968 and disappearance of live eggs or alevins between the two dates.

	Live eggs and alevins per square meter				Percentage of live eggs or alevins that disappeared between dates
	1 Dec. 1967		25 Mar. 1968		
Area	Eggs	Alevins	Eggs	Alevins	
Upper	899	575	0	382	74
Middle	769	345	0	260	77
Lower	463	249	0	108	85

[4]Seasonally, stream discharge in Sashin Creek is usually highest in fall and lowest in summer. Discharge in winter months may also be low, but is normally above summer levels. Because unseasonably low winter discharge could reduce oxygen delivery to embryos below the normal seasonal pattern, I compared the low monthly discharge during December, January, February, and March for 1967-68 with low discharge patterns in the same months for the period 1951-52 to 1966-67. The low mean monthly discharge from Sashin Creek during December, January, February, and March ranged from 18 to 62 ft^3/s and averaged 33 ft^3/s for the 16-yr period. The mean minimum monthly discharge during these same 4 mo in 1967-68 was 30 ft^3/s (U.S. Geological Survey 1969), suggesting that low streamflow levels during these months in 1967-68 were near normal.

In addition to the increasing oxygen requirements due to growth and development of live embryos, Brickell (1971) found that rates of oxygen consumption by dead intact pink salmon eggs exceeded those of early stage live eggs fourfold: 0.0018 mg O_2/whole dead egg per h versus 0.0004-0.0005 mg O_2/7-day-old live egg per h. He noted even greater oxygen consumption for dead eggs when the chorion was pierced or slit or the egg was fragmented: mean oxygen consumption of fragmented dead eggs in constant-flow cylinders was 0.017 mg O_2/egg per h, which exceeds the rate Wickett (1954) found for 7-day-old live alevins. It follows that alevins that die shortly after hatching, because of their soft, exposed, and readily oxidizable tissue, would have higher rates of oxygen consumption than whole intact dead eggs, live eggs, or early stage live alevins.

These increases in oxygen consumption upon death of developing pink salmon embryos are the rationale for suggesting a "snowball effect"—rapidly increasing deaths of embryos once lethal oxygen concentrations were approached. With high densities of live embryos already placing excessive demands on the oxygen and each death increasing the demand, the resulting heavy mortality could have caused fry production to plunge below that expected from lower initial egg densities—an excellent example of Neave's (1953) theory of compensatory mortality.

Disappearance of Dead Eggs Versus Disappearance of Dead Alevins

To test the hypothesis that dead alevins disappear within the streambed more rapidly than dead eggs, I conducted a small study in Sashin Creek in the winter of 1968-69 to consider the relative persistence of dead eggs and alevins in the streambed. A series of Vibert boxes (small plastic perforated containers), each containing a mixture of streambed gravel, 10 dead eggs, and 10 dead alevins (all from 1968 brood year pink salmon) were buried in Sashin Creek on 14 December 1968. The boxes were buried about 20.3 cm deep across a riffle in the middle study area. At irregular intervals, pairs of the boxes were removed from the streambed and the contents were preserved for examination.

Alevins disappeared from the Vibert boxes at a much faster rate than eggs (Table 12). Fewer than half of the original number of alevins were still recognizable at the end of 2 wk; after 37 days only one box contained identifiable alevins. Although the dead alevins disappeared rapidly, only a few of the dead eggs disappeared. In a study to determine whether certain stonefly numphs were predators or scavengers on salmon eggs and alevins, Ellis (1970) found in one experiment that dead pink salmon alevins buried in Vibert boxes in a stream essentially disappeared within a 2-wk period.

TABLE 12.—Contents of Vibert boxes with dead pink salmon eggs and alevins buried in Sashin Creek streambed between 14 December 1968 and 14 April 1969.[1]

No. of days buried	Eggs recovered	Alevins recovered	Invertebrates recovered	
			Insect larvae[2]	Planarian worms[3]
0	20	20	0	0
9	20	10	14	4
16	20	4	37	20
24	20	2	40	34
30	20	1	27	144
37	20	4	36	11
44	20	0	55	5
51	19	0	70	3
71	19	0	196	4
86	20	2	72	9
96	20	0	135	6
109	20	0	149	29
121	19	0	102	36

[1]Each box originally contained 10 dead eggs and 10 dead alevins. Two boxes were removed on each sample date and the contents combined for reporting.
[2]Of all insect larvae recovered, 80% were Plecoptera, 16% Diptera, 3% Trichoptera, and 1% Ephemeroptera.
[3]Tentatively identified as *Polycelis borealis*, a species that Kenk (1953) commonly found in clear cold streams in southern parts of Alaska.

Concurrently with the rapid disappearance of dead alevins from the buried boxes was a rapid buildup of invertebrates in the boxes. Although invertebrates are commonly found with salmon embryos (Briggs 1953; McDonald 1960; Nicola 1968), it is frequently impossible to determine if predation or scavenging is occurring. Although some groups of stonefly nymphs are known to attack live salmon embryos (Stuart 1953; Claire and Phillips 1968), Ellis (1970) concluded that nymphs of the carnivorous genus *Alloperla* were basically scavengers rather than predators.

In addition to various insect larvae, a planarian worm tentatively identified as *Polycelis borealis* was commonly found in the boxes buried in Sashin Creek (Table 12). Little is known on the biology or life history of this planarian, but under favorable conditions it appears to rapidly increase its numbers in the streambed, and thus may be particularly important in removing dead alevins. I have observed successive seasonal increases in the relative abundance of planarians in samples taken from the Sashin Creek streambed with the hydraulic sampler in the fall, winter, and spring. Total counts of planarians removed from the streambed with the hydraulic sampler are not pos-

sible,[5] but partial counts indicated that by March the densities of planarians in some parts of Sashin Creek commonly reached several thousand per square meter. A similar seasonal increase in streambed populations of planarians concomitant with the seasonal occurrence of sockeye salmon, *O. nerka*, embryos has been noted elsewhere.[6]

In Sashin Creek there is little doubt that high planarian populations are related to the presence of salmon eggs and alevins, because planarians are scarce in streambed gravels above the impassable falls where salmon do not spawn. However, the precise role of these organisms in the ecology of spawning beds is unknown. To learn something about the role of planarians, I conducted tests with various combinations of planarians and live and dead salmon eggs and alevins in experimental containers. In these tests planarians did not prey on and were not toxic to live embryos, nor did they feed on dead eggs unless the chorion was broken and the egg contents exposed.

EVIDENCE OF OVERSEEDING

In assessing the probability of streambed overseeding in Sashin Creek in the 1967 brood year, it is most useful to compare fry production in 1967-68 with production in other years. Since 1940, production has varied from 50 fry to almost 6 million fry; corresponding parent escapements varied from 8 to 92,085 (Table 1). Only three escapements exceeded that of 1967, and only one of these (1940) produced more fry (about 0.4 million more) (Table 1). When the numbers of fry are plotted against potential egg deposition, a dome-shaped fry production curve is derived for Sashin Creek (McNeil 1969). The relative position of fry production for the 1967 brood year falls near the descending limb of the curve; fry production from the 1941 and 1942 brood years indicates a continuing decrease in fry production as escapements increased (Figure 2).

Data collected since 1961 on the density of eggs in the three study areas at the end of spawning provide a means of more precisely defining the fry production potential of the stream. Plotting fry production as a function of actual egg deposition for each area produces curves that suggest the potential maximum fry production in the upper and middle areas is around 500 fry/m² and the potential in the lower area is about half that number (Figure 3). In 1967 the actual density of eggs deposited considerably exceeded twice the theoretical maximum fry production in all three areas and the fry production was considerably below the maximum; it appears that overseeding occurred in 1967.

Until 1967 the timing of entry of adults into Sashin Creek had usually been an accurate indicator of the freshwater survival of progeny (Merrell 1962; McNeil 1968; Ellis 1969). The presumed biological basis for the correlation between early spawning and high survival was that embryos de-

[5]When large numbers of planarians are excavated with the hydraulic sampler, many elongate their bodies and pass through the meshes of the collecting net.

[6]W. L. Hartman, W. R. Heard, and C. W. Strickland. 1962. Red salmon studies at Brooks Lake biological field station, 1961. Unpubl. manuscr. on file, NWAFC Auke Bay Lab. NMFS, NOAA, P.O. Box 155, Auke Bay, Alaska.

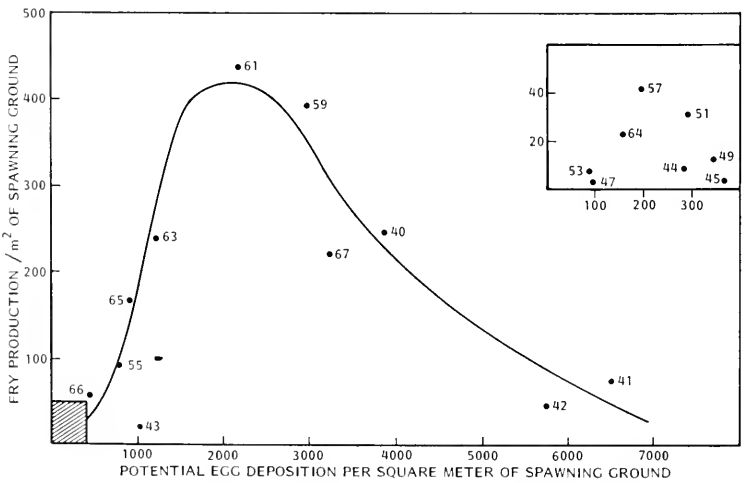

FIGURE 2.—Production of pink salmon in Sashin Creek, 1940-67. The shaded area in the lower left is shown on a larger scale in the upper right corner. Nine generations of the even-year line 1946-62 were excluded because fry productions were all $<1/m^2$. Adult escapement in these years was correspondingly low. The curve (modified from McNeil 1969) is fitted by eye.

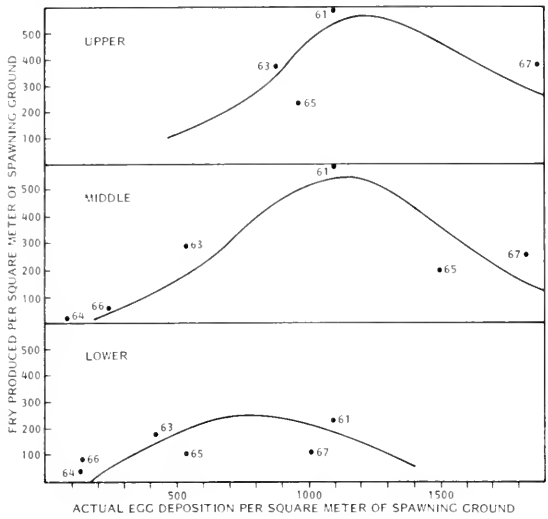

FIGURE 3.—Production curves for pink salmon in three study areas of Sashin Creek, 1961-67, showing relation between number of eggs in the streambed at the end of spawning and number of fry produced. Spawning did not occur in all areas in all years. Location of the 1961 point on the abscissal axis is not precise: success of spawning that year was based on subjective estimates (see McNeil et al. 1964). Curves are fitted by eye.

veloping initially at warmer temperatures had a survival advantage over those developing initially at cooler temperatures (Merrell 1962). In Sashin Creek, spawning closely follows the time of entry into the stream, so that early entry implies early spawning. Although the 1967 spawners entered Sashin Creek on the second earliest date on record, freshwater survival fell well below the predicted level (Figure 4). From the predicted freshwater survival of about 18% shown in Figure 4, the 1967 spawners should have produced 8 million fry.

On the basis of the relation of survival to time of spawning, McNeil (1969) suggested the dome-shaped freshwater production curve for Sashin Creek (Figure 2) may be the result of large escapements, more superimposition, and replacement of the more viable eggs from early spawning by less viable eggs from later spawning. From evidence available, there is little doubt that in Sashin Creek, progeny from early spawners have survival advantages over progeny from late spawners. I suggest, however, that when escapements are large, a point is reached where the number of eggs in the streambed determines ultimate survival, regardless of when spawning occurs.

The local climate and its resulting effects in the stream are extremely variable and have a marked influence on what actually constitutes an overseeded spawning bed at a specific time. Climate influences efficiency of spawning through variations in streamflows, so that overseeding does not occur at a fixed number of spawners. Similarly, streambed overseeding results from a dynamic interaction between the density of eggs in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and prevailing climatic influences on the intragravel environment during the 6 to 8 mo eggs and alevins are in the streambed. Overseeding of streambed gravels will occur at lower egg densities when climatic influences (rainfall, stream discharge, ice cover, etc.) are more adverse to the intragravel environment.

Perhaps the most convincing evidence of streambed overseeding in Sashin Creek is the seasonal change in instantaneous (monthly) mortality coefficients of the 1963, 1965, and 1967 brood

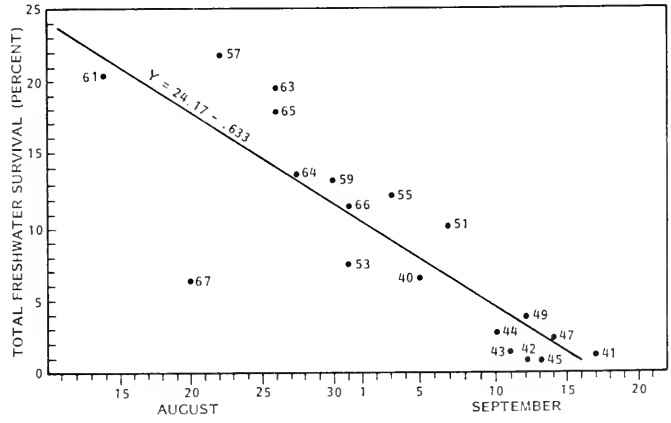

FIGURE 4.—Relation of freshwater survival of pink salmon in Sashin Creek to date when 50% of spawners had entered the stream. Data are from period 1940 to 1967; escapements<1,000 adults are excluded. The curve $Y = 24.17 - 0.633X$ fitted by least squares, where $X = 0$ corresponds to 10 August. Numbered points identify brood years (modified from McNeil 1968).

year progeny (Figure 5). Mortality coefficients for 1963 and 1965, the only years besides 1967 when estimates of live eggs and alevins were made after spawning, at hatching, and before emergence, are from McNeil (1968); the equation and notation for computing the instantaneous mortality coefficients for the 1967 brood year follow McNeil (1966). Time intervals assigned the three periods were 1.4 mo (from potential egg deposition through spawning), 2.0 mo (from spawning to hatching), and 3.7 mo (from hatching to emergence). The survival percentages by time periods are given in Table 6.

The impact of the heavy mortality between hatching and emergence in 1967 brood year progeny is evident in Figure 5. Monthly mortality coefficients during spawning were also high in 1963 and 1967 (0.76 and 0.71); the lower mortality during spawning in 1965 (0.31) probably reflects efficient spawning during the low streamflow condition prevailing that year (McNeil 1968). Mortality from spawning to hatching was similar, but mortality from hatching to emergence was strikingly different in each of the 3 yr (Figure 5). McNeil (1968) suggested the increase in overwinter mortality of 1965 brood year progeny (0.26) over 1963 brood year progeny (0.07) might have been related to a delayed mortality from low concentrations of dissolved oxygen in early embryo development during drought conditions in late summer and early fall in 1965. The number of spawners in 1967 was more than double the number in 1963 and 1965 (Table 1). The overwinter mortality of 1967 brood year progeny (0.42) was considerably higher than the high mortality of the 1965 brood year (0.26). The heavy overwinter mortality experienced by the 1967 brood year progeny may also have been caused by low dissolved oxygen concentrations. However, because no drought conditions existed while the progeny were in the gravel, these poor oxygen conditions probably resulted from the high density of eggs and alevins in the streambed.

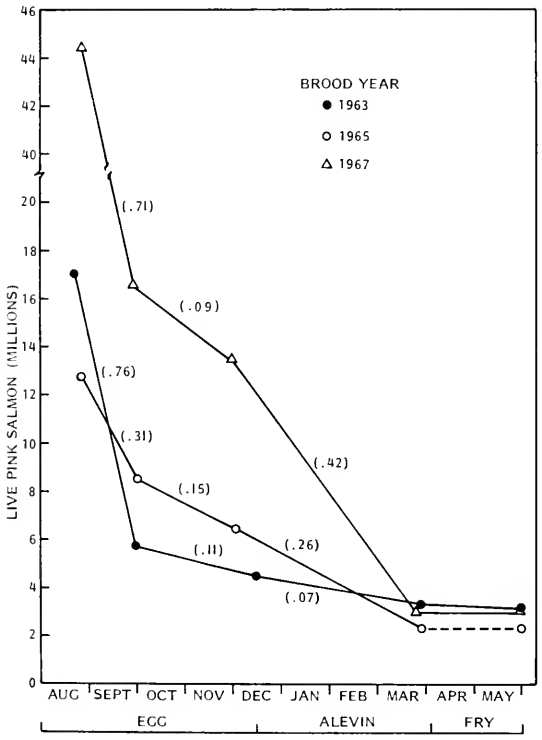

FIGURE 5.—Number of live pink salmon in Sashin Creek at the beginning and end of three periods in freshwater for 1963, 1965, and 1967 brood years. Numbers in parentheses show instantaneous monthly mortality coefficients from the egg through alevin stages. Mortality during fry migration (April and May) for the 1963 and 1967 brood years was negligible when measured as the difference between streambed and weir estimates of total fry production. The dotted extension of the 1965 brood year assumes no mortality during this period.

SUMMARY

1. In 1967, 38,067 pink salmon spawned in Sashin Creek on Baranof Island, Alaska. Fifty-two percent of the spawners (19,639) were females; mean fecundity was 2,260 eggs/female and the potential number of eggs available for deposition totaled 44.4 million.

2. Entry of spawners into the stream was the second earliest on record; based on the previously consistent relation between time of entry and freshwater survival, the production of fry should have been greater than any previously recorded, but the 3 million fry produced were less than half the predicted number.

3. Mean female densities on the spawning grounds were 1.74/m² in the upper area, 1.62/m² in the middle area, and 1.17/m² in the lower area. Densities were higher in the upper area at the beginning of spawning before significant levels of spawning occurred in the middle or lower areas. The tendency for spawners in the odd-year line to utilize the upper area of Sashin Creek may be due to genetic factors, including timing of escapements, and possibly differential marine survival favoring fry produced in the upper area.

4. Survival of progeny of the 1967 spawners was determined a) from stream entry to end of spawning, b) from end of spawning to hatching, c) from hatching to shortly before fry emergence, and d) from shortly before emergence to emergence and downstream migration of fry. In general, survival in each of these time periods was greatest in the upper area, lowest in the lower area, and intermediate in the middle area, a pattern consistent with previous survival studies at Sashin Creek. Total freshwater survival from potential egg deposition to preemerged fry was 10%, 7%, and 4% in the upper, middle, and lower areas, respectively, and 6.8% for the entire stream. The total number of migrating fry agreed closely with the estimates of preemerged fry in the streambed in late March.

5. Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins disappeared within Sashin Creek streambed; 10.7 million of these were alive on 1 December. The high densities of eggs and alevins in the streambed after spawning and at hatching are believed to exceed the streambed capacity for fry production. High overwinter mortalities appear to have occurred shortly after hatching, probably from critical levels of dissolved oxygen in intragravel water. Critical oxygen levels apparently developed under average winter streamflow conditions due to the high biochemical oxygen demand placed on the streambed by high egg and alevin densities.

6. Recently hatched dead alevins disappear rapidly within the streambed because of biochemical decomposition and invertebrate scavenging. In comparison with dead alevins, dead eggs disappear slowly. In Sashin Creek, insect larvae and a planarian, probably *Polycelis borealis*, may be particularly important in removing dead salmon eggs and alevins from the streambed.

7. Several aspects of the historical patterns of pink salmon fry production in Sashin Creek suggest that streambed overseeding occurred in 1967. Fry production from the 1967 spawners falls on the descending limb of the fry production curves, both for the stream as a whole (since 1940) and for the individual stream areas (since 1961). From the historical pattern of time of adult entry and resulting freshwater survival, freshwater survival of 1967 brood year progeny should have been around 18% (or a production of 8 million fry). Survival of progeny during spawning and between spawning and hatching was adequate to reach these predicted levels. Overwinter mortalities (between hatching and emergence), however, were higher than any previously recorded. Compensatory losses during this period were probably due to the presence of too many eggs and alevins in the gravel for existing environmental conditions—streambed overseeding.

8. Overseeding does not invariably occur at some precise density of eggs, but rather is a dynamic interaction between densities of eggs and alevins in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and the prevailing climatological features during the 6- to 8-mo period eggs and alevins reside in the streambed.

ACKNOWLEDGMENTS

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VERTICAL DISTRIBUTION AND PHOTOSENSITIVE VESICLES OF PELAGIC CEPHALOPODS FROM HAWAIIAN WATERS

RICHARD EDWARD YOUNG[1]

ABSTRACT

Vertical distribution data were obtained for 47 species of pelagic cephalopods off Oahu, Hawaii. Peaks in species richness occurred at 500-800 m during the day and in the upper 300 m at night. Over 80% of the individuals occurred in the upper 250 m at night. Approximately 60% of the species underwent diel vertical migration, and most of these migrated into the upper 250 m. In five of nine groups of closely related species, clear differences in habitat were found.

Deepwater spawning appeared to occur in a variety of cephalopods. Two of the bathypelagic octopods brooded their young at or above the upper limit of the remaining adult population. In doing so, the extent of the upward migration of newly hatched individuals was reduced.

Photosensitive vesicles occurred in all species. These organs probably detect downwelling daylight for regulating vertical migration and counterillumination. The vesicles also appeared to form an elaborate system for monitoring bioluminescent light from the animal's own photophores, from within the mantle cavity, and from other animals located outside the visual field.

Cephalopods must occupy a wide variety of ecological roles in the pelagic realm of the open ocean: the highest diversification of families and genera is found in this environment. In order to understand these roles, the vertical distribution of these animals must be determined. A number of papers have treated various aspects of the vertical distribution of oceanic cephalopods (e.g., Pearcy 1965; Clarke 1969; Roper 1969; Gibbs and Roper 1971; Clarke and Lu 1974, 1975; Lu and Clarke 1975a, b; Roper and Young 1975). Their vertical habitats, however, remain poorly known.

Data on the vertical distribution of cephalopods is difficult to obtain: many species are uncommon, and some avoid small trawls. In this study an opening-closing net (modified Tucker trawl) provided unambiguous depth data, and a slightly larger open net (3-m Isaacs-Kidd midwater trawl) added considerable additional data; nevertheless, fast-swimming species were poorly sampled.

Extraocular photoreceptive organs, the photosensitive vesicles, were examined in each species for clues that would indicate the role of light in regulating vertical distribution patterns. The organs in squid, known as the parolfactory photosensitive vesicles, lie near the brain within the confines of the cephalic cartilage. In octopods the organs, known as epistellar photosensitive vesicles, lie within the mantle cavity adjacent to the stellate ganglia. The photosensitive vesicles are paired organs. Each organ, as the name implies, is generally composed of a large number of small vesicles. The individual vesicles contain photosensitive cells similar to those of the retina, and their photoreceptive nature has been well established (Nishioka et al. 1966; Mauro and Baumann 1968; Mauro 1977). The specific functions of the photosensitive vesicles are unknown in both neritic and oceanic cephalopods although many suggestions have been made (see Packard 1972).

Several papers discussing the relationship of vertical distribution to eye structure, bioluminescence and/or development of photosensitive vesicles in selected species have already appeared (Young 1972a, 1973, 1975a, c, d, 1977). Some data on distribution taken during the initial phases of this program have been published by Roper and Young (1975). This paper examines the vertical distribution of all pelagic cephalopods taken off Hawaii and the morphology and orientation of their photosensitive vesicles.

MATERIALS AND METHODS

Specimens were collected off the island of Oahu in the Hawaiian archipelago at long. 158°20′W, lat. 21°20′N over depths between 1,500 and 4,000 m. Collections were made from September 1969 to November 1974 primarily from the RV *Teritu*. Over 3,300 specimens were taken in horizontal tows during about 1,000 h of trawling time.

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Cephalopods were collected primarily with two types of nets: a 3-m opening-closing modified Tucker trawl and a 3-m Isaacs-Kidd midwater trawl (IKMT). Details of the trawling with the Tucker trawl are given by Walters (1976). When the Tucker trawl failed to close or close completely, the trawl was considered an open tow. Tows usually were made at 5 to 6 km/h for a period of 3 h. Twilight periods were generally avoided. Tows made with net closed indicated the catch contained almost no contamination. Contamination from previous tows was minimized by carefully cleaning the net after each tow. The trawl tended to wander vertically when open; this was most severe in deep tows. During the latter part of the program, acoustic depth telemeters allowed trawl depths to be continuously adjusted and greatly reduced wandering. The distribution figures indicate the extent of this wandering. Trawl depths usually were determined with a time-depth recorder attached to the trawl.

Clarke (1973) discussed trawling methods with the IKMT. The trawl was lowered quickly then towed horizontally at 5 to 6 km/h for usually 2 h. Retrieval was rapid with the ship moving slowly ahead. Vertical wandering of the net was not as serious as with the Tucker trawl. All specimens captured with the IKMT were assumed to come from the modal trawling depth of the net, or if no clear mode was present, from the midpoint of the effective vertical range of the tow. The occasional capture of a specimen during setting or retrieval of a net results in an anomalous depth record below the animal's normal habitat. Contamination of the catch by animals from previous tows occasionally occurred with the IKMT. This contamination is especially serious as the error may be impossible to detect.

IKMT data for a few of the most abundant species are presented both as catch per trawling effort and as actual catch figures (Table 1). The remaining distribution figures are designed to show animal size vs. depth relationships and to indicate the precision and reliability of the data (e.g., fishing range of the tow, open or opening-closing tow). As a result, corrections in the data for unequal sampling at various depths could not be made. This bias was especially critical at depths <400 m during the day and at depths >1,000 m during the day and night where sampling was low. The magnitude of this error can be determined from Table 2, which lists sampling time in each 100-m depth interval.

Depth data for most species taken over the entire trawling period have been combined. Therefore, short-term variation in depth distributions may be obscured. Where sufficient data exist to determine general distribution patterns based on Tucker trawls alone, these data are presented separately. For species with insufficient data, data from both trawls are combined in the figures. In most cases larvae, which usually have a different vertical distribution than adults, have been excluded from the distribution figures and the

TABLE 1.—Depth distribution, capture rates, and numbers of the most abundant cephalopod species captured by the Isaacs-Kidd midwater trawl. Day captures for *Pterygioteuthis giardi* are included in Figure 4. R = capture rate in numbers per 1,000 m^3 of water sampled. N = actual number captured. ND = no data.

	Day						Night							
	Abraliopsis sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Abraliopsis* sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Pterygioteuthis giardi*	
Depth (m)	R	N	R	N	R	N	R	N	R	N	R	N	R	N
0-50	ND	ND	ND	ND	ND	ND	5.4	14	15.2	39	1.5	4	5.8	15
50-100	ND	ND	ND	ND	ND	ND	17.9	52	62.1	180	6.5	19	7.9	23
100-150	ND	ND	ND	ND	ND	ND	3.2	8	23.3	57	7.3	18	2.0	5
150-200	0	0	0	0	0	0	5.2	14	14.1	38	15.9	43	2.2	6
200-250	0	0	0	0	0	0	1.0	1	0	0	3.1	3	0	0
250-300	ND	ND	ND	ND	ND	ND	1.0	1	1.0	1	6.5	6	4.3	4
300-400	3.0	4	2.3	3	6.9	9	0	0	0	0	0	0	0	0
400-500	10.9	14	42.3	54	14.1	18	4.9	3	4.9	3	4.9	3	0	0
500-600	7.4	9	72.2	87	20.7	25	3.4	2	6.9	4	5.1	3	0	0
600-700	22.8	26	8.7	10	14.9	17	0	0	1.4	1	0	0	0	0
700-800	1.0	2	5.3	10	3.2	6	2.8	3	0	0	0	0	0	0
800-900	3.6	3	8.5	7	1.2	1	0	0	0	0	0	0	0	0
900-1,000	2.1	2	1.0	1	2.1	2	0	0	0	0	0	0	0	0
1,000-1,100	1.5	1	20.1	13	1.5	1	0	0	0	0	5.4	1	0	0

TABLE 2.—Trawling time in minutes. Since trawls of two different sizes were used, a correction factor of 0.6 was applied to the trawling times of the Tucker trawl to compute the adjusted total trawling time. This factor represents the approximate difference in effective mouth areas of the two nets. Open tows = time of each tow was assigned to one depth. Opening-closing tows = time of each tow was apportioned among depth zones traversed by the trawl. IKMT = Isaacs-Kidd midwater trawl.

	Tucker trawl				IKMT		Total adjusted to IKMT	
	Open		Opening-closing		Open			
Depth (m)	Day	Night	Day	Night	Day	Night	Day	Night
0-50		1,091		939		2,562		3,780
50-100	180	1,112		614		2,897	108	3,932
100-150		781	27	591		2,442	16	3,265
150-200	144	530	84	870	130	2,689	267	3,529
200-250		536	186	320	177	944	289	1,458
250-300	146		31	871		911	106	1,434
300-350	180		203	514	452	605	682	913
350-400	180	180	460	407	839	552	1,223	904
400-500	360	502	1,529	1,413	1,276	605	2,409	1,754
500-600		376	1,748	927	1,204	577	2,253	1,359
600-700		133	1,683	1,420	1,139	714	2,149	1,646
700-800	313	220	1,638	838	1,862	1,052	3,033	1,687
800-900			1,244	519	820	179	1,566	490
900-1,000	180	30	709	184	917	179	1,450	307
1,000-1,100		182	464	64	646	182	924	330
1,100-1,200	195		230	156	180	195	435	289
1,200-1,300	200	300	380		180		528	180
1,300-1,400	10	256	234	98			146	212
1,400-1,500			67	106			40	64
1,500-1,600				30				18
1,600-1,700			8	38			5	23
1,700-1,800			104	267			62	160
1,800-1,900			84	228			50	137
1,900-2,000			48	28			29	17
2,000-2,100			15	27			9	16
2,100-2,200			72	29			43	17
2,200-2,300			43	33			26	20
2,300-2,400				8				5

text. Specimens captured during twilight periods, with a few exceptions, have also been excluded from the charts.

Species examined are listed in Table 3. Larvae or juveniles of several additional species were captured but are not included in this study. These are: *Tremoctopus violaceus*, *Argonauta* sp., *Cranchia scabra*, *Thysanoteuthis rhombus*, *Onykia* sp. One pelagic species reported from Hawaii by Berry (1914), *Iridoteuthis iris*, was not taken. This species belongs in the genus *Nectoteuthis* and probably lives in association with the ocean floor.[2]

Photosensitive vesicles of most species were sectioned. Material was fixed either in glutaraldehyde-osmium tetroxide or Bouin's solution and was embedded in Epon 812[3] or paraffin. All vesicles sectioned contained cells with photosensitive processes and, therefore, appeared to be functional. In only a few cases did the general histology of the organs add to our understanding of their function. As a result, histological details are not included for most species.

In order to quantify the size of vesicles, an attempt was made to obtain dry weights. Many types of vesicles proved difficult to remove and clean completely. Vesicles from a series of similar-sized *Pyroteuthis addolux*, which are easily removed, were weighed and found to vary by a factor of 1.5. Because of the large individual variations and inaccuracies due to difficulties in isolating many types of vesicles, this method of quantification was abandoned. As a result, camera lucida drawings of photosensitive vesicles provide the only measure of organ size: their relative size can be approximately determined by comparison with the brain size.

RESULTS

Pyroteuthis addolux Young 1972

Vertical Distribution

During the day, 39 specimens captured by the Tucker trawl indicate a vertical range for this

[2]Roper, C., and R. Young. Review of the Heteroteuthinae. Unpubl. manuscr.

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

TABLE 3.—Species of cephalopods considered.

Order Teuthoidea
- Family Enoploteuthidae
  - *Pyroteuthis addolux* Young 1972
  - *Pterygioteuthis microlampas* Berry 1913
  - *Pterygioteuthis giardi* Fischer 1895
  - *Abralia trigonura* Berry 1913
  - *Abralia astrosticta* Berry 1909
  - *Abraliopsis* sp. A, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. B, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. C, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. A, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. B, n.sp. being described by L. Burgess
  - *Thelidioteuthis alessandrinii* (Verany 1851)
- Family Ommastrephidae
  - *Symplectoteuthis oualaniensis* (Lesson 1830)
  - *Hyaloteuthis pelagicus* (Bosc 1802)
  - *Nototodarus hawaiiensis* (Berry 1912)
- Family Histioteuthidae
  - *Histioteuthis dofleini* (Pfeffer 1912)
  - *Histioteuthis celetaria pacifica* (Voss 1962)
  - *Histioteuthis* sp. under study by N. Voss
- Family Neoteuthidae
  - *Neoteuthis* sp.
- Family Bathyteuthidae
  - *Bathyteuthis abyssicola* Hoyle 1885
- Family Ctenopterygidae
  - *Ctenopteryx siculus* (Verany 1851)
- Family Onychoteuthidae
  - *Onychoteuthis compacta* (Berry 1913)
- Family Octopoteuthidae
  - *Octopoteuthis nielseni* Robson 1948
- Family Cycloteuthidae
  - *Cycloteuthis serventyi* Joubin 1919
  - *Discoteuthis laciniosa* Young and Roper 1969
- Family Brachioteuthidae
  - *Brachioteuthis* sp.
- Family Chiroteuthidae
  - *Chiroteuthis* n.sp., being described by Roper and Young
  - *Chiroteuthis picteti* Joubin 1894
  - Chiroteuthidae n.gen., n.sp. being described by Roper and Young
  - *Planktoteuthis lippula* (Chun 1908)
  - *Grimalditeuthis bomplandi* (Verany 1837)
- Family Mastigoteuthidae
  - *Mastigoteuthis famelica* (Berry 1909)
  - *Mastigoteuthis inermis* Rancurel 1972
- Family Joubiniteuthidae
  - *Joubiniteuthis portieri* (Joubin 1912)
- Family Cranchiidae
  - *Liocranchia valdiviae* (Chun 1906)
  - *Liocranchia reinhardti* (Steenstrup 1856)
  - *Leachia pacifica* (Issel 1908)
  - *Phasmatopsis fisheri* (Berry 1909)
  - *Taonius pavo* (LeSueur 1821)
  - Sandalops melancholicus Chun 1906
  - *Helicocranchia beebei* Robson 1948
  - *Bathothauma lyromma* Chun 1906

Order Octopoda
- Family Bolitaenidae
  - *Eledonella pygmaea* Verrill 1884
  - *Japetella diaphana* Hoyle 1885
- Family Amphitretidae
  - *Amphitretus pelagicus* Hoyle 1885
- Family Vitreledonnelidae
  - *Vitreledonnella richardi* Joubin 1918

Order Vampyromorpha
- Family Vampyroteuthidae
  - *Vampyroteuthis infernalis* Chun 1903

Order Sepioidea
- Family Sepiolidae
  - *Heteroteuthis hawaiiensis* (Berry 1909)

species of 375 to 510 m; most captures came from 450 to 500 m (Figure 1). IKMT data lumped into 100-m increments show most day captures between 400 and 700 m (Table 1). At night, 38 of the 41 specimens captured by the Tucker trawl indicate a vertical range of about 110 to 225 m; most specimens came from 150 to 200 m. Three specimens were captured during the night in opening-closing tows near their day habitat at depths between 360 and 480 m. Each of these three specimens was taken in a separate tow during a cruise in November 1972 within a few days of new moon. Although the upper 200 m was not sampled on this cruise, these captures indicate that at least part of

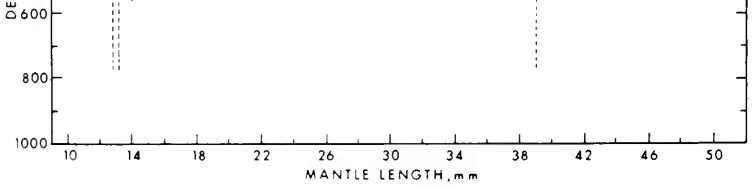

FIGURE 1.—Vertical distribution of *Pyroteuthis addolux*. Symbols for Figure 1 and subsequent figures: open circles represent day captures; closed circles represent night captures. A bar with a circle indicates an opening-closing tow with the bar representing the depth range of the tow and the circle the most likely depth of the capture (the modal depth, or if no clear mode is present, the midpoint of the vertical range of the tow). A circle without a bar indicates a capture in an open tow. A bar without an associated symbol indicates an open oblique tow. Such bars do not always intersect the zero depth line as some gradual oblique tows were made between specific depths. Solid bars represent night captures. Dashed bars represent day captures. A small dot represents a presumed contaminant.

the population was not migrating during this period. IKMT data lumped into 50-m increments show that most night captures were made between 50 and 200 m with peak catches between 150 and 200 m.

Photosensitive Vesicles (Figure 2A)

The organs are very similar to those described by R. E. Young (1977) in *Pterygioteuthis microlampas*. *Pyroteuthis addolux* has two sets of organs. The dorsal organs (the more dorsal set) lie embedded in the posterodorsal wall of the cephalic cartilage and adjacent to the optic lobes of the brain. Each ventral organ lies deeply embedded in the posteroventral surface of the cephalic cartilage. Except for a thin medial extension on each ventral organ, all organs are thick, compact, and approximately circular to square in outline. The histological structure of the dorsal and ventral organs is similar. The integument adjacent to both the dorsal and ventral organs lacks pigment and thereby forms distinctive "windows" for the passage of light.

Nerves from both dorsal and ventral organs enter the peduncle complex of the brain and their fibers disperse in the base of the peduncle lobe near its broad junction with the olfactory lobe.

Pterygioteuthis microlampas Berry 1913

Vertical Distribution (Figure 3)

The vertical distribution has been described by R. E. Young (1977). During the day, 48 specimens captured with the Tucker trawl indicate a depth range of 450 to 575 m; 85% of the specimens were taken between 450 and 500 m. IKMT data lumped into 100-m increments (Table 1) show most day captures between 400 and 600 m. At night 56 specimens taken by the Tucker trawl indicate a depth range of 25 to 180 m; nearly 85% of the captures were made between 50 and 105 m. IKMT data lumped into 50-m increments indicate a range of 0 to 200 m with a strong peak in the 50- to 100-m depth zone. The night distribution was not affected by moonlight (R. E. Young 1977).

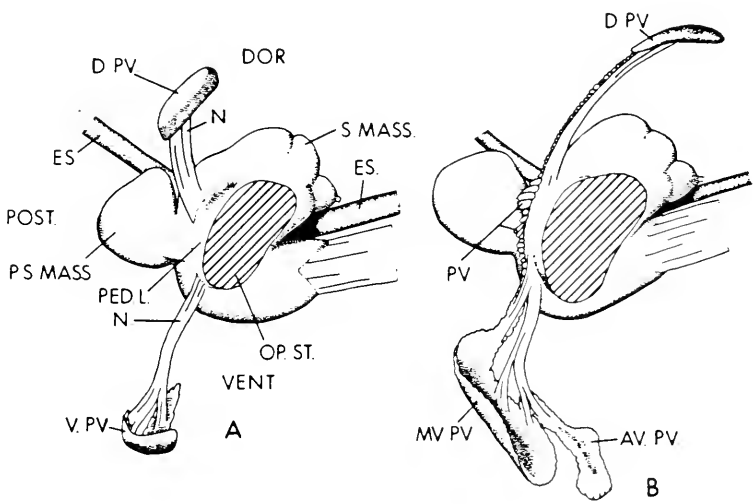

FIGURE 2.—A. Photosensitive vesicles of *Pyroteuthis addolux*. This illustration and most subsequent drawings show a side view of the brain. The optic stalk has been cut (as indicated by cross-hatching) and the optic lobe removed. The esophagus can be seen passing through the brain. Three major subdivisions of the brain are apparent (i.e., the supraesophageal mass, the posterior subesophageal mass, and the middle subesophageal mass.) A large nerve tract which extends anteriorly to the anterior subesophageal mass was cut (indicated by dotted line) and the latter portion of the brain is not shown. B. Photosensitive vesicles of *Abraliopsis* sp. B. Abbreviations for Figure 2 and subsequent figures of photosensitive vesicles: AV. PV.—Anteroventral photosensitive vesicles; C. PV.—central photosensitive vesicles; DOR.—dorsal; D. PV.—dorsal photosensitive vesicles; ES.—esophagus; GILL—gill; H. RET. M.—head retractor muscles; INT.—intestine; M. S. MASS—middle subesophageal mass of the brain; MV. PV.—midventral photosensitive vesicles; N.—nerve; OP. ST.—optic stalk; PED. L.—peduncle lobe; PIG. S.—pigment screen; POST.—posterior; P. PV.—posterior photosensitive vesicles; P. S. MASS—posterior subesophageal mass of the brain; PV.—Photosensitive vesicles; V. PV.—ventral photosensitive vesicles; S. MASS—supraesophageal mass of the brain; VENT.—ventral.

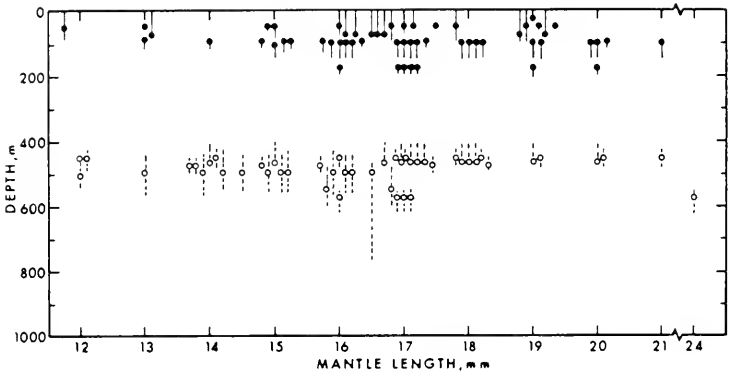

FIGURE 3.—Vertical distribution of *Pterygioteuthis microlampas*. From R. E. Young (1977). Symbols as in Figure 1.

Photosensitive Vesicles

The organs have been described by R.E. Young (1977). They are essentially the same as in *Pyroteuthis addolux*.

Pterygioteuthis giardi Fischer 1895

Vertical Distribution (Figure 4)

During the day 30 specimens captured from both trawls indicate a depth range from about 390 to 525 m; over 90% of the captures were made between 390 and 450 m. One IKMT tow captured eight badly damaged specimens at 630 m, well below their zone of maximum abundance. The previous tow had captured six specimens at 390 m that were in excellent condition; specimens from the deeper tow probably are contaminants. The depth distribution of this species may be biased by the relatively low sampling effort between 350 and 400 m.

At night, 39 captures with the Tucker trawl indicate a depth range of 15 to 180 m; over 75% of the specimens came from 15 to 50 m. IKMT data lumped into 50-m increments (Table 1) show the maximum abundance at depths of 0 to 100 m.

Photosensitive Vesicles

The organs are essentially the same as in *Pyroteuthis addolux*.

Abralia trigonura Berry 1913

Vertical Distribution (Figure 5)

Fifty specimens were captured by both trawls. Excluding presumed contaminants, the day captures were made between 390 and 650 m with nearly 80% between 450 and 560 m. At night captures were made between 30 and 200 m with over 75% between 50 and 100 m.

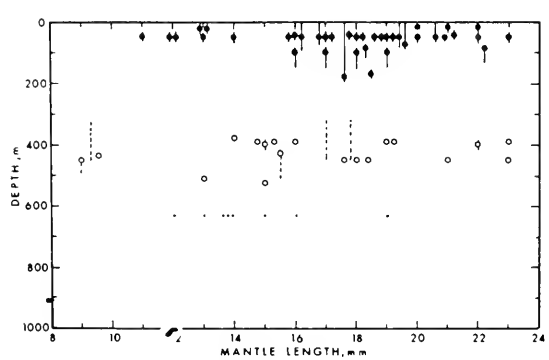

FIGURE 4.—Vertical distribution of *Pterygioteuthis giardi*. Symbols as in Figure 1.

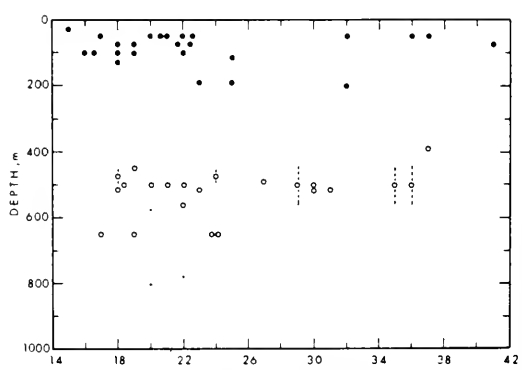

FIGURE 5.—Vertical distribution of *Abralia trigonura*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 6)

The arrangement of organs is similar to *Abraliopsis* sp. described by Young (1973). Four sets of organs are present; all lie adjacent to the cephalic cartilage. One set is located dorsally, one posteriorly, and two ventrally. Each dorsal organ is situated in a concavity of the cephalic cartilage at the posterodorsal edge of the head. The organ is compact, dorsoventrally flattened and circular to triangular in outline. The posterior organs are located on the posterior surfaces of the optic lobes. Each is approximately elliptical and very flat. The posterior organs have a strong yellow pigment which does not fade after fixation. Other organs contain an orange pigment that is lost after fixation. The posterior organs lie immediately anterior and lateral to the opaque liver and directly anterior to the attachment zone of the transparent head retractor muscles (Figure 6B). The ventral organs on each side consist of two, narrowly joined, flattened lobes. One of these, the anteroventral lobe, is located somewhat anterior and medial to the other. The anteroventral lobe has its medial and anterior ends in a deep depression of the cephalic cartilage. The anteromedial edge of each lobe nearly makes contact with its counterpart of the opposite side. The more posterior of the two lobes, the midventral lobe, lies between the ventral surface of the optic lobe and the cephalic cartilage.

Circular windows, similar to those described in *Abraliopsis* sp. (Young 1973), and characterized by a reduced number of chromatophores, are present above each dorsal organ. A large ventral window, totally lacking chromatophores, lies on the ventral surface of the head above the funnel and below the ventral vesicles.

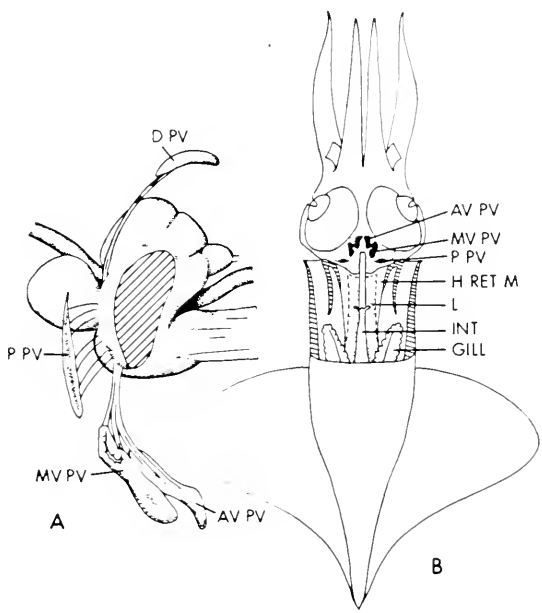

FIGURE 6.—A. Photosensitive vesicles of *Abralia trigonura*. B. Ventral view of *A. trigonura* with portion of mantle removed. This illustration shows the relationship between the posterior photosensitive vesicles, the opaque liver (L), and the mantle cavity. Abbreviations as in Figure 2.

Abralia astrosticta Berry 1909

Vertical Distribution

No specimens were captured during the present program. However, one specimen was taken in a gill net set overnight by T. Clarke on the bottom in 180 m. The National Marine Fisheries Service, NOAA, has captured 44 juveniles (7-38 mm ML (Mantle length)) in pelagic trawls between 10 and 130 m at night and 10 adults in a benthic shrimp trawl at 110 m at night near Hawaii. The type was captured in a bottom dredge between 354 and 650 m, presumably during the day. Roper and Young (1975) indicated that this animal lives near the ocean floor even when migrating.

Photosensitive Vesicles

The organs and associated windows are basically the same as in *A. trigonura*.

Abraliopsis sp. A

Vertical Distribution (Figure 7)

Sixty-seven specimens were captured. Exclud-

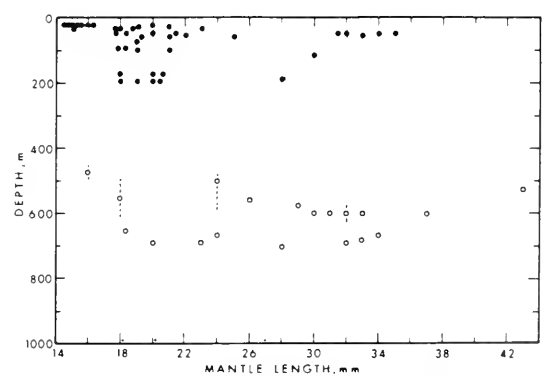

FIGURE 7.—Vertical distribution of *Abraliopsis* sp. A. Symbols as in Figure 1.

ing presumed contaminants, specimens captured during the day came from depths of about 475 to 700 m; 80% were taken between 550 and 700 m. At night, captures were made between about 20 and 200 m; nearly 80% were taken in the upper 100 m.

Photosensitive Vesicles

The organs and associated windows have been described in detail by Young (1973); they are similar to those of *Abralia trigonura*.

Abraliopsis sp. B

Vertical Distribution (Figure 8)

During the day, 23 specimens taken by the Tucker trawl indicate a depth range of 500 to 650 m; most captures came from 500 to 600 m. IKMT data lumped into 100-m increments indicate most specimens came from 400 to 700 m.

At night, 19 specimens from the Tucker trawl probably came from depths between 50 and 100 m. IKMT data lumped into 50-m increments show a strong peak in the 50- to 100-m interval. A few IKMT captures were made as shallow as 15 m.

Photosensitive Vesicles (Figure 2B)

The dorsal and anteroventral organs are similar to other species of *Abraliopsis* and *Abralia*. The posterior lobes, however, are absent, and the midventral lobes are enlarged and extended dorsally. In addition, a thin string of vesicles extends from each midventral lobe dorsally between the brain and the optic lobe to join with the dorsal lobe. The structure of this string is slightly variable, and in some specimens the vesicles found about at midbrain level are slightly enlarged and elongate (Figure 2B). The yellow pigment characteristic of the posterior lobes in related species does not occur in any of the lobes of this species.

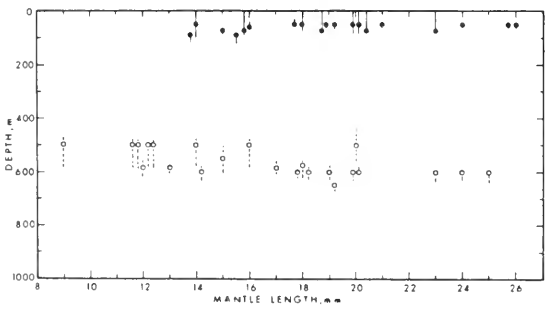

FIGURE 8.—Vertical distribution of *Abraliopsis* sp. B. Symbols as in Figure 1.

Abraliopsis sp. C

Vertical Distribution (Figure 9A)

Only 12 specimens were captured. During the day, five specimens were taken between 500 and 600 m. At night, all of the captures were made in the upper 100m.

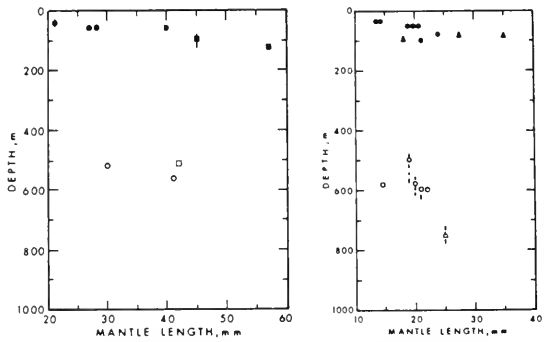

FIGURE 9.—A. Vertical distribution of *Enoploteuthis* sp. A (circles) and *Enoploteuthis* sp. B (squares). B. Vertical distribution of *Abraliopsis* sp. C (circles) and *Thelidioteuthis allesandrinii* (triangles). Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *Abralia trigonura* and *Abraliopsis* sp. A except that the posterior lobe is smaller, slightly more medially located, and continuous with the midventral organ. This latter connection, however, does not have the yellow pigment that the posterior organ possesses. Also, a few scattered vesicles lie on the posterior margin of the nerve from the dorsal organ.

Enoploteuthis sp. A

Vertical Distribution (Figure 9B)

During the day, two captures were made between 500 and 600 m; and at night, three captures were made in the upper 100 m.

Photosensitive Vesicles (Figure 10A)

The organs are similar to *Abralia trigonura*

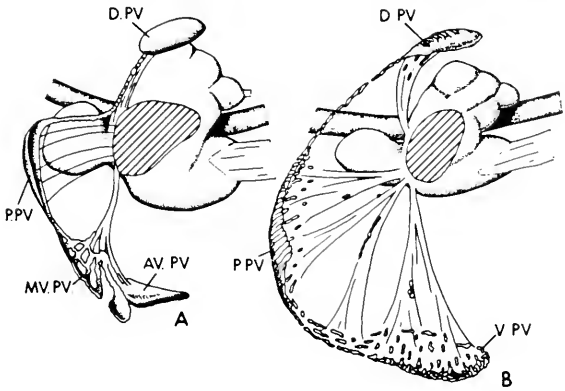

FIGURE 10.—A. Photosensitive vesicles of *Enoploteuthis* sp. A. B. Photosensitive vesicles of *Thelidioteuthis alessandrinii*. Abbreviations as in Figure 2.

with the following exceptions. The midventral organ has a more irregular shape, is less compact, and has a narrow connection with the posterior organ. The posterior organ is continuous with the dorsal organ via a strand of vesicles that extends over the optic lobe. Except for a short segment adjacent to the dorsal organ, this strand contains yellow pigment as does the posterior lobe.

Enoploteuthis sp. B

Vertical Distribution (Figure 9B)

One specimen was captured during the day at 515 m and three were taken at night between 50 and 150 m.

Photosensitive Vesicles

The vesicles are the same as those of *Enoploteuthis* sp. A except for some differences in the posterior organ. The posterior organ in *Enoploteuthis* sp. B is more elongate, more medially located on the optic lobe, and lacks yellow pigment.

Thelidioteuthis alesandrinii (Vérany 1851)

Vertical Distribution (Figure 9A)

During the day, one specimen was taken in an opening-closing tow between 720 and 780 m. At night, three specimens were taken in open tows between 80 and 100 m.

Photosensitive Vesicles (Figure 10B)

Three sets of organs, dorsal, posterior, and ventral, consist primarily of a loose association of variously shaped, mostly independent vesicles (Young 1977). The organs are broad, flat structures, with the greatest concentration of vesicles along the lateral margins of the organs. The organs lack yellow pigment.

Family Ommastrephidae

Symplectoteuthis oualaniensis (Lesson 1830)

Vertical Distribution

Except for larvae, only one specimen was captured in the midwater trawls. This specimen was taken at night by the IKMT which fished at 100 m. This fast-swimming squid normally avoids our trawls. Members of this species are commonly seen at the surface at night around the night-light and a number have been dipnetted. Little is known, however, of their day distribution, although Young (1975b) had assembled evidence which indicates that they live in the upper few hundred meters but may descend on occasion to great depths.

Photosensitive Vesicles (Figure 11A)

Three sets of organs are present: a dorsal, central, and ventral set. The ventral organ lies within the cephalic cartilage at the posterior end of the head and immediately above the posterolateral portion of the funnel. It consists of a series of flat,

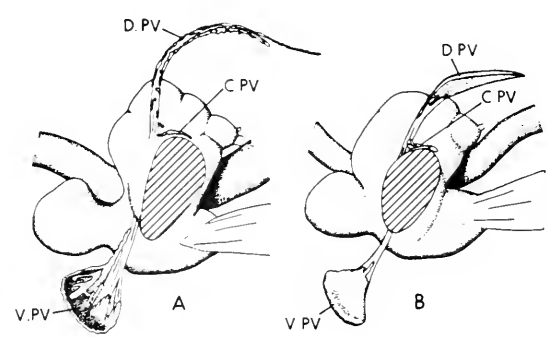

FIGURE 11.—A. Photosensitive vesicles of *Symplecoteuthis oualaniensis*. B. Photosensitive vesicles of *Hyaloteuthis pelagicus*. Abbreviations as in Figure 2.

elongate vesicles that are most numerous at its ventral end. The central organ consists of a few small, flat, elongate vesicles located on the dorsal surface of the optic stalk. The vesicles of the dorsal organ are scattered along a broad arching nerve that extends from the peduncle lobe dorsally then anteriorly along the dorsomedial margin of the optic lobe. The vesicles are flat and irregularly shaped.

Hyaloteuthis pelagicus (Bosc 1802)

Vertical Distribution

The single specimen captured was taken in an opening-closing tow between 1,700 and 2,200 m during the day. The specimen was a gravid female: the ovary was packed with mature eggs, the nidamental and oviducal glands were greatly enlarged, and numerous discharged spermatophores were attached to the lips surrounding the mouth. Specimens in similar condition as well as immature specimens have been captured frequently at a depth of about 100 m at night by the National Marine Fisheries Service, NOAA, in Honolulu using a large Cobb trawl. *Hyaloteuthis pelagicus* typically avoids our midwater trawls. The single day capture demonstrates that this species is capable of descending to great depths. Unfortunately, nothing is known of its normal day habitat.

Photosensitive Vesicles (Figure 11B)

Three sets of organs similar to those of *S. oualaniensis* are present. A small central organ lies just dorsal to the optic stalk and consists of a relatively small number of rather large vesicles. Each dorsal organ lies above the dorsomedial side of the optic lobe and is a large, compact triangular organ with irregularly shaped vesicles. The ventral organ is a flat, compact, oval organ which abuts against the cephalic cartilage above the lateral base of the funnel.

Nototodarus hawaiiensis (Berry 1912)

Vertical Distribution

No specimens have been taken in our midwater trawls; however, 63 specimens were captured in 40-ft shrimp trawls by the National Marine Fisheries Service. Specimens captured during the day came from depths of 230 to 710 m, although only a single capture was made below 420 m. Night captures range from 110 to 410 m. During the late summer and early fall, this species is commonly taken by dip net or near-surface jig at night off the island of Hawaii.

Photosensitive Vesicles (Figure 12A)

Three sets of organs are present similar to those in *S. oualaniensis* and *H. pelagicus*. The central organ is slightly larger than that of *S. oualaniensis* but is positioned similarly. The dorsal organ consists of a flat strip of vesicles that extends from the central organ dorsally to the cephalic cartilage. The margins of this organ are irregular, and thin strings of vesicles extend away from the organ at various places. Where the dorsal organ connects with the central organ, the two can be distinguished by the sizes of their individual vesicles: the small central organ consists of relatively few large vesicles, while the dorsal organ consists of numerous small vesicles. The ventral organ is compact, flattened, and somewhat club-shaped. It occupies about the same position as the corresponding organs in *S. oualaniensis* and *H. pelagicus*.

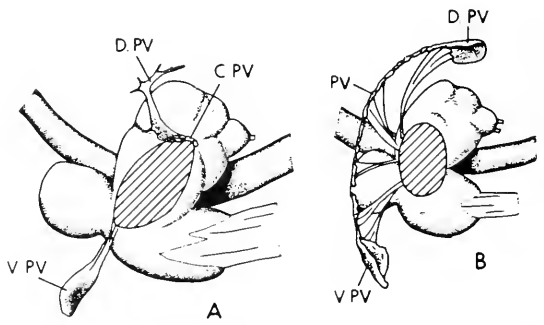

FIGURE 12.—A. Photosensitive vesicles of *Nototodarus hawaiiensis*. B. Photosensitive vesicles of *Histioteuthis dofleini*. Abbreviations as in Figure 2.

Family Histioteuthidae

Histioteuthis dofleini (Pfeffer 1912)

Vertical Distribution (Figure 13)

The vertical distribution of this species has been discussed by Young (1975c). The vertical range is 375 to 850 m during the day; over 80% of the captures came from depths of 500 to 700 m. At

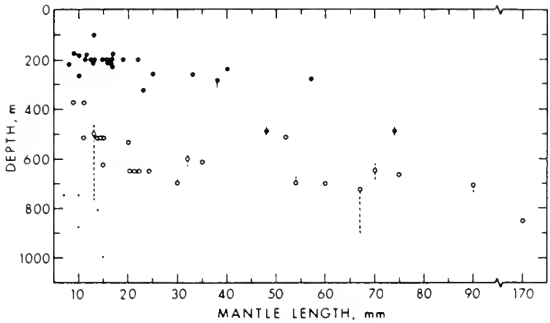

FIGURE 13.—Vertical distribution of *Histioteuthis dofleini*. From Young (1975c). Symbols as in Figure 1.

night, the range is 100 to 500 m; over 85% of the captures came from depths of 150 to 300 m. During both the day and night, larger individuals tend to be found at slightly greater depths.

Photosensitive Vesicles (Figure 12B)

Histioteuthis dofleini has two sets of vesicles, a dorsal and a ventral set, joined by a narrow strand of vesicles. The dorsal and ventral organs are flat and approximately the same size. The dorsal organs lie dorsal to the optic lobes, and the ventral organs lie above the lateral bases of the funnel (R. E. Young 1977).

Histioteuthis celetaria pacifica (Voss 1962)

Vertical Distribution (Figure 14A)

A single day capture came from 550 m. Four night captures came from depths of about 250 to 400 m.

Photosensitive Vesicles

The vesicles are similar to those of *H. dofleini* except that the dorsal and ventral organs are more compact.

Histioteuthis sp.

Vertical Distribution (Figure 14A)

Two day captures came from depths of 575 and 665 m, and four night captures were made between depths of 165 and 275 m.

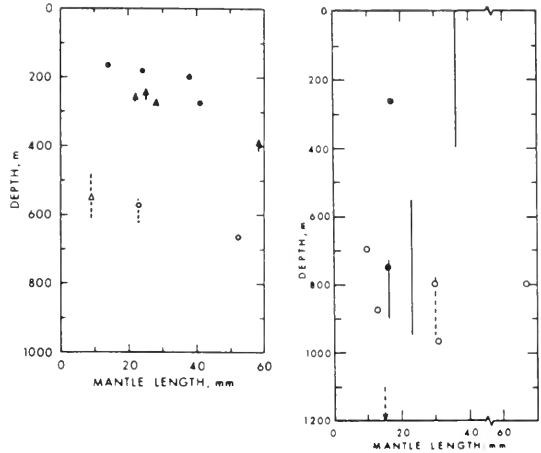

FIGURE 14.—A. Vertical distribution of *Histioteuthis celetaria pacifica* (triangles) and *Histioteuthis* sp. (circles). B. Vertical distribution of *Bathyteuthis abyssicola*. Symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *H. dofleini*.

Neoteuthis sp.

Vertical Distribution

A single small specimen was taken in an IKMT tow that fished between the surface and 350 m at night. Roper and Young (1975) reported nine specimens from the Atlantic Ocean taken in open tows between 1,300 and 2,000 m at night and one specimen taken in a closing net at 900 m at night.

Photosensitive Vesicles (Figure 15A)

Neoteuthis sp. has only one set of organs. Each organ consists of a small grapelike cluster of globular vesicles arising from the medioposterior surface of the peduncle lobe and extending ventrally below the optic stalk.

Bathyteuthis abyssicola Hoyle 1885

Vertical Distribution (Figure 14B)

Five of six specimens captured during the day were taken between 700 and 975 m. The remaining specimen was taken in an oblique IKMT tow that fished between 1,100 and 1,900 m. At night, two specimens were taken in the upper 400 m, a

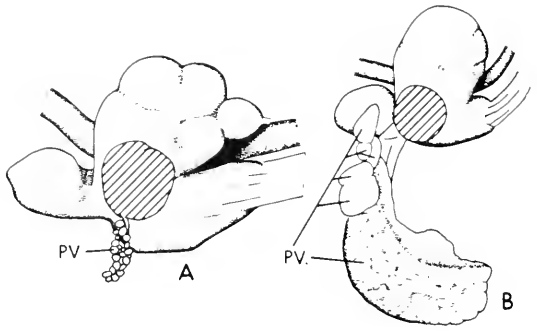

FIGURE 15.—A. Photosensitive vesicles of *Neoteuthis* sp. B. Photosensitive vesicles of *Bathyteuthis abyssicola*. Abbreviations as in Figure 2.

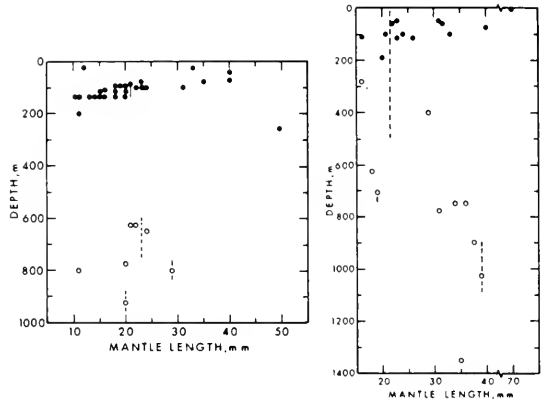

FIGURE 16.—A. Vertical distribution of *Ctenopteryx siculus*. B. Vertical distribution of *Onychoteuthis compacta*. Symbols as in Figure 1.

third was taken in an opening-closing tow at about 750 m, and the fourth in an open oblique tow that fished between 550 and 950 m.

Photosensitive Vesicles (Figure 15B)

The organs have been described in detail by Young (1972a). One set of very large organs is present. Each organ is located adjacent to the posteroventral surface of the eye and above the posterolateral edge of the funnel. Posterior to the organ the skin is only lightly pigmented and forms a "window."

Family Ctenopterygiidae

Ctenopteryx siculus (Vérany 1851)

Vertical Distribution (Figure 16A)

Seven of eight specimens captured during the day came from depths of about 625 to 800 m; the other specimen came from about 925 m. At night 28 specimens were captured between depths of 25 to 260 m; over 80% of the specimens were taken between 50 and 150 m.

Photosensitive Vesicles (Figure 17A)

Ctenopteryx sicula has a single pair of large and highly organized organs. Each organ consists of a single elongate and flattened but curved vesicle. Each organ extends from the posterior end of the supraesophageal mass, beneath the optic stalk, and anterior to the middle subesophageal mass where it joins with its counterpart from the opposite side. The organ, therefore, occupies a groove between the central brain and the optic lobes. The area where the two vesicles join lies just above the funnel approximately at the point where the funnel adductor muscles (bridles) attach to the cephalic cartilage. An iridophore sheath is continuous and encloses both organs in this region, but the vesicles do not actually fuse. That is, the lumen of each vesicle remains separate. The vesicles broaden slightly at their dorsal end and in the region of the junction. The anterodorsal walls of each vesicle are convex and lined with dense layers of iridophores; light enters through the

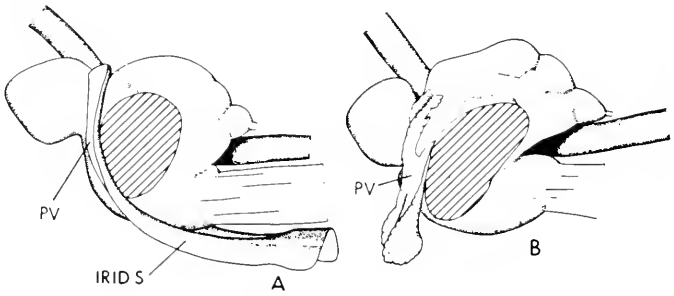

FIGURE 17.—A. Photosensitive vesicles of *Ctenopteryx siculus*. B. Photosensitive vesicles of *Onychoteuthis compacta*. IRID. S.—Iridophore screen. Otherwise, abbreviations as in Figure 2.

posteroventral surfaces. The sensory processes within the vesicles are highly organized, particularly in the ventral portions. The wall of the organ is not particularly thick, and usually has two irregular layers of sensory-cell bodies. The sensory processes arise from all sides of the vesicles; they are straight, parallel, and fill the lumen in the ventral parts of the organ. The sensory processes are about 30 to 50 μm long and lack a detectable core. The dorsal end of the organ lacks the iridophore sheath and has a slightly convoluted wall; the sensory processes are somewhat more widely spaced and do not fill the lumen of the vesicle.

Family Onychoteuthidae

Onychoteuthis compacta (Berry 1913)

Vertical Distribution (Figure 16B)

Twenty-five specimens were captured. Eleven specimens taken during the day came from depths of 240 to 1,350 m. At night, 12 of 14 captures were made between the surface (dip net) and 115 m. The two remaining captures came from depths of 190 and 310 m.

Photosensitive Vesicles (Figure 17B)

Onychoteuthis compacta has a single set of organs. Each organ consists of a large number of small, tightly packed vesicles. Each organ is located on the posterior edge of the optic stalk and extends ventrally and slightly laterally below the central brain along the medial side of the optic lobe. The ventrolateral portion of the vesicle lies directly posterior to the side of the liver and just medial to the head retractor muscles and immediately above the funnel.

Family Octopoteuthidae

Octopoteuthis nielseni Robson 1948

Vertical Distribution (Figure 18A)

Three specimens captured during the day came from depths of about 650 to 765 m. The six night captures came from depths between 100 and 200 m.

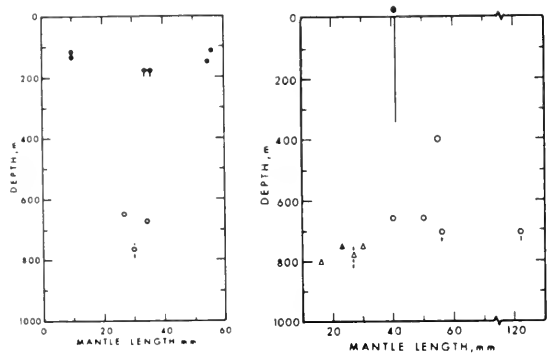

FIGURE 18.—A. Vertical distribution of *Octopoteuthis nielseni*. B. Vertical distribution of *Cycloteuthis serventyi* (triangles) and *Discoteuthis laciniosa* (circles). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 19A)

Two sets of organs are present. A compact ventral organ lies embedded in the thick cephalic cartilage at the anterolateral edge of the statocyst and just medial to the insertion of the head retractor muscles. This organ consists of large, globular, independent vesicles tightly packed together. A series of narrow, very elongate vesicles lie along the nerves from the organ. The central organ lies on the posterior surface of the optic stalk adjacent to the peduncle complex. This large and rather irregularly shaped organ consists of numerous small vesicles.

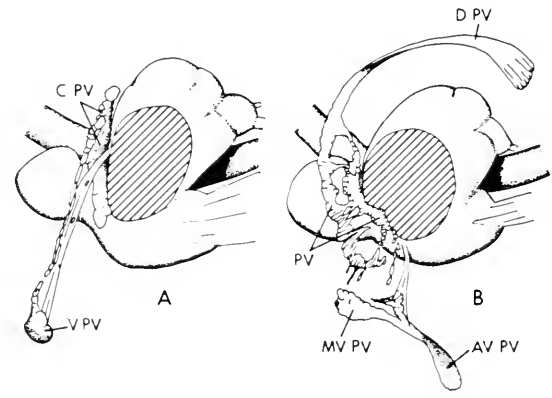

FIGURE 19.—A. Photosensitive vesicles of *Octopoteuthis nielseni*. Photosensitive vesicles of *Cycloteuthis serventyi*. Abbreviations as in Figure 2.

Family Cycloteuthidae

Cycloteuthis serventyi Joubin 1919

Vertical Distribution (Figure 18B)

Three specimens were taken between 750 and 800 m during the day. The single night capture came from an IKMT that fished at 750 m; however, the specimen may be a contaminant, as Roper and Young (1975) listed most of the known night captures of this species from the Atlantic in the upper 200 m.

Photosensitive Vesicles (Figure 19B)

The arrangement of vesicles is complex. On each side of the head, two flattened lobes are located ventral and lateral to the central brain in approximately the positions of the anteroventral and midventral lobes of the *Abraliinae*. The midventral lobe sometimes connects to a complex series of vesicles extending dorsally. These latter vesicles consist of two series: a more posterior series of irregular flattened vesicles lying on the posteromedial surface of the optic lobe; and a thicker, irregular, and rather extensive series of vesicles lying between the optic lobe and peduncle complex. These two series interconnect at various points. At about the level of the optic gland, a thin dorsal organ extends up the medial wall of each optic lobe and onto its anterodorsal surface. This terminal portion gradually widens but remains thin.

Discoteuthis laciniosa Young and Roper 1969

Vertical Distribution (Figure 18B)

Five specimens were taken during the day between 400 and 700 m, although the shallowest capture came from a tow that dipped briefly to 480 m. At night, a single specimen was taken in an oblique tow from the surface to 350 m.

Photosensitive Vesicles (Figure 20A)

The arrangement of vesicles is complex. A broad, flat, irregular ventral lobe is located between the posteroventral surface of the optic lobe and the cephalic cartilage, and opposite the insertion of the head retractor muscles. The broad, flat nerve passing to this lobe bears a series of often isolated vesicles or irregular strands of vesicles which, nearer the brain, join a single, somewhat flattened cord. This central organ extends dorsally and expands somewhat near the optic gland. Although this general pattern holds between specimens, considerable variation in the size of various parts of the central organ occurs.

Family Brachioteuthidae

Brachioteuthis sp.

Vertical Distribution (Figure 21)

Three specimens were captured during the day between 800 and 975 m. Only the mantle of a fourth specimen was present in a day tow at 450 m. The previous tow fished at 900 m and captured one of the other three specimens; the shallow capture is probably a contaminant. Seven of the eight specimens captured at night were taken between 30 and 235 m. The remaining specimen was taken at 1,125 m in an open tow and was a gravid female with sperm masses embedded in the buccal membrane.

Photosensitive Vesicles (Figure 20B)

A single set of organs is present. Each organ is situated on the posterior margin of the optic stalk

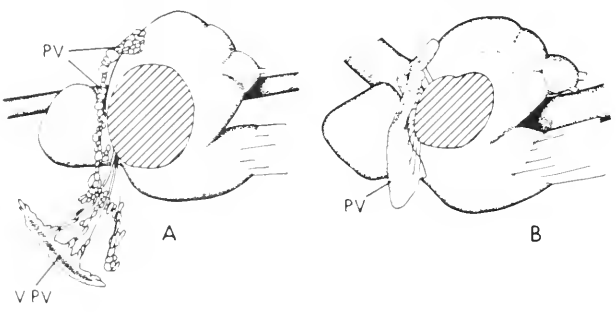

FIGURE 20.—A. Photosensitive vesicles of *Discoteuthis laciniosa*. B. Photosensitive vesicles of *Brachioteuthis* sp. Abbreviations as in Figure 2.

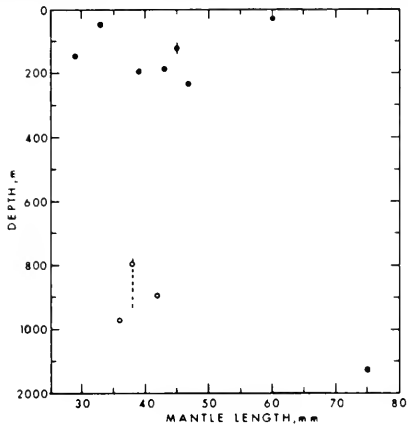

FIGURE 21.—Vertical distribution of *Brachioteuthis* sp. Symbols as in Figure 1.

and extends from the optic gland ventrally and laterally to the level of the ventral surface of the central brain. Each organ consists of numerous small tightly packed vesicles.

Family Chiroteuthidae

Chiroteuthis sp.

Vertical Distribution (Figure 22A)

Three specimens captured during the day were taken between 700 and 800 m. At night, eight specimens were captured between 15 and 750 m; however, six of these came from the upper 200 m.

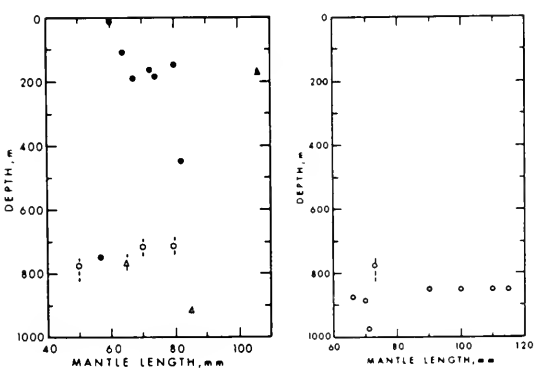

FIGURE 22.—A. Vertical distribution of *Chiroteuthis* sp. (circles) and *Chiroteuthis picteti* (triangles). B. Vertical distribution of Chiroteuthidae gen. sp. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 23A)

One set of small organs is present. Each organ arises on the posterior margin of the optic stalk and extends from the optic gland ventrally to about the level of the ventral surface of the central brain. The organ consists of many small, tightly packed vesicles. Growth of the vesicles from the juvenile stage on is allometric. While the size of each organ increases slightly, the number of component vesicles decreases.

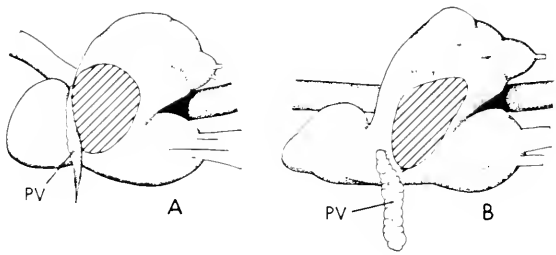

FIGURE 23.—A. Photosensitive vesicles of *Chiroteuthis* sp. B. Photosensitive vesicles of Chiroteuthidae gen. sp. Abbreviations as in Figure 2.

Chiroteuthis picteti Joubin 1894

Vertical distribution (Figure 22A)

Two day captures were made between 750 and 950 m, and a single night capture was made at 175 m.

Photosensitive Vesicles

The organs are essentially the same as in large specimens of *Chiroteuthis* sp. A.

Chiroteuthidae Gen. Sp.

Vertical Distribution (Figure 22B)

All eight specimens of this species were captured during the day between 775 and 975 m.

Photosensitive Vesicles (Figure 23B)

The organs are very similar to those in *Chiroteuthis* spp. One set is present. Each organ consists of small circular vesicles tightly packed into a well-defined organ that attaches to the posteroventral margin of the optic stalk.

Planktoteuthis lippula (Chun 1908)

Vertical Distribution (Figure 24)

Eighteen specimens were captured. Two captures between 200 and 300 m are young animals that probably had not descended to the adult depths. With the exception of a night capture at about 625 m, the remaining animals all came from depths of over 700 m. Among these deeper captures, there is an indication of ontogenetic descent. The largest specimens were captured in an oblique IKMT tow between 1,100 and 1,900 m.

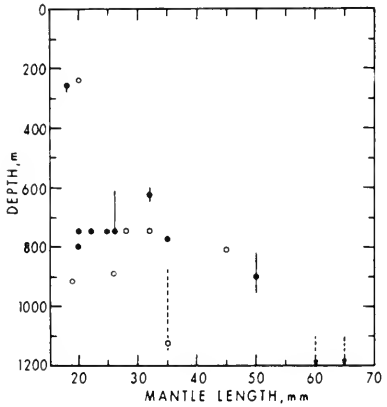

FIGURE 24.—Vertical distribution of *Planktoteuthis lippula*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25A)

One set of small organs is present. Each organ is attached to the ventral edge of the optic stalk and consists of a few globular vesicles.

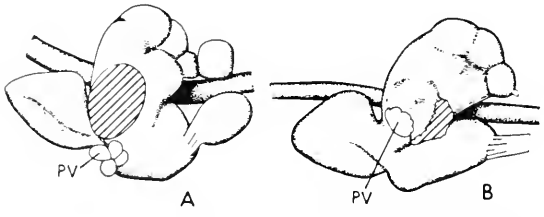

FIGURE 25.—A. Photosensitive vesicles of *Planktoteuthis lippula*. B. Photosensitive vesicles of *Grimalditeuthis bomplandi*. Abbreviations as in Figure 2.

Grimalditeuthis bomplandi (Vérany 1837)

Vertical Distribution (Figure 26A)

Three small specimens were taken at night in the upper 350 m and probably are individuals that had not descended from the larval depths. The larger specimens were all captured during the day between 750 and 1,275 m. The two largest specimens were the two deepest captures.

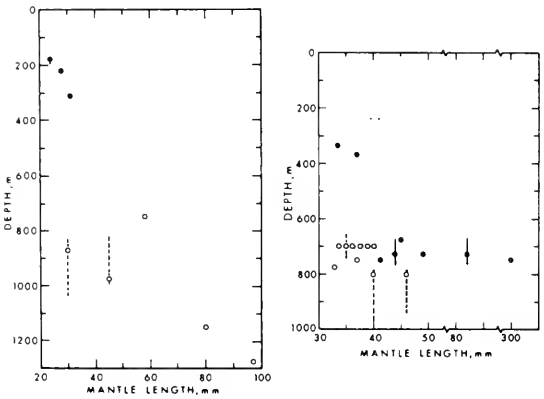

FIGURE 26.—A. Vertical distribution of *Grimalditeuthis bomplandi*. B. Vertical distribution of *Mastigoteuthis famelica*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25B)

One set of organs is present. Each organ consists of a small circular cluster of vesicles attached to the posteroventral margin of the optic stalk.

Family Mastigoteuthidae

Mastigoteuthis famelica (Berry 1909)

Vertical Distribution (Figure 26B)

Excluding contaminants, 16 of 18 specimens were taken between 675 and 800 m, both day and night. In addition, three specimens were probably contaminants. Two of these are assigned to a trawl that fished at 240 m during the day. These were probably captured during the previous tow at 700 m, which contained three specimens. Two shallow night captures of small animals may indicate that some of the population moves upward at night. However, since specimens of 41 mm ML or less are not far past the larval condition, these two specimens may represent animals in transit from the larval habitat.

Photosensitive Vesicles (Figure 27A)

Mastigoteuthis famelica has two sets of organs.

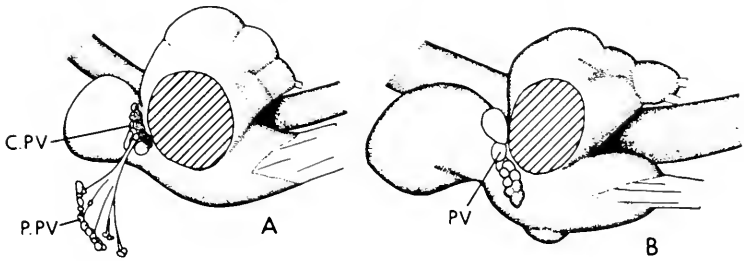

FIGURE 27.—A. Photosensitive vesicles of *Mastigoteuthis famelica*. B. Photosensitive vesicles of *Joubiniteuthis portieri*. Abbreviations as in Figure 2.

The central organs are located on the posterior margin of the optic stalk and consist of a dozen or so independent spherical vesicles. The posterior organs lie on the posterolateral surfaces of the optic lobes opposite the lateral attachment of the head retractor muscles. Each organ consists of a string of several layers of circular or oval vesicles. A few scattered vesicles occasionally occur along the nerves passing from the posterior organ.

Mastigoteuthis inermis Rancurel 1972

Vertical Distribution (Figure 28)

Fifteen specimens were captured during the day at depths of 675 to 870 m; most came from depths of about 700 to 800 m. Ten specimens captured at night came from depths of 255 to 725 m with most specimens being taken between 250 and 450 m.

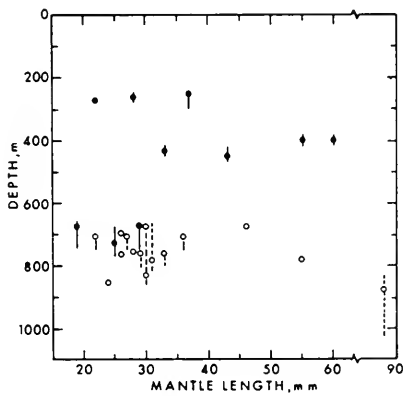

FIGURE 28.—Vertical distribution of *Mastigoteuthis inermis*. Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *M. familica* except that the central organ is flatter and broadly continuous with the posterior organ. The posterior organ extends slightly beyond the insertion of the head retractor muscles and is less elongate.

Family Joubiniteuthidae

Joubiniteuthis portieri (Joubin 1912)

Vertical Distribution

Three specimens, all taken at night, were captured. One (42 mm ML excluding tail) was taken in an oblique tow between the surface and 425 m. A second specimen (64 mm ML) was taken in an opening-closing tow that fished between 480 and 550 m, and a third (85 mm ML) was taken in an open tow that fished at 1,125 m. Roper and Young (1975) listed the two known day captures of this species from the Atlantic Ocean as 800 to 900 m and 2,500 m.

Photosensitive Vesicles (Figure 27B)

One set of small organs is present. Each organ consists of a small number of globular vesicles that form a compact organ. Each organ is attached to the posteroventral margin of the optic stalk.

Family Cranchiidae

Liocranchia valdiviae (Chun 1906)

Vertical Distribution (Figure 29)

Both larvae and adults captured by the Tucker trawl are plotted. IKMT captures have been added where data are weak: specimens >24 mm ML and all specimens captured above 600 m during the day. One hundred fourteen specimens are plotted. Although only a few shallow day captures were made, the vertical distribution pattern is clear: animals between 5 and 15 mm ML predominate in

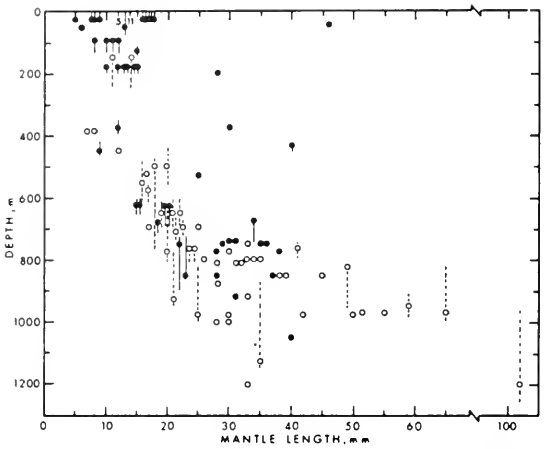

FIGURE 29.—Vertical distribution of *Liocranchia valdiviae*. Symbols as in Figure 1.

the upper few hundred meters. Descent to adult depths begins within the 5- to 15-mm ML size range or occasionally larger. Most specimens 15 to 25 mm ML are captured between depths of 500 and 700 m, while most animals ≥25 mm ML are found deeper than 700 m with progressively larger specimens found at progressively greater depths. Diel vertical migration does not occur. Five large specimens captured at depths of 40 to 525 m at night, however, indicate that some specimens occasionally wander into the upper depths at night. Mature specimens were not captured.

Photosensitive Vesicles (Figure 30A)

Liocranchia valdiviae has a single set of small organs. Each organ is elongate and extends along the posterior side of the optic stalk. Each organ usually consists of three elongated vesicles. A strip of dark brown screening pigment with irregular margins extends along much of the anteromedial edge of the ventral half of the organ. The broad dorsal vesicle either lacks screening pigment or has only a trace of it. The slender middle vesicle has a narrow, often discontinuous strip of pigment which widens ventrally. The ventral vesicle, which is the largest, has a broad, continuous layer of screening pigment.

The vesicles of *L. valdiviae* grow allometrically. At 30 mm ML the vesicles are small, and screening pigment consists of a single small patch on the ventral vesicle. In the largest specimen (102 mm ML), the pigment screen is very extensive and covers much of the anterior surface of the dorsal as well as ventral portions of each organ. The dorsal and ventral vesicles in each organ are somewhat broader in this specimen, making the organ more dumbbell shaped.

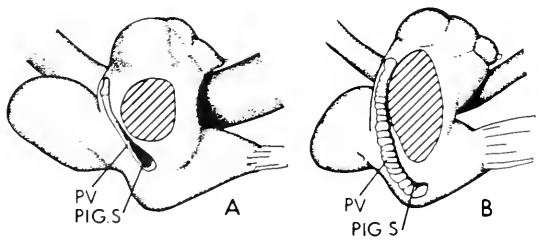

FIGURE 30.—A. Photosensitive vesicles of *Liocranchia valdiviae*. B. Photosensitive vesicles of *L. reinhardti*. Abbreviations as in Figure 2.

Liocranchia reinhardti (Steenstrup 1856)

Vertical Distribution (Figure 31)

All 12 juvenile specimens were captured at night. Ten of the 12 specimens were taken in the upper 100 m; the other 2 came from 150 to 200 m. A single mature specimen was captured at 775 m in a Tucker trawl that failed to close on retrieval. This specimen was a female that had recently spawned: remnants of what appeared to be sperm reservoirs were attached to the inner right wall of the mantle near the base of the funnel; the nidamental glands were gelatinous and extremely swollen; the ovary was depleted; and the muscular tissue of the mantle, fins, head, and arms was flaccid.

Unfortunately, there are no data on the day distribution of this species in Hawaiian waters.

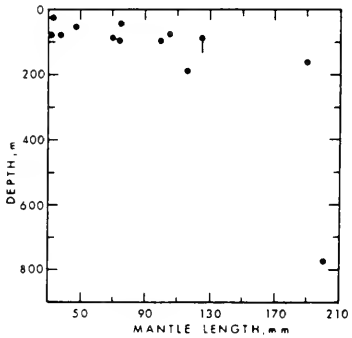

FIGURE 31.—Vertical distribution of *Liocranchia reinhardti*. Symbols as in Figure 1.

However, in the tropical North Atlantic, two specimens of *L. reinhardti* (44 and 48 mm ML) were captured during the day in opening-closing tows between 510 and 600 m, while a 75-mm ML specimen was taken in an open tow that fished between 390 and 800 m (C.C. Lu pers. commun.). Also, M. Clarke (1969) reported specimens of 46 and 69 mm ML from depths between 450 and 810 m during the day in the Atlantic.

Photosensitive Vesicles (Figure 30B)

The organs of *L. reinhardti* have been described by Messenger (1967a). This species has a single large set of organs lying along the posteromedial surface of the peduncle lobe. Each organ consists of a linear array of 20 to 25 tightly packed vesicles. The vesicles are elongated in a transverse direction except for those at the dorsal and ventral ends which are nearly circular. The vesicles are separated from one another by a heavy brown pigment screen which also covers most of the convex anterior side of the organ. Most vesicles within each organ thus form elongate cups which presumably admit light only from one surface. The dorsal vesicle, however, lacks screening pigment from the posterior lateral and dorsolateral surfaces. The ventral vesicle is larger, with photosensitive processes twice as long as those of the dorsal vesicle. It lacks pigment on its ventral and anterior surface. The curvature of the organ and the arrangement of screening pigment allows light to enter different vesicles from a wide range of angles.

Specimens ≤47 mm ML have no screening pigment on the vesicles while those ≥70 mm ML exhibit pigment as described above. The vesicles in the largest specimen (spent female) are slightly larger (especially the ventral vesicle) relative to the brain size than in smaller specimens.

Leachia pacifica (Issel 1908)

Vertical Distribution (Figure 32)

The vertical distribution of *L. pacifica* has been described elsewhere (Young 1975a). This species reaches about 80% of its maximum length in near-surface waters. Large specimens (45-60 mm ML) are found throughout the water column between 30 and at least 1,800 m with those taken from progressively deeper water exhibiting progressively greater sexual maturity. Gravid females were taken at depths >1,300 m.

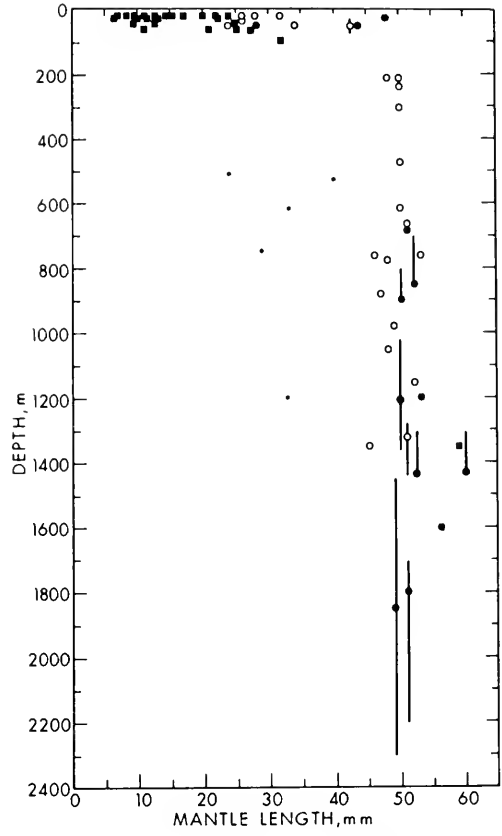

FIGURE 32.—Vertical distribution of *Leachia pacifica*. From Young (1975a). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 33A)

Leachia pacifica has a single set of organs located on the posteroventral surface of the peduncle lobe. Each organ consists of 4 or 5 cup-shaped vesicles that are closely packed into a small oval organ. A dark brown screening pigment covers

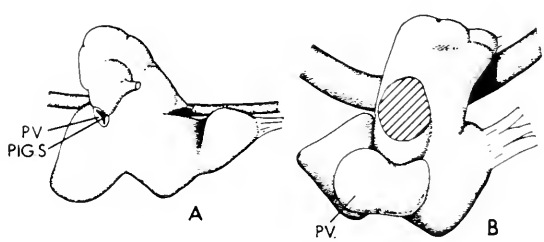

FIGURE 33.—A. Photosensitive vesicles of *Leachia pacifica*. B. Photosensitive vesicles of *Sandalops melancholicus*. Abbreviations as in Figure 2.

much of the anterior and slightly dorsal surface of each organ. This pigment is also found in the walls between some vesicles, tending to isolate them from one another. Although the vesicles are minute in the larva and very small in the adults, a small positive allometric growth of the vesicles seems to occur. Screening pigment first appears on the vesicles between about 20 and 30 mm ML. In the adult, the screening pigment is most extensive and covers the entire anteromedial surface of the organ.

Phasmatopsis fisheri (Berry 1909)

Vertical Distribution (Figure 34)

Over 300 specimens of *P. fisheri* were captured but most were larvae. Metamorphosis occurs at a size of 40 to 50 mm ML.

During the day, six larvae were captured between 150 and 250 m. Seventeen juvenile and adult specimens were captured between about 625 and 800 m; most captures were made between 650 and 775 m.

At night, larvae ≤30 mm ML were taken primarily in the upper 50 m; larvae 31 to 40 mm ML were found throughout the upper 200 m. Fourteen juveniles and adults were taken at night between 90 and 225 m; most captures were made between 100 and 200 m.

Photosensitive Vesicles (Figure 35)

Phasmatopsis fisheri has a single set of large organs. Each organ consists of a broad, elongate vesicle that extends from the optic gland on the dorsal surface of the optic stalk ventrally over the posterior surface of the peduncle complex onto the side of the ventral subesophageal mass, where it bends slightly dorsally. Each organ is thick laterally and medially. Most of the anterior, medial, and lateral surfaces of each organ are covered by dark brown pigment screen. The dorsal tip of each organ lacks screening pigment on its lateral portion and has limited pigment screen on its medial portion. The curvature of each organ allows light to enter various parts from a wide range of angles.

The anterior wall of each organ consists of little more than a membrane backed by dense pigment. The posterior wall and the walls of the dorsal and ventral ends of each organ contain 4 or 5 layers of sensory-cell bodies. Sensory processes are longer (215 μm) and thinner (inner diameter 2 to 4 μm) in the ventral parts of the organ than in the dorsal

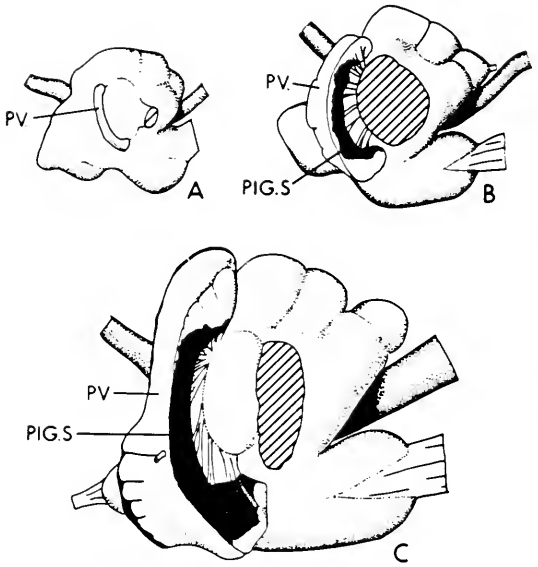

FIGURE 35.—Photosensitive vesicles of *Phasmatopsis fisheri*. A. Larva, 35 mm ML. B. Juvenile, 70 mm ML. C. Adult, 130 mm ML. Abbreviations as in Figure 2.

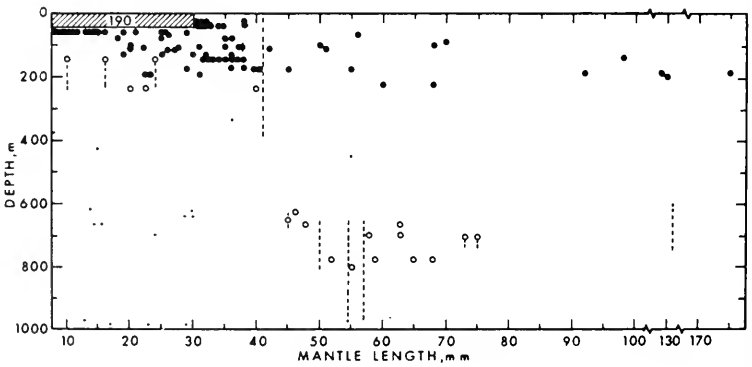

FIGURE 34.—Vertical distribution of *Phasmatopsis fisheri*. Symbols as in Figure 1.

parts (length 155 μm, inner diameter 3 to 6 μm). The processes are long and slender and organized in a straight, parallel alignment.

Each organ is small in larvae and lacks screening pigment. At 35 mm ML, the vesicles form a narrow strip along the posterior surface of the peduncle lobe (Figure 35A). The largest larvae have relatively small organs without screening pigment; the youngest juveniles have large organs that are heavily pigmented. In the juvenile and adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the brain. The ventral half of the organ is particularly enlarged and the organs on each side of the brain contact broadly (but do not fuse) below the ventral midline of the brain.

Taonius pavo (LeSueur 1821)

Vertical Distribution (Figure 36)

The vertical distribution of *T. pavo* has been described by Young (1975d). Larvae probably live in the upper 400 m, although only one capture was made. Juveniles were found primarily between 600 and 650 m, and adults were captured between 725 and 970 m. Diel vertical migration does not occur.

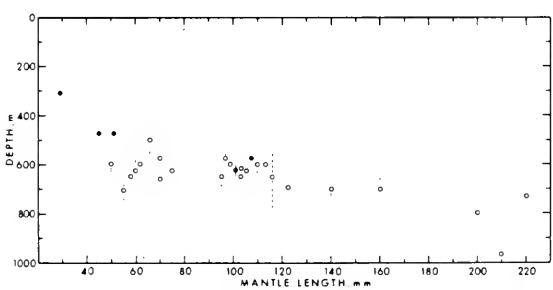

FIGURE 36.—Vertical distribution of *Taonius pavo*. From Young (1975d). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 37)

Taonius pavo has a single set of organs located on the posteroventral side of the peduncle complex. Each organ consists of a single oval vesicle. No screening pigment is present. The large size of the vesicle in a 220-mm ML specimen belies its internal structure. The large central region of the

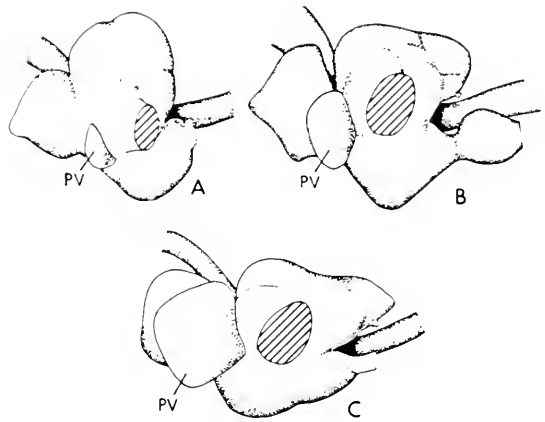

FIGURE 37.—Photosensitive vesicles of *Taonius pavo*. A. Larva. B. Juvenile, 140 mm ML. C. Adult, 220 mm ML.

lumen is unoccupied. Sensory processes occupy about 1/5 (i.e., about 230 μm) of the lumen diameter on the anterior, posterior, and dorsal sides and slightly more (about 300μm) on the ventral sides. The processes are loosely packed and intertwined to a large extent dorsally and more tightly packed ventrally. Inner diameters of the processes vary greatly from about 3 to 30 μm. The wall on the dorsal half of the organ contains about two layers of sensory-cell bodies compared with about three layers ventrally. In a 140-mm ML juvenile, the dissected vesicle was also hollow, with an even thinner region of the lumen occupied by sensory processes. The organs exhibit positive allometric growth (Figure 37).

Sandalops melancholicus Chun 1906

Vertical Distribution (Figure 38)

The vertical distribution in this species has been reported by Young (1975d). Larvae were found in the upper 400 m. Juveniles were captured between 450 and 674 m, and two adults were captured near 800 and 1,075 m. Diel vertical migration does not occur.

Photosensitive Vesicles (Figure 33B)

Sandalops melancholicus has a set of organs located along the ventral surface of the peduncle complex. Each organ consists of a single bilobed vesicle (R. E. Young 1977). Slight positive allometric growth of the vesicles occurs between the juvenile and adult stages.

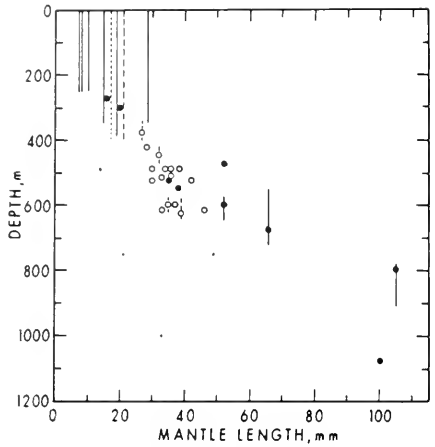

FIGURE 38.—Vertical distribution of *Sandalops melancholicus*. From Young (1975d). Symbols as in Figure 1.

Helicocranchia beebei Robson 1948

Vertical Distribution (Figure 39)

Including larvae, 47 specimens were captured. Although day and night captures are not well intermingled in Figure 39 (due largely to sampling inequities), the data indicate that this species does not migrate. Rather, it seems to undergo ontogenetic descent. The youngest specimens were captured between 100 and 200 m. Progressively larger specimens were generally taken at progressively greater depths, although the relationship of size to depth is not very precise. The deepest capture was probably at 1,200 m. Mature specimens were not captured.

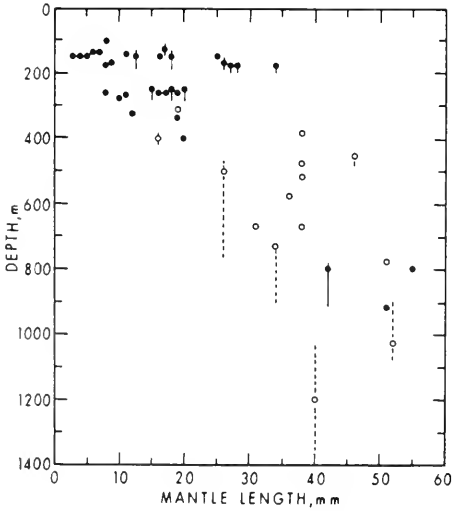

FIGURE 39.—Vertical distribution of *Helicocranchia beebei*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 40A)

One set of organs is present. Each organ consists of a single small oval vesicle located on the posterior surface of the peduncle complex. No screening pigment is present. Very slight, if any, positive allometric increase in the size of the vesicles occurs from juveniles to the largest specimens.

Bathothauma lyromma Chun 1906

Vertical Distribution (Figure 41)

Although only 12 specimens were captured, a general pattern of ontogenetic descent is evident.

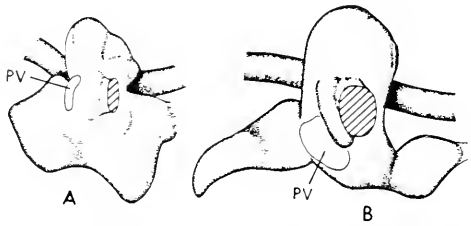

FIGURE 40.—A. Photosensitive vesicles of *Helicocranchia beebei*. B. Photosensitive vesicles of *Bathothauma lyromma*. Abbreviations as in Figure 2.

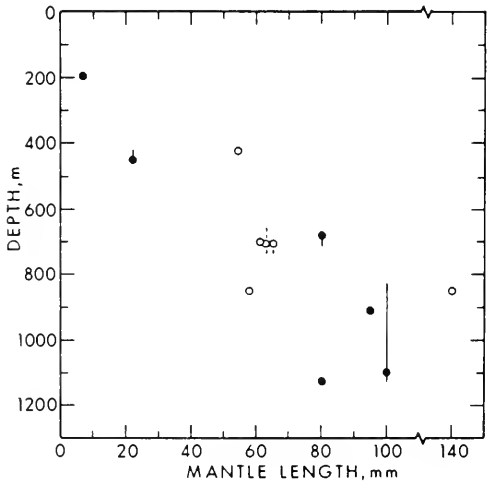

FIGURE 41.—Vertical distribution of *Bathothauma lyromma*. Symbols as in Figure 1.

Day and night captures were in the same depth range, indicating that diel vertical migration does not occur. The three specimens captured at the greatest depths were gravid females. The specimen captured at 910 m had sperm receptacles imbedded in the back of the head and in the anterodorsal surface of the mantle. The nidamental and oviducal glands were greatly enlarged and the entire visceropericardial coelom was packed with large eggs. The muscular tissue was slightly flabby. The specimen captured at 1,125 m exhibited almost identical features. The specimen captured at about 1,100 m had similarly placed sperm reservoirs, less extensively enlarged nidamental and oviducal glands, and lacked eggs (apparently due to damage during capture). This specimen exhibited no sign of muscular degeneration. The mantle cavity of this specimen had two very long arms from another specimen (presumably a male) attached to the inner wall of the mantle. The largest specimen was an immature female. Its size was largely due to its fixation in a relaxed state. In this species, the pen is extraorinarily delicate and accurate measurements of contracted, crumpled specimens are nearly impossible.

Photosensitive Vesicles (Figure 40B)

Bathothauma lyromma has a single set of organs. Each organ consists of a flat oval vesicle located on the posteroventral surface of the peduncle complex. No screening pigment is present. Slight positive allometric growth of the vesicles occurs from juveniles to adults.

Galiteuthis pacifica (Robson 1948)

Vertical Distribution (Figure 42)

The 27 specimens captured indicate a broad vertical range for this species. Fourteen of the 19 captures of specimens >20 mm ML came from depths of 700 m or more. The data indicate that diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles of this species are similar to those of *G. phyllura* described by Young (1972a). A single set of organs is present. Each organ consists of a large oval vesicle attached to the posteroventral surface of the peduncle complex. Considerable positive allometric growth of the vesicles occurs.

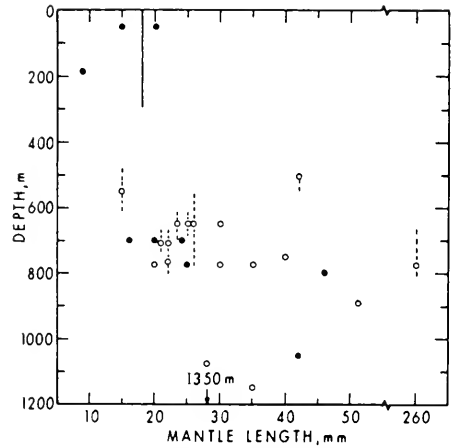

FIGURE 42.—Vertical distribution of *Galiteuthis pacifica*. Symbols as in Figure 1.

Order Octopoda

Family Bolitaenidae

Eledonella pygmaea Verrill 1884

Vertical Distribution (Figure 43)

Eighty specimens were captured. Day and night captures were in the same depth range (except above 300 m where day trawling was minimal), indicating that diel vertical migration does not occur. Most specimens between 5 and 15 mm ML

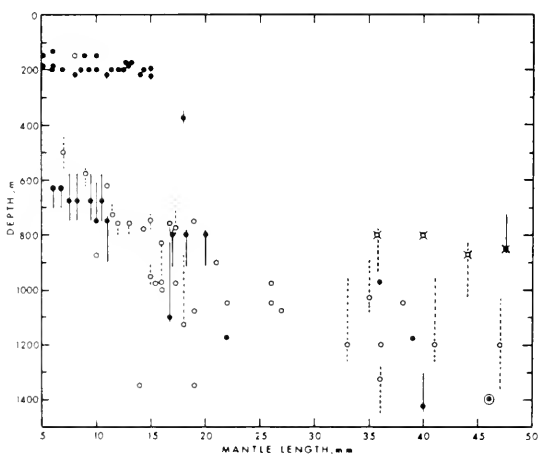

FIGURE 43.—Vertical distribution of *Eledonella pygmaea*. Circles with crosses represent brooding females. Double circle represents a gravid female. Otherwise symbols as in Figure 1.

were captured either around 200 m or below 600 m. Apparently the size at which young begin their descent to adult depths is rather variable. The deep captures exhibit a clear pattern of ontogenetic descent. At 25 mm ML or larger all specimens (excluding brooding females) were captured between depths of 975 and 1,425 m. Four females, apparently brooding, were captured between about 800 and 870 m.

The pigmentation of the female changes as she becomes gravid: the chromatophores over the mantle and especially over the aboral surface of the arms and web become more numerous, and the oral surfaces of the arms and web develop an even denser pigmentation. Nearly all iridophores are lost. At the same time the arms and the web become thicker. The web between the dorsal six arms becomes more extensive, and the web between the two ventral arms is reduced. These dark octopods spawn and apparently brood their young (Young 1972b). Five specimens taken from horizontal tows exhibited this increased pigmentation. In four cases, the ovary was depleted, and in the fifth, captured at 1,400 m, the eggs were not fully mature, but were considerably larger than in an immature female of approximately the same size. In two cases egg strings with developing embryos were found in the same trawl with dark and presumably brooding females.

No mature males were taken. However, judging from the development of the hectocotylus, the penis, and the spermatophore glands, two specimens captured at 1,200 and 1,425 m were nearly mature. Another slightly less mature specimen was taken at 1,325 m. Three still less mature specimens were taken between 1,175 and 1,200 m, while a large male taken at 1,025 m was the least developed of all.

Photosensitive Vesicles (Figure 44A)

The photosensitive vesicles consist of a single pair of organs; each organ is a spherical vesicle attached to the posterior margin of the stellate ganglion.

Japetella diaphana Hoyle 1885

Vertical Distribution (Figure 45)

Seventy-four specimens were captured. Diel vertical migration does not occur. Specimens <20 mm ML were captured mostly in two regions, between 170 and 270 m and between 500 and 800 m,

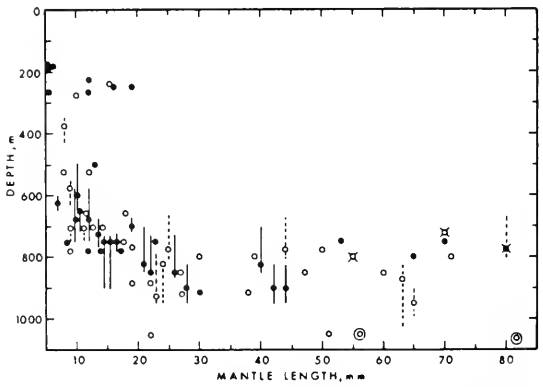

FIGURE 45.—Vertical distribution of *Japetella diaphana*. Circles with crosses represent brooding females. Double circles represent gravid females. Otherwise symbols as in Figure 1.

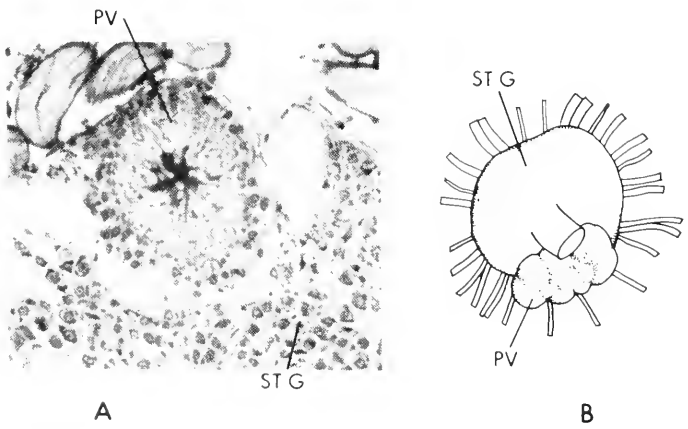

FIGURE 44.—A. Section through the photosensitive vesicle of adult *Eledonella pygmaea*. B. Photosensitive vesicles of *Amphitretus pelagicus*. ST. G.—Stellate ganglion. Otherwise symbols as in Figure 1.

where they exhibited an ontogenetic descent. The depth range for specimens ≥20 mm ML was 725 to 1,065 m; nearly 90% of the animals occur between 700 and 950 m and nearly 60% between 750 and 850 m. Gravid and brooding females were found at the extremes of this range. Two gravid females were captured at 1,050 and 1,065 m while three spent and presumably brooding females were taken between 725 and 800 m. As in *E. pygmaea*, the gravid and spent females have a very heavy pigmentation and lack most of the iridophores present in younger specimens. Five such females were captured in horizontal tows. One gravid female with a sperm mass embedded in the gelatinous tissue between the second and third arms was taken at 1,050 m. Another taken at 1,065 m had been gutted in the trawl but had not spawned: the musculature was firmer than in spent females, and the catch contained a large number of octopod eggs which undoubtedly came from the ruptured ovary. Three specimens taken between 725 and 800 m probably had spawned: two had depleted ovaries and the third was gutted but had deteriorated musculature. In the same tow with the last specimen were four newly hatched larvae, presumably from the brood of the female. One large, heavily pigmented female taken in an oblique tow had the remnants of an egg string dangling from one of the large suckers of the third arm. Two eggs were completely engulfed by the sucker, while a third dangled from the broken egg string extending from the sucker. No mature males were taken.

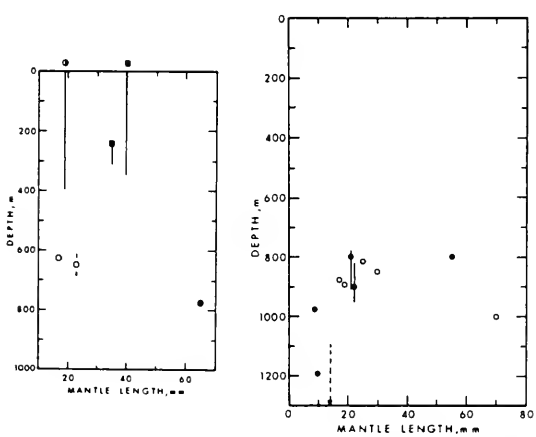

FIGURE 46.—A. Vertical distribution of *Amphitretus pelagicus* (squares) and *Vitreledonella richardi* (circles). B. Vertical distribution of *Vampyroteuthis infernalis*. Half-closed circles represent a twilight capture. Otherwise symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *E. pygmaea*.

Family Amphitretidae

Amphitretus pelagicus Hoyle 1885

Vertical Distribution (Figure 46A)

Two specimens were taken at night in the upper 350 m.

Photosensitive Vesicles (Figure 44B)

Amphitretus pelagicus has one set of organs. They lie on the stellate ganglia immediately anterior to the entry points of the pallial nerves. Each organ consists of a large complex of a dozen or more generally circular vesicles which cover most of the anterior wall of the ganglion.

Family Vitreledonnelidae

Vitreledonnella richardi Joudin 1918

Vertical Distribution (Figure 46A)

Four specimens were captured. One small specimen was taken in an oblique twilight tow between the surface and 400 m. Two other small specimens were taken between 600 and 650 m during the day. One large specimen was captured at 775 m during the night.

Photosensitive Vesicles

An organ consisting of a single spherical vesicle is located on the posterior margin of each stellate ganglion.

Order Vampyromorpha

Family Vampyroteuthidae

Vampyroteuthis infernalis Chun 1903

Vertical Distribution (Figure 46B).

Eleven specimens were captured. Ten of the 11 were taken between depths of 800 and 1,200 m. The remaining specimen came from an open oblique tow that fished between 1,100 and 1,900 m. Diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles have been described in detail by Young (1972a). One set is present. They are located in the dorsal wall of the mantle cavity at the base of the funnel. Each organ consists of a small cluster of spherical vesicles.

Order Sepioidea

Heteroteuthis hawaiiensis (Berry 1909)

Vertical Distribution (Figure 47)

The distribution of this species has been discussed by R. E. Young (1977). During the day, specimens ≤17 mm ML were taken between 250 and 350 m; larger specimens were taken between 375 and 650 m. At night, most specimens <17 mm ML came from depths between 150 and 200 m; larger specimens were taken between depths of 110 and 550 m. Males and females mature at about 15-16 mm ML.

Photosensitive Vesicles (Figure 48)

Two sets of organs are present (R. E. Young 1977). The more dorsal set lies on the posterior margin of the peduncle complex and consists of a short and narrow string of tiny vesicles. An even

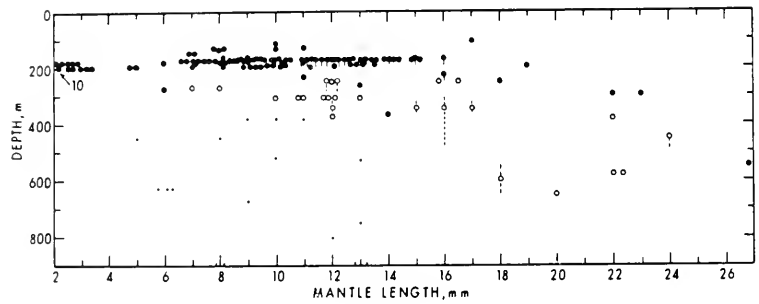

FIGURE 47.—Vertical distribution of *Heteroteuthis hawaiiensis*. From R. E. Young (1977). Symbols as in Figure 1.

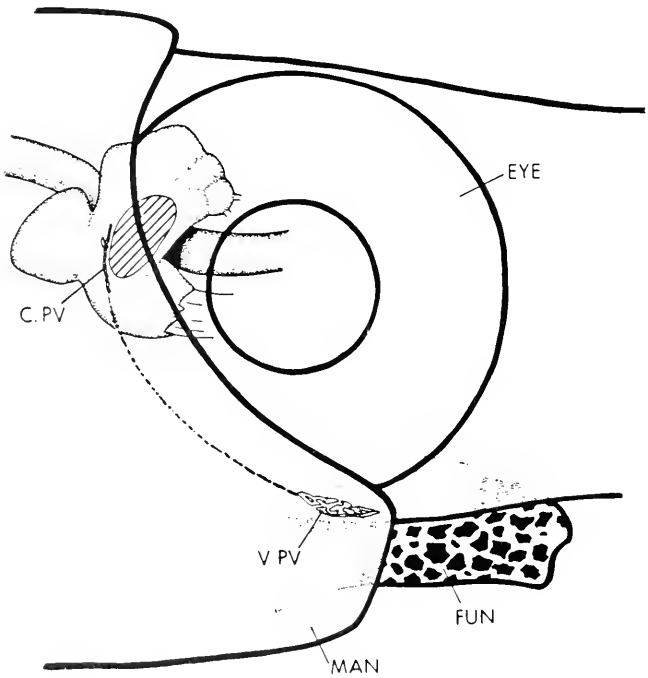

FIGURE 48.—Photosensitive vesicles of *Heteroteuthis hawaiiensis*. In this figure the outline of portions of the head and mantle are superimposed to give a clear perspective of the peculiar arrangement of vesicles in this species. EYE—eye; FUN.—funnel; MAN.—mantle. Otherwise abbreviations as in Figure 2.

narrower string of tiny vesicles extends ventrally around the eyes and joins a rather large but extremely thin, loosely associated group of vesicles that lies over the lateral base of the funnel.

DISCUSSION

Vertical Distribution

The numbers of cephalopod species taken in different 100-m depth zones for the upper 1,400 m showed a broad peak between 500 and 800 m during the day (Figure 49). An abrupt increase in the number of species near 400 m was obscured by the method of analysis: eight species occurred for the first time between depths of 375 and 450 m. To indicate faunal change, the number of species found for the first time in each zone (i.e., depth zones containing species upper range limits) were compared with zones where species found in lesser depths were absent for the first time (i.e., depth zones immediately below the lower range limits) (Figure 49).

The peak at 700-800 m in the summed plot of species added and species lost indicates that many species dropped out in the 600-700 m zone and many were added in the 700-800 m zone. The chart also indicates that only two species were encountered for the first time at 800 m or below. One was the poorly sampled *Brachioteuthis* sp. and the other was deep-living *Vampyroteuthis infernalis*. The data indicate peak species richness in the upper few hundred meters with relatively little change between 300 and 1,000 m during the night (Figure 49).

Numbers of individuals in different depth zones in the upper 1,400 m (exclusive of young individuals, captures in oblique tows, and contaminants) were also examined (Figure 50). During the day, the greatest abundance of individuals occurred between 400 and 700 m. This peak reflects the dominance of the enoploteuthids, especially *Pyroteuthis* and *Pterygioteuthis* spp. The high rate of capture in the 300- to 400-m zone was due in part to a few species whose upper limits extended slightly above 400 m. Nevertheless, an abrupt increase in number occurred in the 400- to 500-m zone. The rates of capture below 1,000 m were unreliable due to the small amount of trawling.

The night data in the upper 400 m were lumped into 50-m increments due to greater control over trawling depths in near-surface waters. The largest catches at night were made in the upper 200 m. In this region two peaks were apparent (Figure 50). The peak in the 50- to 100-m zone was largely due to *Pterygioteuthis microlampas*, the

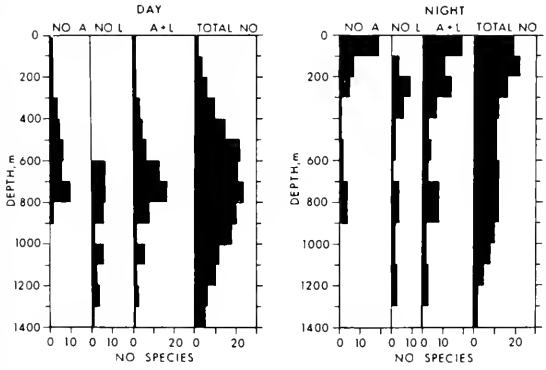

FIGURE 49.—Numbers of species versus depth. The histograms were based on species ranges from midwater trawl data. Data were lumped into 100-m depth increments and were not corrected for unequal trawling times at different depths. Data for some species were very meager. Young stages found in near-surface waters that can be distinguished by an abrupt change in habitat or by a metamorphosis have been eliminated from the figures. No. A—number of species added (i.e., found for the first time in a given depth zone). No. L.—number of species lost (i.e., absent from a given depth zone but present in the shallower zone). A + L—sum of two previous histograms. Total No.—total number of species in each depth zone.

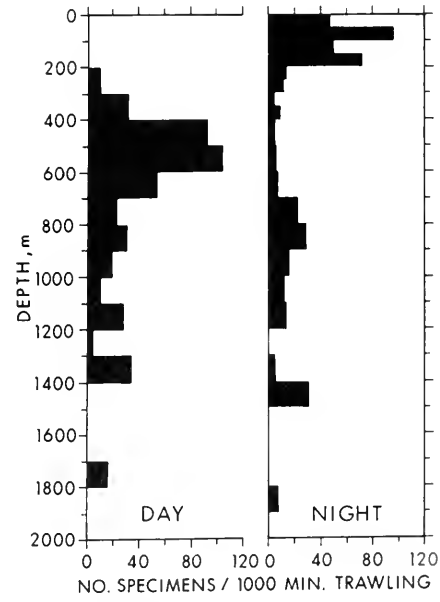

FIGURE 50.—Total catch rate of numbers of cephalopod specimens from both trawls.

most abundant species in the collection. The peak in the 150- to 200-m zone was largely due to *Pyroteuthis addolux* and *Heteroteuthis hawaiiensis*; young *Histioteuthis dofleini* also contributed considerably. Young *Eledonella* were also found in this zone although they were excluded from the figures as "larvae."

The zone between 200 and 700 m was sparsely inhabited at night. The peak between 700 and 1,000 m represented the deep nonmigrating population. The capture rate in this region was almost identical to the day capture rate at the same depths: deep-living migrators were few.

The total rate of capture for the water column during the day was 459 specimens/1,000 min of trawling. Surprisingly, the total capture rate at night was only 309 specimens/1,000 min. This difference was largely due to smaller-than-expected catches at night in the upper 200 m of the few most abundant species. The reason for the low night catches is unknown. Another estimate of the number of animals in the upper 250 m at night was obtained by assuming that the day peak from 300 to 700 m (minus the night catch at these depths) shifted into this upper zone at night (see below). On this basis, nearly 80% of the individuals occurred in the upper 250 m at night. If one considers also the abundant ommastrephids which avoided midwater trawls but occurred in near-surface waters at night, then only a small percent of the total number of individuals would remain below 250 m at night.

In many species, most of the population shifted upward at night. Such day-night differences existed in at least 25 of the 47 species examined, based on present data and literature records. Adequate data were lacking for ommastrephids and *Neoteuthis* sp. Therefore, where the vertical ranges are known, nearly 60% of the species exhibited diel shifts in habitat. Species not exhibiting diel migrations belonged primarily to the Cranchiidae (seven species) and the Octopoda (five species).

At least 18 of the 25 species that exhibited diel migrations occurred almost exclusively in the upper 250 m at night. These included all 11 enoploteuthids, *Liocranchia reinhardti*, *Phasmatopsis fisheri*, *Ctenopteryx siculus*, *Octopoteuthis neilseni*, *Brachioteuthis* sp., *Chiroteuthis* sp., *Onychoteuthis compacta*, and young *Heteroteuthis hawaiiensis*. Two species for which the data were incomplete (*Cycloteuthis serventyi* and *Chiroteuthis picteti*) probably belonged to this category as well. Therefore, at least 80% of the migratory species occurred in the upper 250 m at night.

Amesbury (1975) examined vertical zonation of midwater fishes during the day off Hawaii. He concluded that the water column could be divided into three regions: epipelagic, mesopelagic, and bathypelagic zones. The boundary between the epipelagic and mesopelagic zones occurred at about 400 m and was marked by a sharp increase in the numbers of individuals. This boundary appeared to apply equally well to cephalopods. The boundary between the mesopelagic and bathypelagic zones occurred at about 1,200 m. This boundary was marked by a noticeable decrease in fish numbers and represented the greatest day depths of vertically migrating fish. This lower boundary was not applicable to cephalopods; there was no comparable decrease in numbers of individuals; and this depth seemed to be well below the range of vertical migrators. Amesbury further divided the mesopelagic zone into upper and lower zones with the boundary at about 650 to 700 m. Cephalopods exhibited maximum species turnover at about this depth, as well as changes in light-related adaptations in some species (Young 1975d). Although fish and cephalopod distributions differed with respect to the lower boundary, the distribution of cephalopods generally supported Amesbury's zonation.

In spite of the rather small size of the collection, some evidence of vertical habitat separation among closely related species emerged. Three of the more abundant species belong to the subfamily Pyroteuthinae: *Pyroteuthis addolux*, *Pterygioteuthis microlampas*, and *P. giardi*. In general body proportions and armature, *P. microlampas* was more similar to *Pyroteuthis addolux* than to its congener. During the day, these two species occupied the same depths around 500 m. At night, their populations peaked at distinctly different depths: *Pterygioteuthis microlampas* occurred primarily between 50 and 100 m, while *Pyroteuthis addolux* occurred primarily between 150 and 200 m. Although the data were less clear for *Pterygioteuthis giardi*, this species seemed to center around 400 m during the day and in the upper 100 m at night with about half of the population in the upper 50 m. Thus this species was shallower than its two relatives during the day and tended to be shallower at night, although broad overlap occurred with its congener.

Two species of the genus *Abralia* occurred off Hawaii. *Abralia trigonura* was a common vertical migrator in the area sampled of the open ocean, while *A. astrosticta* was never taken there. *Abralia astrosticta* seems to be a vertical migrator that moves in close proximity to the ocean floor (Roper and Young 1975).

Two species of *Mastigoteuthis* were taken. Both species shared the same day habitat at 700 to 800 m. At night, the population of *M. inermis* spread upward in the water column 400 or 500 m. Although the data were few, *M. famelica* appeared to spread little or not at all.

One of the clearest cases of habitat separation of congeners occurred in *Liocranchia*. *Liocranchia valdiviae* was taken in lower mesopelagic depths during the day and it did not migrate. *Liocranchia reinhardti* was taken in near-surface waters at night and apparently occurred in upper mesopelagic depths during the day.

Although the octopods *Japetella diaphana* and *Eledonella pygmaea* are placed in separate genera, they are very closely related. Both were taken in deep waters and did not migrate. The adults (except brooding females) were taken at distinctly different depths: *E. pygmaea* occupied depths from 975 to 1,425 m while *J. diaphana* occupied depths primarily from 700 to 950 m. Young stages prior to descent were found in near-surface waters. In this habitat *E. pygmaea* was captured primarily at 200 m or just above while *J. diaphana* was captured primarily below 200 m. Young stages of both species in the process of descent occupied depths of about 400 to 800 m or more. The data indicated, however, that at any given size, except for those just beginning descent, the young of *E. pygmaea* occupied greater depths than the young of *J. diaphana*.

In the genus *Abraliopsis* three species were taken: *Abraliopsis* sp. A and *Abraliopsis* sp. C form the most closely related species pair. The available data show no obvious habitat differences. Although the more common *Abraliopsis* sp. A reached a considerably larger size than species C (43 mm ML vs. 33 mm ML), young individuals of species A, however, apparently cooccurred with species C of the same size. The day and night habitats of *Abraliopsis* sp. B were not separable from its two congeners.

Three other groups of congeners were taken (i.e., in *Enoploteuthis*, *Histioteuthis*, and *Chiroteuthis*). No differences in habitats were found within these groups; however, the data were extremely sparse.

Reproduction

Young (1972b) presented evidence for brooding in *Eledonella pygmaea* (incorrectly reported as *Bolitaena microcolyla*) and suggested that brooding occurs in all pelagic octopods. Additional evidence from the present study substantiated the brooding habit for *E. pygmaea*. In addition, evidence indicating brooding in the octopod *Japetella diaphana* was found. This species underwent changes at maturity similar to *E. pygmaea*. Further, newly hatched young have been found in the same trawl with spent females, and in one case the remnants of an egg string was found attached to an arm sucker of such a female.

In both species, gravid or near-gravid females were taken only at the lower limits of the species' vertical range. Although mature males were not taken, those nearest maturity were also taken in the lower parts of the depth range. Apparently, mating takes place at the lower depth limits of the population. Brooding females, on the other hand, were found only at the upper limit of the adult population in *J. diaphana* and only well above the upper limit of the remaining adult population in *E. pygmaea*. The brooding females of both species occurred around 800 m. Presumably the females migrate upward to around 800 m either just before or just after spawning. The increased risk of predation above 800 m probably prevents the female from further upward movement: the numbers of fishes increase greatly above 800 m (Amesbury 1975), and visual detection of the large silhouette presented by a brooding female should be possible above about 750 to 775 m (Young and Roper 1977). The upward movement must be unrelated to feeding since brooding females do not feed (Young 1972b). The upward migration may simply decrease the distance the young must travel after hatching to their larval habitat near 200 m.

A number of cephalopods may spawn at the lower end of their depth range. Evidence for deep-spawning was found in several vertically migrating species. A single spent female of *Liocranchia reinhardti* was captured at 775 m at night, well below its normal night habitat in the upper 200 m. A single gravid, mated female of *Brachioteuthis* sp. was captured at 1,125 m at night; its normal night habitat is in the upper 200 m. *Heteroteuthis hawaiiensis* migrated vertically and exhibited

narrow vertical ranges day and night until sexual maturity was reached; a poorly defined ontogenetic descent then ensued. Unfortunately, no other clues to spawning depth are known.

The nonmigrating species that exhibit a gradual ontogenetic descent would be expected to spawn at the lower end of their range. Indeed, this appeared to happen in *Bathothauma lyromma*. The most dramatic example occurred in *Leachia pacifica*. Young (1975a) demonstrated that this species descends near the time of sexual maturity from near-surface waters to depths of 1,000 to 2,000 m to mate and spawn.

Larvae of most pelagic oceanic cephalopods occur in near-surface waters. Upward migration of larvae would seem to be a formidable task for species that spawn at great depths. The deep-living octopods apparently carry their young partway up presumably to lighten this task. Perhaps squid egg masses are positively buoyant and float to the surface. There are a number of observations of egg masses of pelagic cephalopods floating at or near the ocean surface (see Clarke 1966). However, these have yet to be shown to belong to a deep-spawning species.

Photosensitive Vesicles

These vesicular organs were present in all Hawaiian pelagic cephalopods and they occurred in a great variety of shapes, sizes, and locations. In many squids, the organs were subdivided into as many as four sets of separate organs. In squid, the organs were always found within the confines of the cephalic cartilage and were located either on the optic stalk (central organs) or dorsal, posterior, or ventral to the optic stalk (dorsal, posterior, and ventral organs, respectively). The separate organs often faced different directions (i.e., their broadest surface faced a dorsal, posterior, or ventral direction).

These separate organs were frequently associated with distinctive "windows" in the overlying skin bearing few if any chromatophores. Such windows seem to be unnecessary since most cephalopods can become quite transparent by contraction of their chromatophores. The windows in combination with the more pigmented surrounding skin, however, may restrict light to specific receptors and thereby improve the directionality of the organs. In a few cases (e.g., *Phasmatopsis fisheri* and *Ctenopteryx siculus*), the organ was not subdivided but elongate and curved, allowing different portions of a single organ to face various directions. A directional response of each portion was insured either by heavy pigment (e.g., *P. fisheri*) or silvery iridophores (*C. siculus*) which shielded one surface of the organ. Not all species, however, had vesicular organs that could discriminate between dorsal, posterior, and ventral sources of light. Some species had undivided central organs (e.g., *Sandalops melancholicus*, *Taonius pavo*) without apparent screening devices which therefore are nondirectional. In others, the total area surveyed by a nondirectional organ was restricted by its cryptic position (e.g., *Vampyroteuthis*). Clearly not all cephalopods use these organs in the same way.

General trends between organ size and habitat depth during the day occurred in these animals. Teuthoids and sepioids found in the upper 400 m (neritic species and young *Heteroteuthis hawaiiensis*) generally had small organs. Species found primarily between 400 and 700 m generally had large, complex organs. These included most enoploteuthids, histioteuthids, probably *Discoteuthis laciniosa*, *Liocranchia reinhardti*, and young *Taonius pavo*. Between 700 and 800 m, species with large, complex organs (i.e., *Ctenopteryx siculus*, *Phasmatopsis fisheri*, *Thelidioteuthis allessendrinii*, *Cycloteuthis serventyi*, probably large *Octopoteuthis nielseni*, adult *Taonius pavo*, and *Galiteuthis pacificus*, and *Bathyteuthis abyssicola*) cooccurred with species which had small organs (i.e., chiroteuthids, *Mastigoteuthis*, *Grimalditeuthis bomplandii*, large *Liocranchia valdiviae*, and probably *Neoteuthis* sp.). Many of the small-vesicle species had ranges that extended well below 800 m, where they were joined by other small-organ species (i.e., *Vampyroteuthis infernalis* and probably *Joubiniteuthis portieri*).

The relationship of organ size to habitat depth was especially marked in young *Phasmatopsis fisheri*. The epipelagic larvae of *P. fisheri*, which may grow to 40 and 50 mm ML had small central vesicles. Upon metamorphosis and descent to the adult day habitat (650-775 m), the organs became greatly enlarged (Figure 34). As growth continued, however, a gradual positive allometric growth of the organs occurred without a clear increase in habitat depth.

A number of species did not follow these general trends. Several cranchiids exhibited gradual ontogenetic descent; one of these (*Helicocranchia beebei*) had small organs, while the others (*San-*

dalops melancholicus and *Bathothauma lyromma*) had large organs. *Leachia pacifica*, which had small organs, spent most of its life in epipelagic waters and then descended to depths >1,000 m. *Onychoteuthis compacta* seemed to range widely during the day and had rather large organs (its habitat, however, is poorly known). *Brachioteuthis* had similar organs but probably occurred below 800 m during the day. The ommastrephids had a complex arrangement of organs, yet these animals were primarily epipelagic. In juveniles of many species (e.g., enoploteuthids), the size of the organs (relative to the size of the brain) may be large; yet their absolute size was small when compared with adults occupying the same depths.

Compared with squid, all octopods had small organs. With the probable exception of the tubular eyed *Amphitretus pelagicus*, octopods probably do not occupy depths between 400 and 700 m during the day except as juveniles in transit to greater depths. *Amphitretus pelagicus* is the only pelagic octopod that exhibited clear modification of its organs. In contrast to the small organs, each consisting of a single vesicle, of other octopods, this animal has a larger organ composed of many separate vesicles.

Presumably the general trends with depth were related to depth gradients in both downwelling daylight and bioluminescent light. Downwelling daylight decreases exponentially with depth. Bioluminescent activity should increase from 400 to 600-800 m then decline rapidly if numbers of midwater fishes at various depths (see Amesbury 1975) provide an index to bioluminescent activity during the day. While many vesicles may detect both downwelling skylight and bioluminescent light, we will examine evidence for these two functions separately.

The eyes of some mesopelagic animals can probably detect silhouettes at depths of 750 to 775 m (Young and Roper 1977). Presumably some photosensitive vesicles are at least as sensitive as the eyes, especially when we consider the large size and apparent high pigment density of some (see Young 1972a). The large dorsal organs of squid were positioned so they are exposed to downwelling daylight. Large central organs appeared to be exposed to this light in species lacking dorsal organs.

Some experimental evidence indicates that midwater cephalopods detect downwelling light with these vesicular organs. A number of cephalopods have been seen to conceal themselves with bioluminescent light (Young and Roper 1977). This counterillumination requires that the intensity of downwelling light is precisely determined by the animal, and the photosensitive vesicles seem the likely photoreceptor (Young 1973, 1977). Recently R. E. Young, C. F. E. Roper, and J. Walters (in manuscr.) covered the dorsal organs of *Abraliopsis* sp. B while it was counterilluminating and recorded a 90% drop in its luminescence. They concluded that the dorsal organs detect downwelling light. Since animals can detect downwelling light with these organs for counterillumination, they may use this photic information for other purposes as well.

Vertical migration in many midwater animals is closely associated with changing light levels (Boden and Kampa 1967). Since cephalopods migrate during twilight periods, light cues received by the vesicular organs may serve to trigger or regulate their migrations. This view is supported by three sources of evidence. First, nerves from the vesicles pass into the peduncle complex of the brain. Messenger (1967b) suggested, on the basis of experimental evidence in *Octopus*, that this complex is part of a visuomotor system: visual information from the eyes enables this complex to exercise control over locomotion. Secondly, experimental evidence on the function of the photosensitive vesicles in neritic *Octopus* strongly suggests that these organs regulate diurnal activity patterns (R. Houck pers. commun.). Finally, most migrating cephalopods have large vesicular organs positioned to detect downwelling light. The only exceptions are species of *Mastigoteuthis* and *Chiroteuthis*, whose migration patterns are not as distinct as in other species.

If dorsal and central organs function primarily in the detection of downwelling light, we may have a clue to the peculiar arrangement of vesicular organs in ommastrephids. The ommastrephids were the only squids that had central organs on the dorsal surface of the optic stalk as well as dorsal organs. In *Nototodarus hawaiiensis*, these two organs differ morphologically (the small central organ has large component vesicles and the large dorsal organ has small vesicles), but the organs are adjacent to one another. The structural differences suggest separate functions for the organs, yet their close proximity indicates that both will be exposed to the same source of light. The same argument holds for these organs in other ommastrephids, although the two organs are

somewhat further separated. The ommastrephids have the unusual habit of usually living in epipelagic waters but occasionally descending to great depths (Roper and Young 1975). Perhaps the central organs function in epipelagic waters while the dorsal organs operate only in deep water. Certainly there are considerable problems associated with a single organ functioning over such a wide range of light intensities.

Certain photosensitive vesicles appear to detect bioluminescent light rather than downwelling skylight. The small vesicular organs in the deep-living *Vampyroteuthis infernalis* are shielded from downwelling skylight (Young 1972a). Vesicular organs are present in the blind bathypelagic octopod *Cirrothauma murayi* (J. Z. Young in Packard 1972) which lives in depths where detectable surface light is absent. Certain photosensitive vesicles of many other species were shielded from downwelling light. Such organs presumably detect bioluminescent light. Young (1973, 1977) demonstrated that certain vesicular organs in some species were directly exposed to the animal's photophores, presumably for counterillumination purposes.

The detection of bioluminescence is not limited, however, to the animal's own photophores. With only a few exceptions all species examined had some means of "viewing" various parts of the mantle cavity with their vesicular organs. In many cases, the organs seemed precisely placed for this purpose (see Figure 6). In most species with large opaque livers (e.g., ommastrephids, enoploteuthids, histioteuthids, bathyteuthids, cycloteuthids, octopoteuthids, and mastigoteuthids), some organs extended laterally or ventrally past the liver, enabling a "view" of the mantle cavity. In other species with the liver far back in the mantle cavity (e.g., cranchiids, *Brachioteuthis*, *Ctenopteryx*), only central organs were present. In *Vampyroteuthis infernalis*, the organs lay within the mantle cavity and could only be exposed by light originating within this cavity, the funnel, or at the mantle opening. This animal, like most other cephalopods, had no photophores in these locations. The photosensitive vesicles in octopods were also located within the mantle cavity. The view of the mantle cavity is obscured only in *Onychoteuthis*, *Chiroteuthis*, *Joubiniteuthis*, and Chiroteuthidae gen. sp., although most of these species could still detect light from within the funnel and at the entrance to the mantle cavity.

Young (1972a) suggested that the photosensitive vesicles in *Vampyroteuthis* detect small glowing organisms that are carried into the mantle cavity with the respiratory current. In the deep sea, a glowing organism within the mantle cavity could reveal the squid's location and have disasterous consequences. J. Z. Young (1977) extended this idea to octopods. Nevertheless, this suggestion seems unlikely to have broad application in explaining the consistent relationships between vesicle location and mantle cavity "visibility"; however, no alternative function has been found.

Some squid may detect bioluminescent light originating outside the animal. The large vesicular organs in the deep-living *Bathyteuthis abyssicola* are not exposed to its own photophores and probably detect bioluminescence from animals located outside its restricted visual field (Young 1972a). In *Ctenopteryx siculus*, the elongate vesicular organs joined in the midventral line over the funnel and were there shielded dorsally and laterally by a thick layer of iridophores. The ventral part of this organ would detect light originating within the funnel. Yet, the high organization and sophisticated structure of the vesicles seem overly matched for such a task. This organ probably "looks" ventrally through the funnel to the area below the squid. Similar arguments could be made for certain lobes in other squids.

The photosensitive vesicles in many cephalopods apparently form an elaborate system for monitoring bioluminescent light from their own photophores, from within the mantle cavity, and from the immediate vicinity of the animal that lies outside the visual field

The great variety of photosensitive vesicles found among the species of pelagic cephalopods off Hawaii presumably reflects a variety of functions for these organs associated with the detection of both downwelling and bioluminescent light. The morphology and placement of these organs have provided some clues to these functions. A full understanding of this complex sensory system, however, must await experimental studies on living animals.

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Note added in proof: The correct name for the species listed here as *Phasmatopsis fisheri* is *Megalocranchia fisheri* (N. Voss. In press. Studies on the cephalopod family Cranchiidae. A revision of the genera, with a key for their determination. Bull. Mar. Sci.)

SYSTEMATIC SAMPLING IN A PLANKTONIC ECOSYSTEM

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ABSTRACT

Two sampling studies, computer simulation and field, investigated the consequences of applying restricted systematic sampling (at predetermined depths) to estimate total chlorophyll in the water column. Comparison was made with stratified random designs with one and two samples per strata. Systematic sampling appeared more accurate than most stratified random designs. However, when repeated over restricted spatial or temporal intervals, systematic designs tended to produce biased estimates. In the central Pacific, an interval of several days, or 100-200 km, appeared necessary for natural population fluctuations to average out the bias inherent in a restricted systematic sampling design.

Underlying sampling theory is the assumption of random collection of samples. This is the only satisfactory method of assuring a representative sample from an unknown population. In pelagic ecology (and undoubtedly in other fields) this assumption is generally neglected and surveys are conducted at fixed geographic positions, at fixed spatial or temporal intervals, and/or at fixed depths, without recourse to randomization. The implicit assumption is that the natural complex variability of pelagic populations provides the necessary element of randomization.

Two types of sampling strategies are frequently called systematic. The present study is concerned with the situation in which the sampling positions are fixed according to some pattern determined by the investigator and are not necessarily at equal intervals; this will be termed restricted systematic sampling (RSS) to distinguish it from the strategy in which only the sampling interval is fixed and the location of the first sample in the first interval is determined at random (randomly located systematic sampling; Yates 1948). Among the alternate sampling strategies which provide the requisite randomization, unrestricted random and stratified random sampling (SR) have received the most attention. In unrestricted random sampling, samples are selected individually from the entire population by some random process, such as by numbering all sampling units and selecting from them by means of a random numbers table. In SR, the population is first divided into subpopulations from each of which one or more samples are selected at random. SR is useful because it ensures that the samples are distributed throughout the entire population.

Three characteristics of sampling designs are of interest (Figure 1): 1) bias, any consistent deviation between the true population parameter and repeated estimates based on the same sampling design; 2) precision, the variability of successive estimates about their mean when a sampling design is repeated on the same population; and 3)

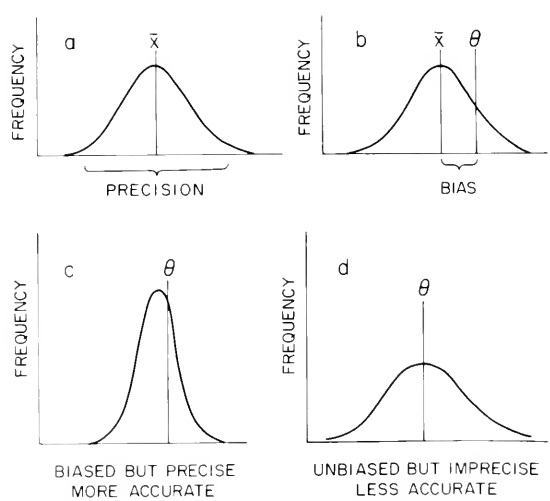

FIGURE 1.—Normal frequency distributions used to illustrate: a) precision, the spread of observations about their mean value ($\bar{x}$); b) bias, the deviation of the mean of repeated observations from the true parameter (θ); c) a distribution which is biased but precise; and d) a distribution which is unbiased but imprecise. Distribution c will be more accurate than distribution d, in spite of the bias, if the average deviation of observations from θ is smaller.

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accuracy, a concept including both freedom from bias and high precision and which, in the absence of bias, is equivalent to precision. The practical determination of precision, in its strictest sense, is restricted to quasi-static populations in which the population remains unchanged between collections of replicate samples (forests or soil types or mussel beds, etc.). In the case of RSS, the concept of precision has no meaning in this type of population because successive application of the same sampling design to the same population will give identical results. Such static populations do not exist in a planktonic system because spatial and temporal variability produce continual change. Thus, in the present study, the concept of a population is expanded to incorporate spatial and temporal fluctuations in which case the precision of RSS has a real value.

Theoretical aspects of systematic random sampling strategies have been considered by many (e.g., Yates 1946, 1953; Deming 1950; Cochran 1963; Sukhatme and Sukhatme 1970). Empirical investigations have been restricted to terrestrial systems, particularly to surveys of vegetation types or timber volumes (e.g., Hasel 1938; Osborne 1942; Finney 1948b, 1950; Numata and Nobuhara 1952; Bourdeau 1953; Milne 1959). The results from these studies indicate that randomly located systematic sampling often gives more accurate estimates than other procedures (Hasel 1938; Osborne 1942; Madow 1946; Yates 1946, 1948; Finney 1948a; Bordeau 1953; Milne 1959; Grieg-Smith 1964) especially when the sampled population has positive correlation between neighboring units (Cochran 1946; Milne 1959; Sukhatme and Sukhatme 1970). Because of the greater precision and greater convenience of systematic sampling, some workers have recommended its use for terrestrial surveys (Hasel 1938; Yates 1946; Milne 1959). On the other hand, it has been shown that irregular distributions or pronounced patterns of variation, especially periodicity or linear trends, may cause systematic designs to give biased estimates or estimates of reduced precision (Madow and Madow 1944; Finney 1950; Bourdeau 1953; Sukhatme and Sukhatme 1970); nor does the precision necessarily improve with increasing sample size (Madow 1946; Bordeau 1953).

Of the random designs, SR generally offers greater precision than unrestricted random sampling (Yates 1953; Milne 1959) and, with a constant number of samples, this precision increases as the number of strata increases (Yates 1953). The most precise design is one with one sample per strata, but this (like a systematic sample) offers no internal estimate of error (Finney 1948a, b).

The success of systematic sampling clearly depends upon the nature of the sampled population. If individuals or properties in a population are distributed at random, all strategies will be equivalent. Pronounced pattern, however, may increase or decrease the effectiveness of systematic designs. Thus, quite aside from the theoretical objections to systematic sampling, uninformed application of any systematic sampling is to be discouraged.

Although Strickland (1968) warned that discrete samples may give a poor representation of the vertical distributions of highly stratified substances, such as chlorophyll, a thorough study of the consequences of systematic sampling in the ocean has not been conducted, even though most populations have marked gradients, especially along the vertical axis. This may be attributed to the logistical difficulties of enumerating an oceanic population in its entirety, in contrast to a timber stand in which every individual may be observed, counted, measured, and mapped.

The present study is restricted to the consequences of applying RSS in the vertical direction. The distribution investigated is that of chlorophyll in an oligotrophic oceanic environment. Total chlorophyll in the water column is a frequently used index of plant crop and it is most often estimated from a series of restricted systematic samples. The major question is whether such sampling produces any bias in the estimate of total chlorophyll, or whether the temporal and spatial heterogeneity of the chlorophyll distribution is sufficient to average out the biases of individual determinations. Of secondary concern is whether there is a significant difference in precision or accuracy between estimates derived from RSS and those derived from SR.

The area of study is the North Pacific Central Gyre in the vicinity of lat. 28°N, long. 155°W. The region is one of relatively low spatial and temporal variability (Venrick et al 1973; Gregg et al. 1973; McGowan and Williams 1973; Eppley et al. 1973; Haury 1976). Thus, it is an environment in which any adverse characteristics of RSS are expected to be magnified. The general features of the distribution of chlorophyll in the North Pacific Central Gyre have been summarized (Venrick et al. 1973). Most of the year, surface concentrations are low (0.02-0.06 mg/m^3), and there is a narrow subsur-

face maximum layer (0.10-0.20 mg/m^3) centered between 90 and 120 m.

The present study was conducted in two parts. In part A, a computer was used to sample nine semiartificial populations derived from continuous vertical profiles of chlorophyll fluorescence. Changes in the fluorescence per extractable chlorophyll unit with depth (Kiefer 1973) and smoothing of small-scale features during the pumping procedure result in a profile which represents only the grosser features of the true distribution. From the vertical profiles, the total population along the vertical axis was calculated, allowing the accuracy of various sampling strategies to be determined directly. Study B was conducted in the field where restricted systematic and stratified random samples were collected simultaneously from the population. In this study, a real population was studied but the total population could only be approximated.

METHODS

Analytical Procedures

Chlorophyll a was determined fluorometrically according to the procedure of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965). Water for discrete, extracted chlorophyll samples was obtained with Nansen bottles. Water for continuous vertical profiles was obtained with the seawater pumping system described by Beers et al. (1967) and was passed through a fluorometer equipped with a flowthrough door.

Study A

The chlorophyll fluorescence profiles were taken during September 1968, on 9 consecutive days during which time the ship followed two drogues which were set at 10 m depth to follow the mixed layer. These were launched at lat. 27°00'N, long. 155°18'W and moved in a northwesterly direction at speeds between 0.5 and 1.5 kn covering 345 km in 9 days. The profiles were not made at the same time of day. The closest two profiles were separated by 13 h, the most distant by 40 h. Additional aspects of these profiles and accessory data have been published (Scripps Institution of Oceanography 1974).

The fluorescence profiles were read at 1-m intervals and translated into units of approximate chlorophyll down to a depth of 180 m. In order to offset the increase in fluorescence per unit of extractable chlorophyll with depth, one conversion equation was used down to and including the chlorophyll maximum and another below the maximum. The conversion factors were determined by analysis of chlorophyll extracted from discrete water samples collected periodically during the cruise. The surface value of each continuous profile was set to 0.03 mg/m^3 and the minimum value below the maximum to 0.01 mg/m^3; these were the mean values of extracted chlorophyll observed at the surface and at 200 m, respectively. The horizontal scale was adjusted to bring the mean maximum value of all profiles to 0.156 mg/m^3, the average maximum of the discrete samples. A typical adjusted profile is presented in Figure 2.

These semi-artificial populations were sampled with four stratified random designs (Table 1). The success of SR depends upon the extent to which the strata can be made internally homogeneous. In an attempt to achieve this, the stratum boundaries of SR-1 and SR-2 were determined as much as possible by the hydrographic, biological, and chemical

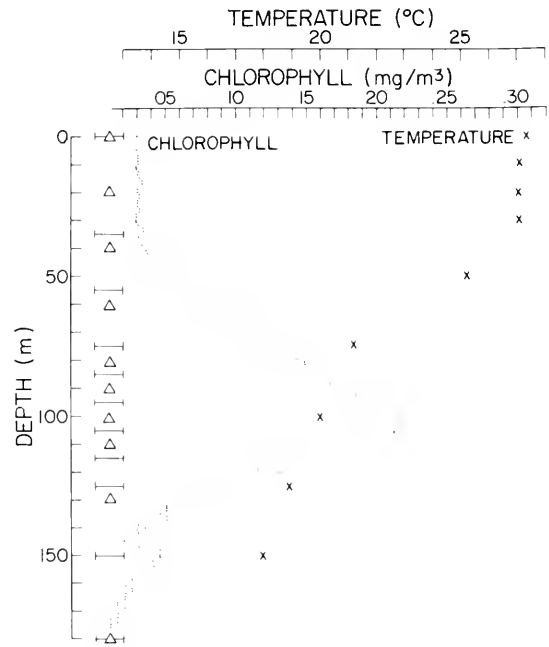

FIGURE 2.—A typical population of chlorophyll values derived from a continuous profile of fluorescence (27 September 1968) and sampled in study A, together with the temperature values from the associated hydrocast. Triangles indicate the location of samples in restricted systematic design 3; bars represent the boundaries of strata used in stratified random design 1.

TABLE 1.—Systematic and stratified random sampling designs used in studies A and B.

Systematic:	RSS-1	RSS-2	RSS-3	RSS-4	Stratified random:	SR-1	SR-2	SR-3	SR-4
	0	0	0	0		0	0	0	0
	20	10	20	45		35	75	15	45
	40	25	40	65		55	95	45	90
Sample	60	35	60	80	Stratum	75	105	75	110
depths	80	50	80	90	boundaries	85	125	90	130
(m)	100	60	90	100	(m)	95	180	100	180
	120	75	100	110		105		110	
	140	100	110	120		115		120	
	160	125	130	137		125		130	
	180	180	180	180		150		150	
						180		180	

characteristics of the environment (Figure 2), and larger strata were assigned to the layers in which environmental gradients were small and several narrow strata were placed in the region of the chlorophyll maximum. The 35-m boundary marked the average depth of the mixed layer; 95 m was the approximate depth of penetration of 1% of the surface radiation, and 125 m represented the beginning of the nutricline. Design SR-1 consisted of 10 strata, each with one sample; in design SR-2, adjacent strata were lumped giving five strata with two samples in each. Designs SR-3 and SR-4 were those used in study B (below) and were thus based on environmental characteristics observed at that time. Each of the nine populations was sampled 20 times with each of the stratified random designs. To facilitate comparison with the systematic samples, for which there was only one cast of each design per profile, it was desirable to examine a series of unreplicated stratified random samples. For this purpose, 10 subsets were selected at random from the replicate casts, each subset containing nine stratified random casts, one from each population. Total chlorophyll was calculated from the mean (arithmetic) concentration per strata times the width of that strata, summed over all strata. This is the classical procedure for summarizing data collected by SR.

Four RSS designs were employed: RSS-1, one sample at the surface and every 20 m thereafter; RSS-2, the design actually employed in September 1968 in which the cast was partially determined by standard hydrographic depths; RSS-3, a design which was based upon complete knowledge of the vertical distributions which were being sampled and which was derived from application of the general rules of sample allocation, i.e., samples were concentrated in the region of maximum variability (the chlorophyll maximum layer); RSS-4, a design based on stratified random design 1 (and therefore more strictly comparable to it) with a sample at the top of the upper stratum (0 m) and bottom of the lowest stratum (180 m) and at the center of all intermediate strata.

Two methods of calculating total chlorophyll from systematic samples were investigated. In the first, the layer between adjacent samples was represented by the arithmetic mean of the two samples (equivalent to integration with linear interpolation). In the second, the layer was represented by the geometric mean of adjacent samples. This latter procedure is sometimes recommended when the population exhibits large, nonlinear changes between adjacent samples. A comparison of the two procedures was made in study A, on the basis of which the method using geometric means was rejected.

Study B

Study B, conducted in June 1977, combined two 10-sample designs, one restricted systematic (RSS-1) and one stratified random (SR-3 or SR-4) into a single 20-bottle cast. The strata boundaries were primarily determined from two preliminary 18-bottle casts which defined the regions of chlorophyll gradients and from a single STD trace which defined hydrographic strata (Figure 3). As in study A, narrower strata were established at the depths of maximum gradients of chlorophyll (the region of the maximum layer). The major differences between designs SR-1 and SR-2 and designs SR-3 and SR-4 were due to a shallower mixed layer and broader, deeper maximum layer observed in June 1977.

Over a period of 21 days, a total of 18 casts were made, 9 employing RSS-1 and SR-3 and 9 employing RSS-1 and SR-4. All casts were located within a rectangle bounded by lat. 28°21.6′N and 28°45.9′N, and by long. 155°14.0′W and 155°33.5′W. Fourteen casts were taken in conjunction with another program between the hours of 2200 and 0300 (with one exception, delayed by winch failure until 0550). Twelve casts were

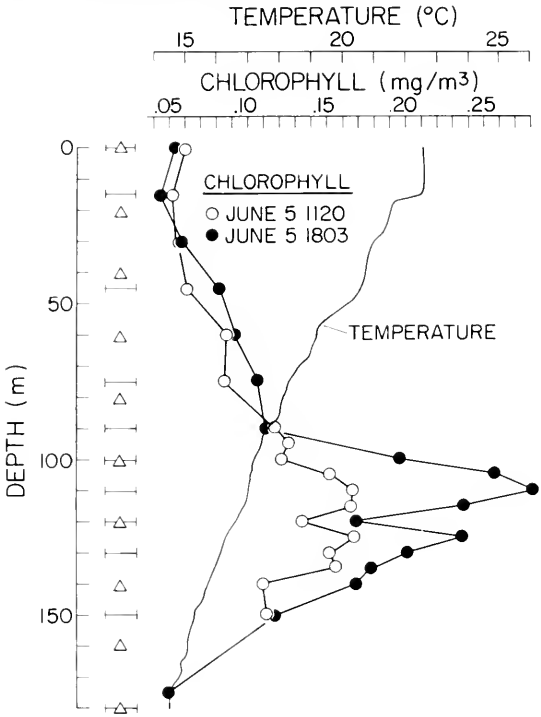

FIGURE 3.—Chlorophyll values observed in two 18-bottle casts preliminary to study B, together with the temperature trace from the associated STD lowering. Triangles indicate location of samples in restricted systematic design 1; bars represent the boundaries of strata used in stratified random design 3.

paired, taken within a few hours and within 3 n.mi. of each other. These have been considered replicate casts.

When the combined systematic-stratified random design called for bottles to be spaced more closely than 3 m, it was necessary to use a messenger heavier than the standard Nansen messenger (such as a Niskin bottle messenger) in order that it develop enough momentum to trip the second bottle. When both sampling designs called for the same depth, the extra bottle was arbitrarily positioned, usually filling in the largest gap in the region of the chlorophyll maximum layer. This "free" sample was used only in the calculations of total chlorophyll in the water column.

Statistical Procedures

Bias is evaluated by the consistency with which n observations ($x_i, i = 1, n$) from a given sampling design fall above or below the true population value and may be measured as a percent of the true value (θ):

$$\left[\frac{\sum (x_i - \theta)}{n} \times 100\%\right] / \theta.$$

Precision is measured by the variance of a series of n observations about their mean ($\bar{x}$):

$$\frac{\sum (x_i - \bar{x})^2}{n-1}.$$

In an analogous way, accuracy is measured by the mean square deviation of a series of observations from the true population total:

$$\frac{\sum (x_i - \theta)^2}{n-1}.$$

Both accuracy and precision are inversely related to their statistical measures, increasing as the numerical value of the measure decreases. Since most scientists are used to thinking in terms of variances and sums of squares, it did not seem desirable to invert these measures to achieve direct correspondence.

In the analysis of the results, limited use was made of the parametric analysis of variance. Most statistical tests were nonparametric tests which make few assumptions about the characteristics of the data (e.g., Dixon and Massey 1957; Tate and Clelland 1957; Conover 1971; Hollander and Wolfe 1973). Unless stated otherwise, the probabilities associated with conclusions in the text are derived from the binomial distribution with $p = \frac{1}{2}$.

In several analyses in these studies, the problem of multiple testing arose, as when all four systematic designs were tested for bias. Unfortunately, the tabulation on most nonparametric procedures is not sufficiently complete to allow correction for multiple testing to be made without making the tests extremely conservative. Since this was deemed undesirable, the probabilities given for the statistical tests are uncorrected. It is unlikely that this makes any real difference in the outcome of these studies which gain most of their force from the similarity of results in the two approaches.

RESULTS

Study A

Integration of values

The results of study A are summarized in Table 2. The total chlorophyll values derived from the four systematic sample designs were calculated by integration with linear interpolation (i.e., using the arithmetic mean of adjacent samples to represent the average chlorophyll in the stratum between them). Use of the geometric mean in this calculation resulted in the true total being underestimated 27 out of 36 times ($P = 0.01$). Nor was there any increase in accuracy (the resultant accuracies, based on use of the geometric mean, were 0.538, 0.987, 0.488, and 0.752 for RSS-1 through RSS-4). The use of the geometric mean in the calculation of total chlorophyll does not appear to be justified.

Bias

The biases observed in the eight sampling strategies are summarized in Table 3. Of the four restricted systematic designs, only RSS-2 gave no signs of bias. Design RSS-3, the "best informed" design, overestimated the true population total in eight of the nine trials ($P<0.05$). RSS-1 overestimated the population only five out of nine times, but the overestimates were clustered toward the end of the series and the underestimates toward the beginning. This temporal trend lies just outside the usual level of significance (run test; $P<0.10$) but it indicates that the time period necessary for the population to provide "random" variability of sufficient magnitude to eliminate bias may be of the order of several days or 100-200 km. The magnitudes of the biases were −4.0% for the period 19-21 September and +3.7% for the period 24-27 September. Similarly, the bias introduced by using RSS-3 to estimate the true population total for 19-25 September was −3.6%.

The peculiar periodicity of bias seen in RSS-4 also indicates a nonrandom interaction between the sampling design and the sampled population

TABLE 3.—Bias of systematic and stratified random sampling designs, Study A.

Date (1968)	Systematic designs				Stratified random designs			
	RSS-1	RSS-2	RSS-3	RSS-4	SR-1	SR-2	SR-3	SR-4
19 Sept.	−	−	+	−	+	− −	−	+
20 Sept.	−	−	+	+	−	− +	[1]0	−
21 Sept.	−	−	+	−	+	− +	[1]0	+
22 Sept.	+	+	+	+	−	− +	[1]0	+
23 Sept.	−	−	+	−	−	− −	−	−
24 Sept.	+	−	+	+	+	− −	+	+
25 Sept.	+	+	+	[1]0	−	− −	−	+
26 Sept.	+	−	−	−	+	− +	−	+
27 Sept.	+	+	+	+	+	− +	+	−

[1]Estimate = true value.

TABLE 2.—Results of study A, a computerized simulation sampling study. The estimated parameter (θ) is total chlorophyll above 180 m; units are milligrams per square meter; time is local time.

Date (1968)	Time	True value (θ)	Systematic designs One cast each				Stratified random designs Means and variances (in parentheses) of 20 replicates			
			RSS-1	RSS-2	RSS-3	RSS-4	SR-1	SR-2	SR-3	SR-4
19 Sept.	1719	8.50	8.00	8.00	8.62	8.39	8.52	8.38	8.39	8.59
							(0.345)	(2.460)	(0.642)	(0.050)
20 Sept.	2312	10.31	9.91	9.98	11.12	10.71	10.29	10.18	10.31	10.24
							(0.244)	(0.987)	(0.182)	(0.513)
21 Sept.	2335	7.35	7.21	6.69	7.57	7.33	7.36	7.16	7.35	7.36
							(0.059)	(0.950)	(0.215)	(0.466)
22 Sept.	2351	6.89	7.23	7.72	7.45	7.18	6.85	6.88	6.89	6.92
							(0.072)	(0.151)	(0.081)	(0.129)
23 Sept.	2025	8.83	7.97	7.51	9.03	8.47	8.62	8.68	8.82	8.78
							(0.801)	(1.780)	(0.341)	(1.227)
24 Sept.	0900	9.68	9.70	9.20	9.94	10.56	9.81	9.57	9.85	9.79
							(0.178)	(1.490)	(0.406)	(1.841)
25 Sept.	0800	11.00	11.84	12.08	11.08	11.00	10.86	10.90	10.92	11.16
							(0.263)	(1.436)	(0.443)	(0.687)
26 Sept.	0830	13.85	14.23	13.14	13.36	13.06	13.92	13.23	13.65	13.90
							(1.123)	(5.323)	(2.289)	(3.954)
27 Sept.	2400	13.90	14.47	14.56	14.94	14.78	14.17	13.60	14.06	13.83
							(0.490)	(3.676)	(1.409)	(3.348)
Accuracy $\frac{\sum(x_i - \theta)^2}{n-1}$			0.308	0.695	0.308	0.320	[1]0.574	[1]1.464	[1]0.779	[1]1.662
Precision $\frac{\sum(x_i - \bar{x})^2}{n-1}$		6.441	8.113	7.729	6.537	6.725	[1]8.004	[1]6.312	[1]7.036	[1]8.540

[1]Mean values from 10 sets of unreplicated casts.

(run test, $P = 0.10$). With the sampling interval employed here, the biases of individual estimates average out over the entire study. Had the interval been twice as large, a consistent overestimate or underestimate would have resulted, with respective magnitudes of +5.8% and −1.9%, until 25 September when the phase relationship appears to have shifted.

Tables 2 and 3 also present the results of the four stratified random designs, based upon the means of 20 replicates. The consistent underestimates resulting from SR-2 were sufficiently unexpected that a second series of 20 SR-2 samples were drawn from each population. This series showed no evidence of bias and, thus, it appears that the initial results were the product of random chance.

Precision

Precision, in its strictest sense, could only be examined in the case of the stratified random designs, for which replicates were available. The designs employing 10 strata, each with one sample, SR-1 and SR-3, offered greater precision than designs with fewer strata. However, there was a highly significant concordance (Kendell coefficient, $P<0.01$) between the precisions of all designs with respect to the profiles giving the most precise result. Examination of the individual profiles indicated that the precision of the results was inversely related to the strength of the chlorophyll maximum and to the amount of small-scale variability along the vertical axis, or, in other words, to the structural complexity of the population. Later, the accuracy of the systematic designs (discussed below) was found to show the same relationship.

For all stratified random designs, the variance between replicates was trivial compared with the variance between the nine populations. Analyses of variance gave $f_{8,19}$ ratios ranging from 54 to 344 (all $P<<0.01$). When all nine profiles were considered to be replicates of the same population, the variance between the nine estimates from each systematic cast could be compared with the variance between single stratified random casts, one from each population (Figure 4A). On this scale, there were no differences in precision between any of the sampling designs. The large variation between populations masked any difference in performance. Thus, when the concept of the sampled population is expanded to include spatial and temporal variations, RSS appears to offer neither advantages nor disadvantages with respect to precision of estimates.

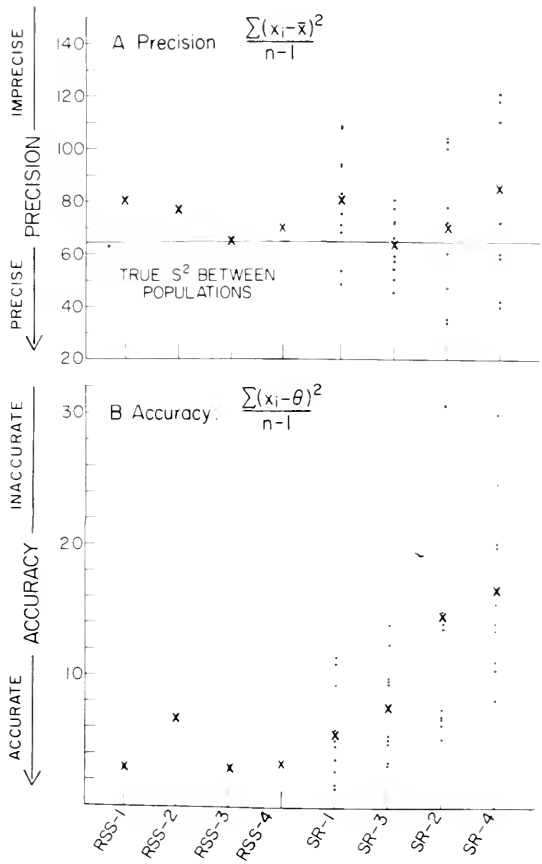

FIGURE 4.—The results of the computer simulation sampling study, study A, showing the relative precisions and accuracies of the four restricted systematic sampling designs (RSS) and four stratified random designs (SR).

Accuracy

The accuracy of the various designs was also compared using sets of unreplicated stratified random casts (Figure 4B). The greater accuracies of stratified random designs SR-1 and SR-3 relative to SR-2 and SR-4 undoubtedly reflected their greater precision; and perhaps the greater accuracy of SR-1 relative to SR-3 was due to selection of more appropriate strata. The systematic designs were generally more accurate than the stratified random designs. Only stratified random design SR-1 achieved the accuracy of the systematic designs.

Most of the chlorophyll work in the central Pacific has been based upon 12 or more sampled depths. Thus, it was encouraging to find that as few as 10 depths, regardless of the sampling strategy, gave a generally satisfactory picture of the amount of chlorophyll in the water column. Of nearly 400 estimates from individual casts, 76% fell within ±10% of the true value. This percent increased to 85% for stratified designs SR-1 and SR-3 and to 94% for the 36 systematic casts. However, to the extent that these fluorescence profiles underestimate the structural complexity of the true chlorophyll distribution, these results probably overestimate the accuracies of the designs.

Study B

The results of the field study were remarkably similar to those of the computer study (Table 4). Bias and accuracy were investigated by assuming that the entire population was exactly represented by the 20 samples in one cast (systematic samples plus stratified random samples plus "free" samples). The results of study A indicate that the discrepancy is not likely to be severe.

TABLE 4.—Results of study B, a field sampling study. The estimated parameter is total chlorophyll above 180 m and the true value (θ) is estimated from the 20 combined samples of the two designs; units are milligrams per cubic meter.

Date (1977)	Local time	θ	x_i bias RSS-1	x_i bias SR-3	x_i bias SR-4
5 June]	2345	18.87	18.73−	18.25−	
6 June]	0220	17.68	17.10−	18.69+	
8 June	0033	15.54	14.06−	18.21+	
9 June	0236	18.11	17.23−	17.55−	
9 June]	2241	16.70	16.22−	17.19+	
10 June]	0550	15.47	14.75−	16.68+	
13 June]	2208	13.26	13.29+	12.31−	
14 June]	0035	13.42	13.47+	13.33−	
15 June	2203	14.53	15.91+	11.19−	
19 June]	2149	11.50	10.91−		9.03−
20 June]	0100	10.29	10.78+		10.78+
21 June	2246	14.25	14.73+		11.42−
22 June	1107	10.67	11.00+		10.17−
23 June]	2333	13.60	13.41−		12.97−
24 June]	0133	12.52	12.16−		12.09−
24 June]	1505	16.83	17.11+		18.11+
24 June]	1632	16.98	17.69+		15.72−
26 June	0822	13.32	13.58+		13.10−
Accuracy:	$\frac{\sum(x_i - \theta)^2}{n-1}$		0.45	2.83	2.31
Precision	(6/5-6/15)	0.492	0.808	0.249	
MS] w/in pairs]	(6/19-6/25)	0.442	0.319		1.591

] indicates pair of replicate casts

Bias

When the 18 casts are considered in chronological sequence, it is evident that RSS tended to deviate from the true value in the same direction on adjacent casts. The direction of bias was the same within five of the six pairs of replicate casts ($0.05<P<0.10$) and a run test over the entire sequence was significant ($P = 0.05$). The absolute magnitude of the bias which would result were the five replicate pairs considered estimates of five population totals ranged from 0.3% to 3.7% with a mean of 2.0%. Within the restricted spatial area of this survey, between 2 and 8 days appear necessary for the natural fluctuations of the population to be sufficient to average out bias inherent in RSS.

Precision

Precision was investigated by means of the six pairs of replicate casts. Stratified random design SR-3 with one sample per strata was more precise than the design with two samples per strata ($f_{3,3} = 6.5$, $P<0.10$). The precision of the systematic design was intermediate and was not significantly different from either.

Accuracy

The accuracies of the two stratified random designs, as measured against the total chlorophyll estimated from all 20 samples, were similar, but the systematic design RSS-1 was significantly more accurate than either (signed rank test, $P<0.05$). Possibly the greater accuracy of the systematic designs, seen in both studies, might be partially attributable to the different arithmetic formulae with which total chlorophyll was calculated since these give somewhat different weights to the individual samples. To test this, the estimates from both the restricted systematic and the stratified random designs were calculated by linear integration. This did not alter the relative accuracies of RSS-1 and SR-3 in study B or of RSS-1 and SR-1 in study A, nor did it eliminate the bias apparent in RSS-1. Thus, it appears to be the sample location rather than the formula by which total chlorophyll is calculated that is responsible for the greater accuracies of the systematic designs.

DISCUSSION

These studies indicate that there is a potential for biased estimates to be derived from systematic samples collected from a planktonic ecosystem.

While it is recognized that the results suffer from small sample sizes, they gain considerable force from the fact that two different approaches give quite similar conclusions.

It appears that RSS, when applied to the vertical distribution of chlorophyll, may actually give estimates of total chlorophyll which are, on the average, closer to the true value than are estimates based on SR. This is consistent with results from terrestrial systems. Stratified random designs frequently result in pairs of samples falling closely adjacent to one another. In populations which are varying continuously, the information contained in such an adjacent pair is largely repetitious. Such redundancy is avoided in RSS because the spacing between adjacent samples is controlled. The relative performance of SR is expected to improve in populations with more discontinuous distributions such that the strata may be defined to be internally homogeneous, giving maximum precision. On the other hand, and perhaps more important, there appears to be a potential for bias in systematic designs, especially when the sampling occurs within restricted spatial or temporal intervals. In the central Pacific, which is relatively homogeneous in time and space, the bias was detectable, but the magnitude was small. Unfortunately, the results cannot be generalized to other environments. The bias may be expected to diminish as increasing environmental complexity increases the small-scale variability of the sampled population. Whether or not bias is therefore negligible in more complicated neritic environments remains to be investigated.

On the other hand, in planktonic environments the natural fluctuations produce variability between replicate casts which is generally large relative to the experimental error associated with a single cast. The increased accuracy of systematic designs is not likely to result in a detectable increase in the precision of the estimate of the mean of several samples. Depending upon the goals of a study, it may also be true that the magnitude of the bias introduced by systematic sampling is insignificant. For instance, it appears that RSS as routinely used on large-scale oceanic surveys probably introduces no serious error. However, increasing attention is being focused on small-scale, local phenomena, and the routine use of RSS for these studies deserves examination. Possible effects of the interaction between bias and sampling scale found in this study include overestimation of fluctuations in total population (if a positive bias occurs with higher populations and a negative bias with lower populations), underestimation of fluctuations (if a positive bias occurs with lower populations and a negative bias with higher populations), or production of artificial fluctuations when in fact the population is stable. Whether or not such artificial effects of RSS might be important enough to overshadow the gain afforded in terms of ease of sample location and data analysis depends upon the particular study under consideration.

Study A demonstrated the dependence of the success of a sampling design upon the interaction of that design with the structure of the population being sampled; thus, it would seem that intelligent application of knowledge about the sampled population should improve the design. It was, therefore, disconcerting to find that RSS every 20 m, RSS-1, consistently performed as successfully as did RSS-3 which was designed by a presumably experienced worker (the author) with total knowledge about the population to be sampled. We must conclude either that the location of samples in RSS-3 was not as intelligent as it might have been, or that the natural variability of the population makes intelligent placement of systematic samples impossible. (The latter interpretation has a certain appeal.) In contrast, the dependence of SR on the selection of strata is apparent in both studies. Many narrow strata give more precise and accurate estimates than do fewer, larger ones, undoubtedly because, in the presence of strong vertical gradients, they better satisfy the criterion of internal homogeneity. The most precise and accurate results are obtained when the number of strata is equal to the number of samples. The disadvantage of this strategy is the absence of direct estimates of variability within strata from which to calculate confidence intervals around the final estimate. This is not usually of concern in planktonic work because small-scale patchiness is of such magnitude that more useful estimates of precision are obtained directly from replicate casts, and thus apply to some spatial and temporal interval, rather than to a single cast.

The logistics of SR in the open ocean presented few major difficulties. The task of allotting samples randomly to strata was time consuming. After the first few casts, the job of sample design was relegated to the computer. Preparation of the cast card demanded more than routine caution (although minor errors were readily assimilated into the randomization procedure). The use of random

sampling also precluded routine sharing of water samples with others whose programs were designed around standard depths, and, with the present high cost of ship time, the pressure for sharing samples is often considerable. Indeed, this study was possible primarily because there was an unusual amount of excess wire time available.

On the other hand, there were advantages to SR quite apart from the general merriment caused by the unorthodox bottle spacing. The results from the occasional closely spaced samples gave continual insight into the vagueries of small-scale vertical stratification. For instance, within the top 30 m, samples separated by 1- and 2-m intervals differed by <3% of their mean. In the region of the chlorophyll maximum, between 75 and 125 m, the same intervals produced deviations of 30% and 40%, indicating sharp layers and frequent inversions.

It is not within the scope of this paper to make generalizations concerning the use of systematic sampling versus SR. The potential advantages and disadvantages of each have been demonstrated in one environment. It is the responsibility of all researchers to evaluate the use of RSS in reference to their specific programs. If a potential problem is recognized, it is hoped that it will stimulate a preliminary sampling study to examine directly the consequences of RSS in the biological system of interest. This worker's experience with SR was satisfactory, and the potential for biased data is sufficiently undesirable that effort will be made to incorporate randomization into future sampling designs. It is hoped that the untidy profiles which will result will be accepted with understanding by the scientific community.

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DISTRIBUTION AND ABUNDANCE OF SMALL FLATFISHES AND OTHER DEMERSAL FISHES IN A REGION OF DIVERSE SEDIMENTS AND BATHYMETRY OFF OREGON

WILLIAM G. PEARCY[1]

ABSTRACT

Demersal fishes were sampled at seven stations located inshore of Heceta Bank, on Oregon's continental shelf, over a 2-yr period with a 3-m beam trawl designed to catch small flatfishes. Two general assemblages of fishes were recognized: a shallow water (74-102 m), sandy-bottom association where Pacific sanddab, *Citharichthys sordidus*, was numerically the dominant species, and a deeper (148-195 m) assemblage, generally on mud, where the slender sole, *Lyopsetta exilis*, predominated. Rex sole, *Glyptocephalus zachirus*, was usually the second most common species at all stations. Dover sole, *Microstomus pacificus*, ranked fourth to sixth by numbers and composed the largest biomass (wet preserved weight) at three stations. Species diversity was lowest at the shallowest station where sediments were well-sorted, fine sands that contained only 0.1% organic carbon.

The biomass of all fishes captured ranged from 0.9 to 2.4 g m^{-2}. These values are low compared with estimates made by others off Oregon and Washington using commercial-sized otter trawls, presumably because of avoidance of the small beam trawl by large fishes.

An analysis of variance of the catches of all fishes combined, of Dover, rex, and slender soles, and of Pacific sanddab revealed few significant effects of sediment, depth or season. Sediment type had a significant effect on the catches of slender sole—largest catches were on a clayey-silt bottom. Catches of sanddab were inversely related to depth of water. Depth-season interactions were significant for all species combined and for rex and Dover soles, numbers were higher at the deepwater stations during winter than summer, indicating seasonal bathymetric movements. Annual variations were marked—total catches and catches of most species were larger for unknown reasons during 1968 and 1969 than 1970.

Based on length-frequency data, age-group 0 (<50 mm standard length) rex sole were found in high proportions at the deepest stations on the outer edge of the continental shelf. Small sanddab (<70 mm) composed a larger proportion of the catch by numbers on sandy silt than on sand where larger fish predominated.

Both sediment type and depth of water have been correlated with the abundance and species composition of benthic animals. According to Thorson (1957), the physical and chemical composition of sediments may be the main factor in determining the general pattern of distributions of infaunal and epifaunal invertebrates on the level sea floor. Direct influence of bottom type on demersal fishes may be less than on infauna and epifauna, but sediments may affect fishes indirectly by influencing the composition and abundance of available benthic food. Depth of water has frequently been related to faunal changes of both benthic invertebrates and vertebrates across the continental shelf and slope (Sanders and Hessler 1969; Alton 1972; Haedrich et al. 1975). In some studies, these faunal changes were related to concomittant changes in both sediment type and depth (Day and Pearcy 1968).

The influence of depth and sediments on the distribution of the benthos, however, is difficult to separate because these factors are usually closely correlated. Sediment texture generally decreases with increasing depth of water. Small particles are transported from regions of high energy waves and currents into deep, low energy sedimentary environments, while coarse sediments, such as sands, generally are deposited close to their continental source in shallow water.

This study is an attempt to analyze the relationships between sediment and depth on the species composition of benthic fishes and the abundance of small flatfishes in a localized region, mainly inshore of Heceta Bank along the continental shelf of Oregon. The bathymetry and sediments are variable in this region (Figure 1). This is an important factor in this study because the resulting sediment

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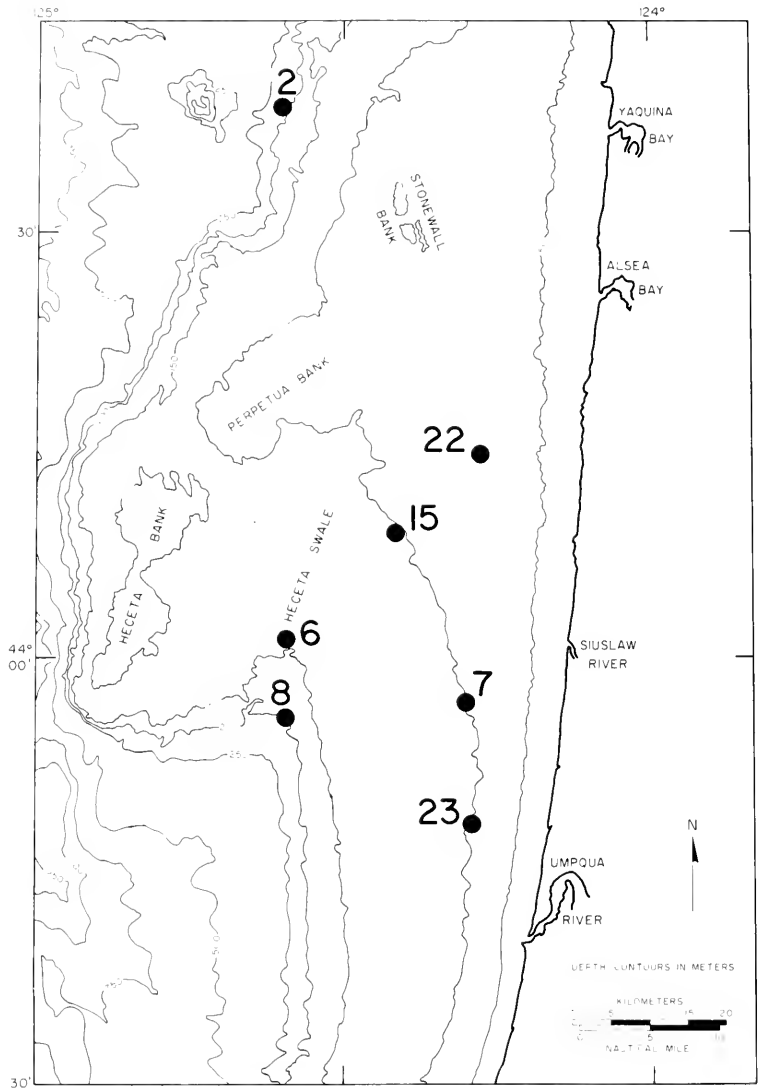

FIGURE 1.—Locations of the seven stations (numbered) off the central Oregon continental shelf that were selected for this study.

types are diverse and do not necessarily grade regularly from coarse sand on the inner shelf to finer sediments with increased depth (Kulm et al. 1975). Because of this heterogenous distribution of sediments, a natural experiment can be designed to differentiate between possible effects of depth and sediment type. Seven stations were selected in an attempt to provide different sediment types at the same depth and the same sediment types at different depths. The region inshore of Heceta Bank produces large commercial catches of flatfishes, such as Dover sole, rex sole, English sole, and Pacific sanddab (Demory et al.[2]).

METHODS

The sediment types for the stations were characterized by the percent sand, silt, and clay, percent of organic carbon and median particle size by Bertrand (1971) and Gunther (1972) (Table 1). A Phleger multiple corer was used to sample sediments. Initially sediments were sampled at the apices of a triangle (sides = 1 n.mi.) and at each

[2]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. Rep., 49 p.

TABLE 1.—Average sediment texture, percent organic carbon,[1] and median particle size[2] at the seven stations off Oregon (from Bertrand 1971). Stations are arranged according to depth.

Item	Station						
	22	7	23	15	6	2	8
	74 m	100 m	102 m	102 m	148 m	190 m	195 m
Clay (%)	0.9	11.7	23.6	7.3	30.3	14.7	35.3
Silt (%)	0.4	22.1	48.1	8.6	66.6	16.8	62.1
Sand (%)	98.7	63.7	28.3	84.1	3.1	68.5	2.6
Organic C (%)	0.1	0.6	1.3	0.4	1.7	1.0	1.6
Median particle size (Mdϕ)	1.88	4.20	6.01	2.99	6.85	4.62	7.22

[1]The percent organic carbon was estimated by the difference in weight between total carbon and calcium carbonate carbon. Total carbon was determined by dry combustion in a Leco induction furnace and measurement of the evolved CO_2 in a Leco gas analyzer. Calcium carbonate was measured by acidifying ground, dried sediment with 0.1 N HCl and measuring the CO_2 evolved (Bertrand 1971). (Reference to trade names does not imply endorsement by the National Fisheries Service, NOAA.)

[2]Md$\phi = \phi 50'$ where $\phi = -\log_2 D$ and D = diameter in millimeters. See Inman (1952).

station at the center of the triangle. The upper 2 cm of the cores were analyzed. Sediment particle size was measured by standard procedures (Krumbein and Pettijohn 1938). The coarse sand fractions were analyzed by the settling tube method (Emery 1938). Particle size of sediments in the vicinity of each station was similar (Bertrand 1971). Sediments were also sampled at each station during each cruise. According to Gunther (1972), seasonal variations of sediment grain size parameters within stations were not significant, but significantly different sediment types were found among stations at about the same depths, and fairly similar sediments occurred at different depths.

Three station-pairs were identified that had rather similar sediment characteristics but were located at different depths (Table 1): 1) Stations 6 and 8 (148- and 195-m depth, respectively) had highest percentages of clay and silt, lowest percentages of sand, and the highest organic carbon of all stations; 2) Stations 22 and 15 (74 and 102 m) had sandy sediments with low percentages of clay, silt, and organic carbon; Station 22, however, was almost entirely (99%) well-sorted beach sand; 3) Stations 7 and 2 (100 and 190 m) had 60-70% sand and intermediate percentages of clay and silt (12-22%) and organic carbon (0.6 and 1.0%). Station 2 had a thin overlying layer of silt that was absent at Station 7 (Roush 1970); 4) Station 23 located at 102-m depth, about the same as Stations 7 and 15, was intermediate in sediment texture and organic carbon between stations 7 and 2 and 6 and 8. Thus, stations were recognized with three different types of sediment at about 100 m and two different types at 190-195 m. These sediment types agree with three types recognized by Kulm et al. (1975) for the continental shelf off Oregon: 1) well-sorted detrital sands (former beach sands) with a high quartz content mainly on the inner shelf; 2) patchy mud facies largely at midshelf depths and concentrated near large rivers; and 3) mixed sand and mud between the sandy facies and the outer edge of the shelf. Glauconite, the principal authigenic constituent of shelf sands, occurs around the rocky outcrops such as Heceta Bank and along the outer edge of the continental shelf.

Fishes were collected in beam trawls 3 m or 2.7 m wide and 76 cm high at the same seven stations on the central Oregon continental shelf (Figure 1). This net has a small mesh size (13-mm stretch measure) and mouth opening and therefore caught mainly small species and juveniles of most commerical species. A total of 115 tows were made on nine cruises between August 1968 and August 1970. Trawls were made during daylight hours. Each station was sampled during the four seasons of each year. The trawl was streamed at a ship speed of 3.7 km/h (2 kn), and descended at 30 m wire/min until a scope of 1:4 was achieved, towed for about 15 min (mean, 16 min, SD 5.3), and then retrieved at 30 m wire/min. Two beam trawl tows were made at each station during each cruise with standardized trawling procedures by the same personnel.

An odometer wheel was mounted outside of each skid to provide estimates of the distance trawled over the bottom. Area sampled was calculated from the circumference of the odometer wheels, the number of revolutions recorded on odometer counters, and the distance between the skids (see Carey and Heyamoto 1972).

The two odometer readings for a tow were usually similar. Where they differed, I used the highest reading and assumed that slippage of the wheel in sediments or jamming by sea pens, etc. caused the low reading. Rigid stops were mounted on the skid frame to prevent turning of the wheels until they contacted the bottom.

The effectiveness of odometer wheels to estimate distance traversed by the beam trawl on the bottom has been assessed by Carney and Carey.[3] They recognized slippage of the wheels in the sediment and failure of the footrope to effectively tend the bottom at all times as possible errors in measuring actual areas sampled. For these

[3]Carney, R. S., and A. G. Carey, Jr. A report on the effectiveness of metering wheels for measurement of the area sampled by beam trawls. Unpubl. manuscr., 17 p.

reasons, catch per tow was used as a supplementary estimate of abundance in addition to catch per square meter derived from odometer readings.

All fishes were preserved with 10% buffered Formalin[4] at sea, and identified, measured (standard length, SL) and weighed (wet preserved weight) ashore.

RESULTS AND DISCUSSION

Fish Assemblages

The rank order of abundance of the 10 most common species are shown in Table 2. Pacific sanddab, *Citharichthys sordidus*, was the numerical dominant at the four shallowest (74-102 m) stations where it composed 25-86% of the total number of fishes captured. At the three deepest (148-195 m) stations, slender sole, *Lyopsetta exilis*, ranked first in abundance where it composed 38-42% of the number of fishes collected. Rex sole, *Glyptocephalus zachirus*, ranked second in abundance at all stations (except at Station 6 where it was third). The high rank of rex sole at all stations corroborates Hosie's [5] observation that rex sole is probably the most widely distributed sole on the continental shelf and upper slope off Oregon, occupying a large bathymetric range with diverse sediments. Dover sole, *Microstomus pacificus*, ranked fourth at the four inshore stations and fifth or sixth at the deeper stations.

Demory's (1971) study off northern Oregon and southern Washington showed that these flatfishes were most abundant at the following depths:

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

[5]Hosie, M. J. 1976. The rex sole. Inf. Rep. 76-2, Oreg. Dep. Fish Wildl., 5 p.

TABLE 2.—Ranks of the 10 most numerically abundant fishes at each of the seven stations, and the presence (+) of these species at other stations if they did not rank among the top 10. Absence of either a number or (+) indicates that a species was not captured at that station.

	Station						
Item	22 74 m	7 100 m	23 102 m	15 102 m	6 148 m	2 190 m	8 195 m
Citharichthys sordidus	1	1	1	1	6	+	4
Glyptocephalus zachirus	2	2	2	2	3	2	2
Microstomus pacificus	4	4	4	4	5	6	6
Lyopsetta exilis	8	5	6	6	1	1	1
Lycodopsis pacificus	+	3	3	10	2	8	3
Xeneretmus latifrons	+	+		+	4	3	7
Cymatogaster aggregata	5	6	7	3	+		
Parophrys vetulus	3	10	8	5			+
Sebastes juveniles					7	5	5
Eopsetta jordani	6	9	+	+	+		+
Sebastes crameri		7	5	+	9	10	10
Asterotheca pentacanthus			+		+	4	+
Poroclinus rothrocki		8	9	+	+		8
Thaleichthys pacificus	9	+	+	+	+	7	+
Allosmerus elongatus				7			
Icelinus borealis	7						
Merluccius productus		+	+	+	8	+	+
Sebastes elongatus					+	+	9
Radulinus asprellus	+	+	+	8	+		
Sebastes diploproa						9	+
Engraulis mordax		+	+	9	+		
Eptatretus stoutii		+	+	+	10	10	+
Microgadus proximus	10	+	+	+	+		
Citharichthys stigmaeus			10				+
Dominance and diversity information							
No. tows	15	15	16	15	17	18	16
No. fish	776	1,921	1,161	1,357	2,175	732	1,091
Percent of no. made up by dominant sp	86	45	25	53	41	38	42
No. spp	19	25	24	24	34	35	34
Diversity (H_e)	0.70	1.62	2.16	1.66	1.77	2.47	2.00
Number and biomass of fishes captured per square meter[1]							
All species (no./100 m²)	1.7	4.0	3.0	2.4	4.0	1.4	1.6
(g/m²)	1.2	2.2	1.4	1.1	2.0	0.9	1.2
(g/m² (TS))	1.2	2.3	1.5	1.7	2.4	0.9	2.0
Dover sole (g/10 m²)	0.2	5.1	3.7	1.4	3.0	2.6	2.8
Rex sole (g/10 m²)	2.2	3.2	2.0	2.4	2.3	0.2	2.0
Slender sole (g/10 m²)	0.1	0.7	0.8	0.1	5.2	0.8	2.5
Pacific sanddab (g/10 m²)	9.8	5.8	2.3	6.6	0.6	0.1	0.4

[1]Based on odometer readings and based on estimates of distance trawled from times and ship's speed (TS).

Pacific sanddab, 37 to 90 m; slender sole, 90 to 183 m; small (≤180 mm TL) rex sole, 55 to 183 m; and small (≤180 mm TL) Dover sole, 55 to 150 m. Therefore the stations sampled in my study were not shallow enough to include all of the major depth range inhabited by Pacific sanddab, rex sole, or Dover sole. Furthermore, large Dover and rex soles are known to be distributed in deeper waters of the upper continental slope off Oregon (Demory 1971; Hosie see footnote 5; Demory[6]), regions unsampled in this study.

The ranks of the dominant species as well as the presence of other species implies a shallow water (74-102 m) and a deepwater (148-195 m) assemblage of fishes. *Cymatogaster aggregata* and *Parophrys vetulus* ranked within the top 10 species at the shallowest Stations 22, 7, 23, and 15 but not at deep Stations 6, 2, and 8 where they were usually absent. *Xeneretmus latifrons* and *Sebastes* juveniles, on the other hand, were only abundant at the deep stations.

Similarity among the stations was calculated as

$$\text{SIMI} = \frac{\sum_{i=1}^{S} P_{1i}P_{2i}}{(Sd_1)\,(Sd_2)}$$

where S is the number of species present at both stations; P_{1i} is the proportion of the ith species at one station; P_{2i} is the proportion of the ith species at a second station; and $(Sd_1)(Sd_2)$ is the product of the square roots of estimators of Simpson's diversity index for Stations 1 and 2. This measure of similarity was used because it is analogous to a correlation coefficient, relates closely to Simpson's measure of concentration, and has maximum and minimum values of 1 and 0 (McIntire and Moore 1977).

Two assemblages of fishes, a deep and a shallow one, were evident based on high similarity in the species composition among the three deepest stations (2, 6, 8) and among three of the four shallow stations (15, 22, 7) (Table 3). Similarity between stations of each of these two groups varied from 0.85 to 0.95. Station 23, another station at about 100 m (like Stations 7 and 15) also had a fairly high similarity with the other shallow water stations. It was similar to Station 7 (0.92 m) but less similar to Stations 15 and 22 (0.77 and 0.65 m). The benthic environment of Station 23 differed from the other three shallow stations in that it had more than twice the percentage of clay and silt found at Station 22, 7, or 15, where sand was the major sediment component.

TABLE 3.—Indices of similarity (SIMI) for the species composition of fishes among each of the seven stations. Stations are arranged by depth.

	Station					
Station	22	7	15	23	6	2
Shallow						
22						
7	0.86					
15	0.94	0.93				
23	0.65	0.92	0.77			
Deep						
6	0.05	0.33	0.14	0.57		
2	0.04	0.26	0.13	0.38	0.85	
8	0.18	0.45	0.29	0.58	0.91	0.95

Based on sediment composition two of the three station pairs were very similar (Table 3): Stations 22 and 15 (SIMI = 0.94), and Stations 6 and 8 (SIMI = 0.91). Stations 7 and 2, another station pair, at 100 and 190 m, had a similarity of only 0.26. This disparity may be explained by the thin layer of silt overlying a predominantly sandy sediment at Station 2. For epifaunal organisms the sediment type at this station may have been more similar to that at Stations 6 and 8 than any other stations. This may explain why Station 2 is so similar in species composition to Stations 6 and 8. However Station 7 showed high similarity (0.92-0.93) with Stations 15 and 23, stations with different sediment types but both at the same depth. Thus clear separation of the effects of depth and sediment was not always possible. Nevertheless the most consistent and obvious assemblages were correlated with depth. Stations of different sediment types had high similarity within the shallow water assemblage.

These results agree with those of Day and Pearcy (1968) who studied the distribution of demersal fishes from 40 to 1,829 m along a transect just north of Heceta Bank. They delineated a species association at depths of 42-73 m on sandy sediments with Pacific sanddab as the dominant species and an association at 119-199 m on silty-sand sediments where slender sole predominated. Because the same species associations sometimes were found on different sediment types, they felt that factors other than sediment texture may govern the distribution of fish assemblages.

Diversity

The number of species of fishes collected was

[6]Demory, R. L. 1975. The Dover sole. Oreg. Dep. Fish Wildl. Inf. Rep. 75-4, 4 p.

highest (34-35) at the deep stations, intermediate (24-25) at the 100-m stations and lowest (19) at the shallow station (Table 2B). Species diversity calculated by the information function (Shannon and Weaver 1963):

$$H_e = -\Sigma_{pi} \ln_{pi},$$

varied between 0.7 and 2.5 at the seven stations. Diversity was lowest at the shallow, sand station where sanddab composed 86% of the catch. Diversity was highest at Station 2, which had the largest number of species, and next highest at Station 23, where the dominant species composed only 23% of the total number of fishes. Since the number of species was similar among the three 100-102 m stations or the three deep (148-195 m) stations, differences in diversity within these two groups are due to variations in the evenness of the proportions of the various species.

The values of diversity are similar to those found by others for demersal fish communities. Margalef (1968) reported that diversity (H) of bottom fishes trawled off the Spanish Mediterranean ranged from 1.0 to 2.4. Haedrich and Haedrich (1974) calculated H = 0.7-1.7 for demersal fishes of Block Island Sound [from the data of Merriman and Warfel (1948) and Richards (1963)], and H = 1.6-1.8 for bottom fishes on the continental slope off southern New England. Haedrich et al. (1975) give a value for H of 1.9 for 141-285 m on the continental slope south of New England.

Biomass Estimates

Based on odometer estimates of distance trawled, numbers varied from 1.4 to 4.0/100 m^2, and biomass ranged from 0.9 to 2.2 g m^{-2} (Table 2). Estimates of the biomass of fishes based on ships's speed (3,700 m h^{-1}), average trawling times on the bottom (16 min) and the width of the beam trawl are in agreement with the estimates that used odometer readings.

The biomass of the four common flatfishes at each station shows that the Pacific sanddab composed nearly all the biomass at Station 22 and also had the largest biomass at Stations 7 and 15. Dover sole predominated in catches at Stations 23, 2, and 8, and slender sole was the dominant fish at Station 6. These trends are similar to those noted earlier for species numbers (Table 2).

Catches of demersal fishes with the small beam trawl at these seven stations are low compared with other estimates made with commercial-sized otter trawls off Oregon and Washington. On the basis of surveys using an otter trawl with a 23-m footrope with 9.9-cm mesh (estimated to have a 9-m horizontal and a 1.5-m vertical mouth opening), Demory and Hosie[7] calculated that the average biomass of fishes on the continental shelf of Oregon was 19 g m^{-2} in 1971-72 and 16 g m^{-2} in 1973-74. Barss et al.[8] employed similar methods to estimate a standing stock of trawlable fishes on the continental shelf and upper slope (18-549 m) of Washington of about 15 g m^{-2}. In both of these studies, a large portion of the catch consisted of rockfishes, *Sebastes* spp., Pacific hake, *Merluccius productus*, other roundfishes, skates, and other elasmobranchs. The average biomass of flatfishes, the type of fishes that their trawl was designed to catch, was 5.7 and 5.4 g m^{-2} for 1971-72 and 1973-74, respectively, off Oregon and 9.0 and 7.5 g m^{-2} for 1975 and 1976 off Washington. Alverson et al. (1964), also using large otter trawls (28-m footrope) with large (11-cm) mesh, provided data from which a biomass of 8.0 g m^{-2} for demersal fish and 3.1 g m^{-2} for flatfishes can be estimated for the continental shelf of Oregon and Washington. Our estimates are also low compared with the values given by Oviatt and Nixon (1973) for New England waters.

Although all these values are approximations dependent on the accuracy of estimates of actual distance trawled and the effective mouth area, the otter trawl catches are several times larger than my beam trawl estimates. Nektobenthic fishes, such as hake and rockfishes, as well as large demersal flatfishes and skates are poorly sampled with the beam trawl because they are not available to the net or they avoid the trawl (see also Day and Pearcy 1968). Thus, retention of small species of fishes and juveniles of large species by the beam trawl, fishes that may escape through the meshes of the larger nets, do not compensate for fishes that avoid the beam trawl or nektobenthic species that range above the bottom.

Kuipers (1975) estimated that the catch efficiency of a 2-m beam trawl decreased exponentially with increasing length of plaice, *Pleuronectes platessa*, from approximately 100%

[7]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. Fish Comm. Oreg., Annu. Rep., 9 p.

[8]Barss, W. H., R. L. Demory, and N. Ten Eyck. 1977. Marine resource surveys on the continental shelf and upper slope off Washington, 1975-76. Oreg. Dep. Fish Wildl. Rep., 34 p.

for plaice under 7 cm to 15-30% for plaice over 15 cm. Riley and Corlett (1965) and Edwards and Steele (1968) estimated catch efficiencies of 57% and <45% for 0-group plaice in 2-m and 4-m beam trawls, respectively. In this study, the 3-m beam trawl caught about one-fourth the biomass of flatfishes per square meter caught by Demory and Hosie (see footnote 7) off Oregon, indicating a low catch efficiency.

The length-frequency distributions of Pacific sanddab and rex sole caught in the beam trawl are compared in Figure 2 with those caught in two larger otter trawls with large-sized mesh by Demory and Robinson[9] off Oregon. The small-meshed beam trawl retained appreciably smaller individuals than the otter trawls, verifying that it was most effective in capturing small flatfishes and that large fishes effectively avoided this small net.

The disparity between the estimates of abundance by otter trawls and the beam trawl may be magnified by the effects of otter doors, bridles, and towing cables. The bridles from the otter doors to the net (sweeplines and dandy lines) in combination with the wake from the doors can herd fishes into the net from a wide area in front of the trawl, thereby increasing the effective mouth opening (Loverich[10]). Thus the abundance estimates cited above that are based on the horizontal spread of otter trawl nets are probably too large. The towing cable of the beam trawl, on the other hand, drags on the bottom immediately in front of the trawl and therefore may frighten fishes away from the net tow path. Size-dependent responses of fishes to the bottom disturbances created by trawl doors, bridles, and cables may contribute to the differences found in size of fishes captured by the two types of trawls. Large fishes, with better swimming capabilities, may be herded more effectively by otter trawl bridles than small fishes. Large fishes may also rapidly swim away from the towing cable of the beam trawl.

[9]Demory, R. L., and J. G. Robinson. 1973. Resource surveys on the continental shelf off Oregon. Fish. Comm. Oreg., Annu. Rep., 18 p.

[10]Loverich, G. 1975. Trawl nets evaluated by expert. Fisherman's News, Sept. 1975 and pers. commun.

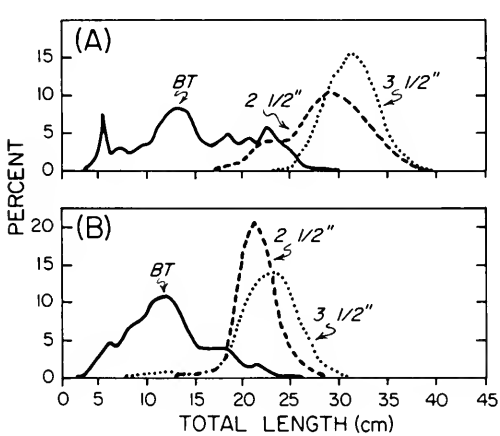

FIGURE 2.—Comparison of length-frequency distributions of (A) rex sole and (B) Pacific sanddab captured in the beam trawl (BT) with 13-mm mesh with those captured by Demory and Robinson (see footnote 9) in 3½-in (89-mm) mesh and 2½-in (64-mm) mesh otter trawls on the continental shelf off Oregon in 1971 and 1972.

Environmental Effects

An analysis of variance, using a linear model with depth as a continuous variable and sediment, season, and year as indicator variables, was completed on the untransformed data for numbers and weight of fishes per square meter and numbers and weight per tow. Sediment was classified as four types based on the percent of sand (2-4, 28, 63-69, 84-99%). Trawls were combined into two seasons, October-April (winter), and May-September (summer). Levels of significance, $P<0.05$ and $P<0.01$, are shown in Table 4. Because of the large number of tests, only effects with $P<0.01$ are considered significant, although $P<0.05$ are shown to provide indications of possible trends. Effects with $P<0.05$ will only be discussed if they reinforce an effect of $P<0.01$, or if two effects of $P<0.05$ were found in the same species-effect category.

Sediment Effects

The number and biomass of slender sole caught per tow appeared to be affected by sediment type (Table 4). This is curious because this species is primarily a pelagic feeder (Pearcy and Hancock 1978). Largest catches per tow were made at stations with high percentages of clay and silt, and lowest catches occurred on sandy sediments. Based on sediment types (and stations), catches of slender sole ranked as follows: 2-3% sand (6-8) >63-69% sand (2-7) >28% sand (23) >84-99% sand (22-15) (see also Table 2). The same trend with sediments is indicated ($P<0.05$) for slender sole weight per square meter, but because catches per square meter were more variable or mean differences were less, differences were not significant at $P<0.01$.

TABLE 4.—Results of an analysis of variance (ANOVA) of the numbers and weights of fishes caught per square meter or per tow[1]; * indicates $P < 0.05$; ** $P < 0.01$. R^2 (coefficients of determination) values are given below.

		All species				Rex sole				Dover sole				Slender sole				Pacific sanddab			
		No		Wt		No		Wt		No		Wt		No		Wt		No.		Wt	
Item	df	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow
Year	2	**	**	**	**	**	*	**		**		**		*	*	*		**		**	
Sediments	3					*							*		**	*	**			*	*
Seasons	1													*							*
Sediment · season	3						*						*			*	*				
Depth	1		*		*			*	*									*	**	*	**
Depth · season	1	**		**		**	*	*		**	*									*	*
Error	95																				
Total	106																				
R^2 (tow)		0.18		0.20		0.23		0.16		0.17		0.16		0.36		0.33		0.28		0.34	
R^2 (m^2)		0.39		0.51		0.47		0.40		0.46		0.43		0.24		0.28		0.36		0.37	

[1]An ANOVA using a square root transformation for the data on all species combined per tow and per square meter gave similar significance effects. The ANOVA was unbalanced because of unequal numbers of observations per station, season, depth, etc. Effects were tested using the extra sum of squares principle (Searle 1971).

The biomass of Pacific sanddab, on the other hand, showed opposite trends ($P < 0.05$) and was large on sandy sediments and small on silt or clay sediments (see also Day and Pearcy 1968; Barss et al. see footnote 8). Since the effect of sediment was not significant for total fish catch by numbers or weight sandy stations with low percent organic carbon, apparently did not support a markedly lower abundance of demersal fishes (Table 2). Although adult Dover sole show a strong preference for mud or silt bottom (Barss et al. see footnote 8; Demory see footnote 6), this trend was not apparent for the small Dover sole caught inshore of Heceta Bank in this study.

A sediment-season effect was indicated for slender sole. They were caught in larger numbers per tow and weight per square meter ($P<0.05$) at the stations with a low percentage of sand (6-8) in the winter than the summer.

Depth Effects

The slope of the regression between depth and number and weight per tow of Pacific sanddab was significant ($P<0.01$) and negative. Catches per square meter on a number and weight basis gave the same trends ($P<0.05$). Sanddab were most abundant in shallow water. Weight of rex sole per square meter and per tow and total fish numbers and weight per tow also tended to decrease ($P<0.05$) with depth.

Depth-season interactions were significant on a square meter basis for all species combined (number and weight) and for numbers of rex and Dover soles. These effects were caused by appreciably larger catches in deep water in winter than summer. Seasonal differences were small in shallow water. This trend for lower catches on the outer edge of the continental shelf during summer than winter was obvious for Pacific sanddab. They were completely absent from the deep stations (2, 6, 8) during the summer but were present at all stations during winter. Seasonal bathymetric migrations, with spawning migrations into deep water in the winter and return to relatively shallow depths in the summer, have been described for Dover sole and rex sole by Hagerman (1952), Harry (1956), Alverson (1960), and Demory (1971). Such movements could explain these depth-season effects.

Seasons

No significant seasonal differences were detected, indicating little seasonal variation in catches of these species when all stations are combined.

Year Effect

On the basis of numbers and weight per square meter and per tow, more fishes were captured in 1969 and 1968 than in 1970 at all stations (Figure 3). This trend was significant ($P<0.01$) for all species combined and for rex sole, Dover sole, and Pacific sanddab. Year effects were also indicated for slender sole ($P<0.05$). I have no cogent explanation for these large annual variations. They could represent actual variations in abundance or availability, due to natural events or increased fishing activity, or to undetected changes in sampling efficiency. Dominant year classes have been reported for these flatfishes off Oregon (Demory and Robinson see footnote 9), which may contribute to these annual differences, though changes in length-frequency distributions were not obvious over this 2-yr period.

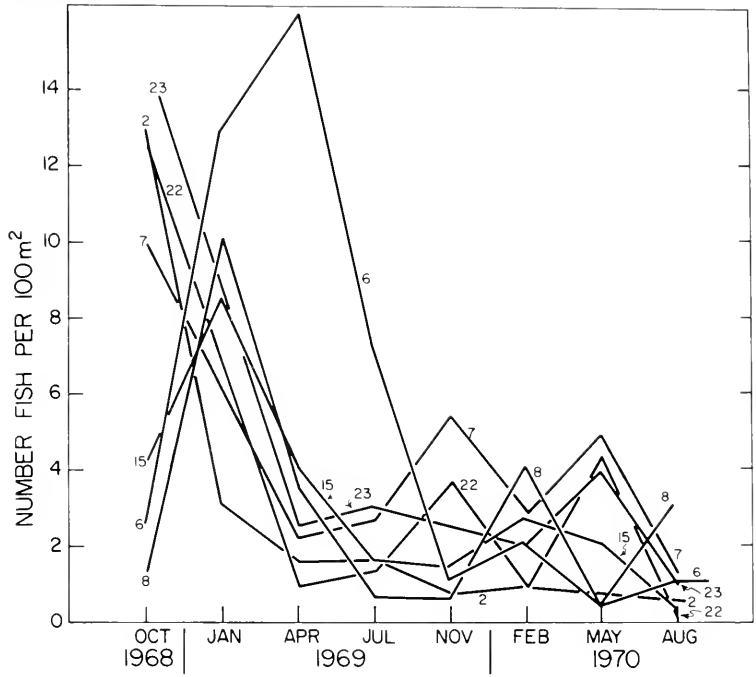

FIGURE 3.—Variations in the total numbers of fishes caught at each of the seven stations, 1968-71. The two tows at each station for each sampling period were averaged.

The amount of variability explained by the regression (R^2) of all effects on catches ranged from 0.16 to 0.51 (Table 4). Values were larger for the analysis based on catches per square meter than catches per tow, except for slender sole. These low values indicate that most of the variability was not accounted for by the variables of sediment, depth, year, and season. Large residual mean squares indicate that sampling variability associated with catches at individual stations is appreciable. Oviatt and Nixon (1973) completed a multiple regression analysis of biomass and numbers of benthic fishes in Narragansett Bay, R.I., with 14 environmental variables. Depth and sediment organic content contributed significantly to the regression for total fish numbers and fish biomass. But an R^2 of only 0.21 was found. In both of these studies, only a small fraction of the total variability was explained by the environmental factors included.

Size-Frequency Distributions

Differences in length-frequency distributions were sometimes obvious among the stations located at different depths or sediment types. For example, the main length mode of rex sole at the 100- and 102-m stations was 125 mm, but at 190- and 195-m depth there was a distinct bimodal distribution with peaks at 45 and 215 mm (Figure 4). These differences imply that young-of-the-year

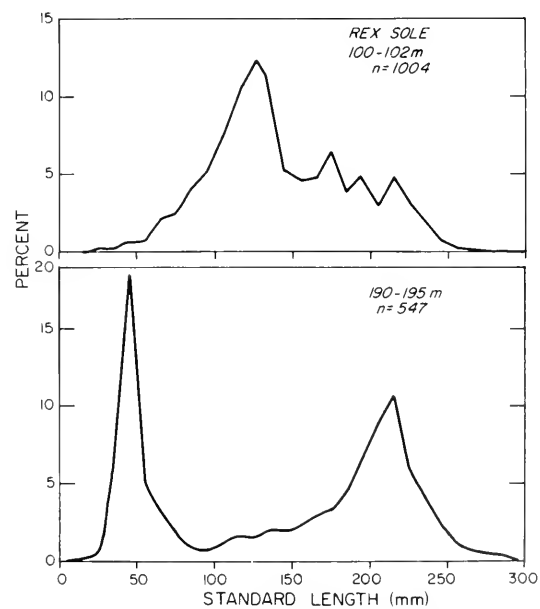

FIGURE 4.—Length-frequency data for rex sole at 100-102 m stations (above) and 190-195 m stations (below).

(<50 mm) and age-groups III-V (200-250 mm) rex sole (see Hosie and Horton 1977 for age-length data) preferentially inhabit deep waters on the outer edge of the continental shelf while intermediate sizes (75-150 mm) inhabit shallower waters of the inner shelf. The peak of young-of-the-year rex sole at 200 m corroborates the conclusion of Pearcy et al. (1977) about the depth of larval settlement and the nursery ground for early benthic life. They concluded that rex sole larvae settle to the bottom mainly on the outer continental shelf during the winter when they are >50 mm SL. Powles and Kohler (1970) and Markle (1975) believed that the nursery grounds of *Glyptocephalus cynoglossus* are also in deep waters off the east coast of the United States.

Small Pacific sanddab (<70 mm) composed a larger proportion of the catch at 102 m where sand was 28% of the sediment (Station 23) than at 74 and 102 m where sand made up over 64% of the sediment (Stations 22, 15) (Figure 5). Young sanddab appear to inhabit deeper water with finer sediments in early life and then aggregate on sandy bottom areas in shallow water where they often dominate the demersal fish fauna. Hence, this trend of decreasing depth with increasing age is similar to that found for rex sole.

SUMMARY

1. Demersal fishes were sampled at seven stations on Oregon's central continental shelf at various seasons of the year during a 2-yr period. A fine-meshed, 3-m beam trawl was used in order to quantitatively sample small flatfishes. The stations ranged from 74 to 195 m deep and had sediment types ranging from nearly 100% sand to clayey-silts with about 3% sand.

2. Stations were selected in an attempt to separate the effects of depth and sediment on the assemblages of fishes and abundances of common species. Three station-pairs were recognized that had similar sediment types but were located at different depths. Separation of sediment and depth effects was complicated however by differences in measured (and possibly unmeasured) factors between station pairs.

3. Two general assemblages of fishes were recognized on the basis of species composition of fishes by numbers, biomass per square meter of dominant species, and similarity indices among the seven stations. These were a shallow water (74-102 m) assemblage dominated numerically by Pacific sanddab, and a deepwater (148-195 m) assemblage dominated by slender sole.

4. Species diversity (H) varied between 1.6 and 2.5 except at the shallow, sand station where it was only 0.7. Dominance was pronounced at this station: 86% of all the individual fishes captured were Pacific sanddab. The largest number of species (34 or 35) was recorded for the three deep stations. These values of H are similar to others for temperate, demersal fish communities.

5. Similarity indices of the species composition of fishes were high for two of the three station pairs with similar sediments. However, indices were also high among the four shallow stations of differing sediment types. Stations that were near each other geographically were similar, indicating the possibility of a proximity effect, but high similarity was also found among deep stations, one of which was over 65 km from the others.

6. An analysis of variance of the number and weight per square meter and per tow of Dover, rex, and slender soles, Pacific sanddab, and all species combined indicates some effects of sediments and depth. Largest catches of slender sole were at the clayey-silt station pair, and largest catches of Pacific sanddab were on sandy sediments. Catches of Pacific sanddab were significantly larger at the shallow stations. Catches of rex sole and all species combined also tended to decrease with increasing depth.

7. Differences in the length-frequency distributions of Pacific sanddab and rex sole were corre-

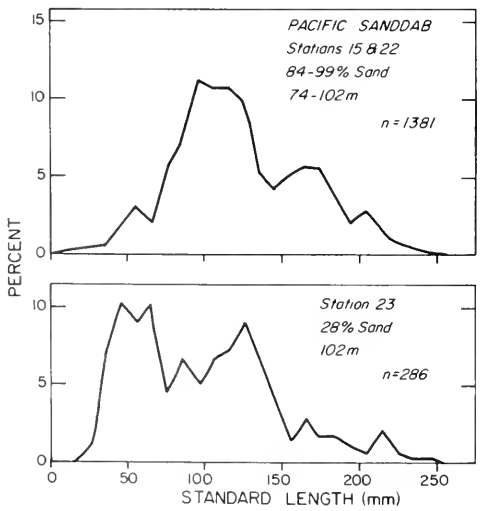

FIGURE 5.—Length-frequency data for Pacific sanddab at stations with 84-99% sand (above) and 28% sand (below).

lated with depth or sediment type. Small sanddab predominated on the silty-sand station, whereas large sanddab preferred sandy sediments. Young-of-the-year rex sole were concentrated on the outer edge of the continental shelf (190-195 m).

8. Catches were sometimes larger in the winter than the summer, especially at the deep stations. This trend, which was noted for all four flatfishes and for all species combined, is probably the result of seasonal bathymetric movements.

9. A pronounced decrease in the catches of most species and total catch per square meter occurred during the 2 yr of this study. Reasons for this decline are unknown.

10. The biomass of benthic fishes ranged from 0.9 to 2.4 g m^{-2} at the seven stations. Biomass was not appreciably lower at the pure sand stations, which had about 0.1% organic carbon in the sediment. This is related to the fact that the Pacific sanddab, the predominant species at this station, is a pelagic feeder (see Pearcy and Hancock 1978).

11. The weight of fishes per square meter caught in the 3-m beam trawl was several times lower than that estimated from larger otter trawls with coarser meshes. Although the beam trawl caught many small flatfishes, large fishes and nektobenthic species effectively avoided this small beam trawl, resulting in low biomass estimates.

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FEEDING HABITS OF DOVER SOLE, *MICROSTOMUS PACIFICUS*; REX SOLE, *GLYPTOCEPHALUS ZACHIRUS*; SLENDER SOLE, *LYOPSETTA EXILIS*; AND PACIFIC SANDDAB, *CITHARICHTHYS SORDIDUS*, IN A REGION OF DIVERSE SEDIMENTS AND BATHYMETRY OFF OREGON

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ABSTRACT

The feeding habits of the Dover sole and rex sole (mainly juveniles) and of slender sole and Pacific sanddab were investigated at seven stations on the continental shelf off central Oregon. Dover sole had a catholic diet, feeding on a large variety of infaunal and epifaunal invertebrates. The composition of the diet varied among stations of different depth and sediment type indicating opportunistic feeding. Pelecypoda were the most important prey on a weight basis at the shallow station (74 m) of well-sorted sand where they were the dominant macrofaunal invertebrate. Ophiuroids, sea pens, anemones, and pelecypods were the most important prey at 100-102 m stations of silty sand or sandy silt. Polychaetes composed over 90% of the diet at the deep stations (148-195 m) of clayey silt or silty sand. The average standing stocks per square meter of Dover sole caught in beam trawl collections and polychaetes in grab samples were positively correlated among stations.

Similarity of the food habits of Dover sole on the basis of food weight or frequency of occurrence was generally higher among stations of similar depth than of similar sediment texture. Similar trends were noted for assemblages of benthic fishes and invertebrates.

Dover sole collected during the winter had the highest percentage of empty stomachs, the fewest prey taxa, and often the lowest frequency of occurrence of prey taxa within a size group. Because seasonal variations were not observed in abundance of macrofaunal food in the sediments, availability of prey may change with season, or more likely, Dover sole feed more intensely and less selectively during summer.

Small (<150 mm standard length) rex sole fed mainly in amphipods and other crustaceans. Large (150-450 mm standard length) rex sole preyed chiefly on polychaetes. The diet of rex sole was less diverse than that of the Dover sole and overlap of diet between the two species was not large.

Both the Pacific sanddab, numerically the most common species of fish at the shallow sand station, and the slender sole, the most common species at the three deep, soft-sediment stations, preyed principally on pelagic crustaceans such as euphausiids, shrimps, and amphipods. Although the biomass of mollusks in the sediments was large at the shallow sand station, they were not consumed by Pacific sanddab. Fish were occasionally an important food for the sanddab.

The objectives of this study were: 1) to describe the food habits of the four species of flatfishes that are common in trawl catches on the central continental shelf off Oregon: Dover sole, *Microstomus pacificus*, rex sole, *Glyptocephalus zachirus*, slender sole, *Lyopsetta exilis*, and Pacific sanddab, *Citharichthys sordidus*; 2) to evaluate the possible effects of depth and sediment, size of fish, and season of capture on their food habits; and 3) to compare the biomass and composition of fish food from grab samples with feeding habits of fishes.

These species are among the most abundant flatfishes in demersal communities of this region of the Pacific Ocean (Alverson et al. 1964; Day and Pearcy 1968; Alton 1972; Demory and Hosie[2]). They dominated the fish catches at the stations where they were captured for this study (Pearcy 1978). In order to know more about the role of these fishes in their ecological communities, including competitive-predatory relationships, more data are required on their food habits.

Hagerman (1952) listed food items found in Dover sole caught in California waters. Pearcy and Vanderploeg (1973) listed general taxonomic groups preyed upon by Dover, rex, and slender soles and Pacific sanddab. Kravitz et al. (1977) gave a detailed account, including species of prey

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[2]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Commer. Fish. Res. Dev. Act, Annu. Rep. July 1, 1974 to June 30, 1975, 9 p.

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consumed by the rex sole and Pacific sanddab caught in a single collection off the central Oregon shelf. This study is, to our knowledge, the most complete study of the food habits of these four species.

METHODS

Fishes were collected during 115 tows with a 3-m beam trawl at seven stations on the continental shelf off central Oregon between August 1968 and August 1970. These stations are classified by four depth categories and the percentage of sand in the sediments in Figure 1. Details on methods and descriptions of the stations are given by Pearcy (1978).

All fishes were preserved at time of capture with Formalin,[3] and the body wall of large (>150-200 mm SL) fishes was incised to insure preservation of stomach contents. Fishes were identified and measured (standard length, SL) in the shore laboratory. Stomachs were removed from 326 Dover sole represented in the catches at all seven stations; and from 614 rex sole, 1,109 slender sole, and 723 Pacific sanddab captured at two or three stations where each of these species was most common.

Stomach contents were removed and empty stomachs were noted. Food organisms were identified to species when possible. Annelids, crustaceans, mollusks, echinoderms, coelenterates, and remaining taxa (major taxa) were weighed to the nearest 0.01 g (wet-preserved weight). Usually these weights were obtained for the contents of a single stomach, but when the contents were insufficient for accurate weighing, taxa from the stomach contents of several fish of the same species and size, and from the same tow, were combined and weighed together to constitute an observation. The number of observations for Dover, rex, and slender sole and Pacific sanddab were 325, 374, 607, and 392, respectively.

Results are reported as the a) percent that each major food taxa constitutes of the total wet weight of food found in stomachs for all seasons combined and for winter and summer seasons separately; and b) the frequency of occurrence (FO) of principal prey, i.e., species or taxa found in 5% or more of the observations for a species or size group of a species for all seasons combined.

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

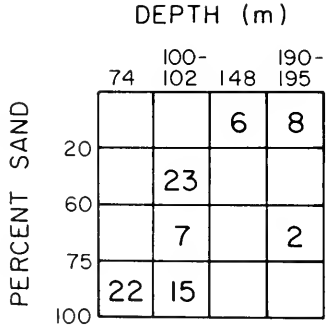

FIGURE 1.—Classification of the seven stations, each indicated by station number, according to depth of water and percent of sand (0-20, 20-60, 60-75, and 75-100%). The stations with similar sediment types but different depths are 6 and 8, 7 and 2, and 22 and 15. (See Pearcy 1978 for additional information.)

RESULTS

General Food Habits

Two general feeding types are indicated by differences in the weights of major food taxa (annelids, crustaceans, mollusks, echinoderms, coelenterates, and other taxa) found in the stomach contents of the four species (Table 1). Dover and rex soles fed largely (64%) on annelids, while slender sole and Pacific sanddab fed mainly on crustaceans (75%). Within these two apparent feeding types, differences occurred among the proportions of prey taxa of secondary importance. For example, crustaceans were more abundant in the diet of rex than Dover sole (31% vs. 11%), whereas mollusks were more abundant in Dover than in rex sole (18% vs. 1%). Annelids composed more of the stomach contents of slender sole than Pacific sanddab (15% vs. 7%).

Based on the average frequency of occurrence of principal prey (FO≥5%) from all sizes of fish and from all stations (Table 2), it is obvious that the food habits within these two feeding types (Dover sole-rex sole vs. slender sole-Pacific sanddab) are not as similar as shown by Table 1. Principal prey of Dover sole, for example, included 11 different identified polychaetes. Rex sole preyed mainly on three identified species of polychaetes. Only one principal prey species of polychaete was common to the diet of both Dover and rex soles. The shrimp *Pandalus jordani*, pelecypods, and ophiuroids were principal prey in the food of Dover but not rex sole, whereas crab larvae, cumaceans, and *Oiko-*

TABLE 1.—Percent by weight that major food taxa composed of the diet of the four flatfishes, all stations and seasons combined.

Taxa	Dover sole	Rex sole	Slender sole	Pacific sanddab
Annelida	64.4	64.8	15.6	7.2
Crustacea	11.2	31.0	75.6	74.8
Mollusks	18.3	1.4	0.7	0
Echinoderms	3.4	0.1	0.1	0
Coelenterates	2.6	0	0	0
Other taxa	0	2.8	8.2	18.0

TABLE 2.—Average frequency of occurrence of principal prey (those occurring in 5% or more of the observations) in the four species, all stations combined.

Prey	Rex sole	Dover sole	Slender sole	Pacific sanddab
Polychaeta				
Sternaspis fossor	12	14		
Myriochele heeri		15		
Nothria geophiliformis	9			
Goniada brunnea	10			
Aricidea neoseucica		6		
Haploscoloplos elongatus		9		
Chaetozone setosa		6		
Terebellides stroemii		6		
Rhodine bitorquata		5		
Typosyllis hyalina		9		
Lumbrineris sp.		6		
Amphicteis sp.		5		
Glyceridae		5		
Unidentified	25	19	7	
Crustacea				
Pandalus jordani		6	7	
Euphausia pacifica			9	7
Crab larvae or juvenile	7			13
Gammarid amphipods	29	24		
Copepods				12
Cumaceans	8			
Unidentified	16	12	21	24
Mollusca				
Pelecypoda		12		
Echinodermata				
Ophiuroidea		12		
Miscellaneous				
Oikopleura spp.	7			
No. observations	347	325	607	392
No. fish	614	326	1,109	723

pleura were principal prey of rex but not Dover sole. Gammarid amphipods occurred frequently in stomachs of both rex and Dover soles; had they been identified to species, the overlap between the diets of the Dover and rex soles would appear even smaller. Overlap in the diets of Dover and rex soles of various size groups were also found to be small.

Gammarid amphipods, the major crustacean prey of Dover and rex soles, were not principal prey for slender sole and Pacific sanddab. Slender sole and Pacific sanddab fed largely on pelagic crustaceans, as indicated by the occurrence of euphausiids in stomachs of both species, by crab larvae and calanoid copepods in sanddab, and by *Pandalus jordani* in slender sole. Slender sole and Pacific sanddab are chiefly pelagic feeders. *Pandalus jordani* is known to migrate off the bottom at night (Pearcy 1970) and hence could have been consumed on the bottom or in midwater by slender sole. We have occasionally caught both slender sole and Pacific sanddab in midwater trawls at night. Barss[4] caught in midwater trawls at night Pacific sanddab that had been feeding heavily on northern anchovy, *Engraulis mordax*. The only good evidence for benthic feeding by either of these two species is the presence of annelids in their diets (Table 1).

Differences Among Stations

The proportions (by weight) of the major taxa in the diet of Dover sole were sometimes markedly different among stations (Table 3). Prey composition and availability may be functions of sediment and or depth. Annelids constituted over 90% of the diet on a weight basis at the three deepest stations (2, 6, and 8), but ≤13% at the shallowest station (22) where the sediment was well-sorted sand. At this shallow station, mollusks and crustaceans were the major food items in the diet. Coelenterates (feeding polyps of sea pens and anemones) and echinoderms (brittlestars) were minor food taxa for Dover sole at all stations except Stations 15 and 23 (102 m depth), where together they composed over one-half the diet. The proportion of fish with food in their stomachs was also higher at these two stations than at any of the other stations.

To illustrate the similarities of the food habits of Dover sole among these stations, we constructed a station-station matrix (Table 4) using an index (C_λ) that Horn (1966) recommended for comparing overlap in exploitation of alternative food sources

[4]Barss, W. H. (compiler). 1976. The Pacific sanddab. Oreg. Dep. Fish Wildl., Inf. Rep. 76-5, 5 p.

TABLE 3.—The average percentage composition of stomach contents of Dover sole on a weight basis at each of the stations.

Taxa	Station (depth in meters in parentheses)						
	22 (74)	7 (100)	15 (102)	23 (102)	6 (148)	2 (190)	8 (195)
Annelids	12.6	59.9	25.0	30.5	91.9	93.4	91.0
Crustaceans	29.6	14.1	3.3	3.1	3.7	3.5	6.5
Mollusks	57.9	23.7	13.5	12.4	3.0	2.2	0.3
Echinoderms	0	1.1	33.8	30.1	1.4	1.1	2.2
Coelenterates	0	1.2	24.3	23.8	0	0	0
Other taxa	0	0	0	0.1	0	0	0
No. fish examined	65	38	22	10	49	91	51
No. fish with stomach contents	28	19	20	10	22	61	32

TABLE 4.—Similarity (C_λ) in the diets of Dover sole at the seven stations based on the percentage of major taxa in their diets on a weight basis (below diagonal) and frequency of occurrence of principal polychaete prey (above diagonal). Stations are arranged by depth.

	Frequency of occurrence						
Stations	22	7	15	23	6	2	8
22		0.04	0	0	0.09	0.06	0
7	0 58		0 64	0 57	0 24	0 54	0.05
15	0 34	0 56		0.59	0 21	0.38	0
23	0 34	0 64	0 99		0.09	0.42	0
6	0.22	0.88	0 44	0 52		0.37	0 42
2	0 21	0.87	0 43	0.52	1 00		0 45
8	0 21	0 88	0 43	0 53	1.00	1 00	

within the same habitat. This measure of similarity varies from 0 to 1.0. The percentages by weight of the major taxa (lower half of Table 4) were identical at the three deepest (148-200 m) Stations: 2, 6, and 8. Stations 15 and 23, both located at 102 m depth, were also very similar. Station 7 at 100 m was fairly similar ($C_\lambda > 0.87$) to Stations 2, 6, and 8 located in deeper water. The percent of major taxa in the diet of Dover sole at the shallow, sand location (Station 22) was not very similar to any other station ($C_\lambda \leq 0.58$).

The frequency of occurrence of principal prey of Dover sole (Table 5) indicates fairly low similarity among different stations for species of polychaetes. Most species occurred at only one or two stations and the assemblage of polychaetes eaten by Dover sole appears to be different at each station. As one would expect, similarity is higher when higher taxa such as gammarid amphipods or pelecypods are considered as a group. For this reason comparisons of similarity among stations should be confined to prey identified to the same taxonomic level.

To examine differences in prey species among stations we calculated the overlap in diet (C_λ) based on polychaetes alone, the most common and speciose prey animals of Dover sole (and the food group that one of us (Hancock) was familiar with taxonomically). The range in overlap of diets based on frequency of occurrence of individual taxa of polychaetes at these stations (Table 5) was appreciably lower than that based on weight percentage of major taxa (upper half of Table 4). Stations 2, 6, and 8, which were very similar on the basis of the weight of major taxa in the Dover sole stomachs, overlapped only moderately on the basis of frequency of occurrence of polychaetes ($C_\lambda = 0.37 - 0.45$). Stations 15 and 23, similarly based on major taxa, were the most similar ($C_\lambda = 0.64$) stations based on frequency of occurrence of polychaetes. Station 23 was the next highest in similarity with Stations 7 and 15. Thus, the polychaete prey of Dover sole were most similar among these three 100-102 m stations.

TABLE 5.—Frequency of occurrence of principal prey of Dover sole from the seven stations.

Taxa	Stn 22	7	23	15	6	2	8
Polychaeta:							
Sternaspis fossor		23	24	6		32	
Myriochele heeri		31	14	6	8	27	
Nothria geophiliformis					9	14	13
Chloeia pinnata						36	16
Melinna cristata						14	
Goniada brunnea		7			8	14	
Aricidea uschakowi		5			9		
Aricidea neosuecica		9			23		
Haploscoloplos leongatus					25	18	8
Owenia fusiformis		10				18	
Maldane sarsi		5	6				
Chaetozone setosa		8		6	8	9	
Terebellides stromenii		11	10				
Tharyx multifilis					6		8
Rhodine bitorquata		13					
Typosyllis hyalina		25		6			
Ammontrypane aulogaster							5
Nephtys cornuta							11
Anaitides groenlandica	10						
Lumbrineris sp		12			6		
Ammontrypane spp.						9	
Amphitteis		9				18	
Aricidea spp							5
Pherusa papillata		7					
Tharyx spp.					9		
Nephtys spp		5		8		8	
Terebellidae						9	
Ampharetidae							5
Maldanidae						9	
Lumbrineridae					11		
Glyceridae		10	8				
Spionidae	10	5			6	9	
Hemipodus borealis	10						
Laonice cirrata		6					
Megelona sp.		5					
Crustacea							
Pandalus jordani	30	7	16			23	8
gammarid amphipod	70	22	22	24	14	45	26
copepod	20						
cumacean		7					8
Diastylis spp							8
Valvifera spp.	10						
Ostracoda	10					14	5
unidentified crustacea							
Mollusca							
Gastropoda		7					
Solenogasters spp		7					8
Pelecypoda	20	20		10	16		8
Yoldia ensifera			8				
Lucina sp						9	
Megacrenella columbiana		10		10			
Tellina salmonea	10						
Acila castrensis	10						
Echinodermata							
Ophiuroidea		11	27	16		23	
sea pen			12				
Miscellaneous							
Nematoda						18	
No. observations	10	91	51	49	64	22	38
No. fish	10	91	51	49	65	22	38

Because stomachs of the other flounders were examined for only two or three stations, few station comparisons could be made. As with Dover sole, the percentage of major taxa in the diets of rex sole at Stations 2, 6, and 7 were similar, and food habits were almost identical at Stations 2 and

TABLE 6.—The average percent by weight that major taxa composed of the diet of rex sole, slender sole, and Pacific sanddab at Stations 7, 6, and 2.

	Rex sole			Slender sole			Pacific sanddab	
Taxa	Stn 7	6	2	7	6	2	7	6
Annelida	58.7	69.7	64 5	1.2	18.5	13.1	8.2	0.1
Crustaceans	39.2	24.8	29.6	92.2	72.3	77 8	71 3	99.9
Mollusks	2.1	1.0	0.5	0.9	0 8	0	0	0
Echinoderms	0	0	0	0	0	0	0	0
Coelenterates	0	0	0	0	0	0	0	0
Other taxa	0	4.5	5.5	5.8	8.5	9 1	20.5	0
No. fish examined	376	210	28	68	844	197	690	33
No. fish with stomach contents	262	160	25	35	403	83	478	13

6 (Table 6). A larger percentage of crustaceans (and the lowest percentage of annelids) was found at Station 7 than at 2 or 6 for both rex and slender soles. But crustaceans were more abundant in the diet of sanddab at Station 6 than at Station 7. Fishes (included as other taxa) were an appreciable part of the sanddab diet at Station 7. Again, differences in availability of food taxa apparently occurred among stations for the same predator species, and different trends in the importance of food taxa are evident for different species of fish at the same stations.

The principal prey were most similar for rex sole at Stations 2 and 6, as were the major taxa by weight. The polychaete *Nothria geophiliformis* and the larvacean *Oikopleura* occurred in over 5% of the observations only at these two stations. It is curious that the planktonic *Oikopleura* was so frequent in the diet of this primarily benthophagus fish. Other prey common at all these stations included the polychaete *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and cumaceans.

Pandalus jordani was a principal prey species for slender sole at Stations 6 and 7 but not at Station 2. The shrimp *Spirontocaris bispinosa* and unidentified fish were found in over 5% of the fish only at Station 6. Copepods were common only at Station 7.

Euphausia pacifica was a principal prey for Pacific sanddab at Stations 6 and 7. *Pandalus jordani* occurred in 26% of the fish at Station 6, but was uncommon at Station 7. Decapod crab larvae and copepods, on the other hand, were common prey only at Station 7.

Variations With Seasons or Size of Fish

Changes in the relative proportions of the major taxa of food consumed by different sizes of the four species of flatfishes are shown for "summer" (May-September) and "winter" (October-April) in Figures 2-5. Because food habits as well as sizes of fishes vary among stations (Tables 3, 6; Pearcy 1978), geographic effects are confounded in these figures.

Annelids usually dominated the diet of all size groups of these juvenile Dover sole during both seasons (Figure 2). Crustaceans appeared to decrease in importance with increasing size of fish during the winter season, but reached peaks in the summer. Mollusks (*Solegasters* spp., *Yoldia ensifera*, and unidentified pelecypods) attained peaks in the diet of intermediate-sized (200-300 mm) Dover sole, and echinoderms (mainly ophiuroids) attained a peak at a larger size of fish.

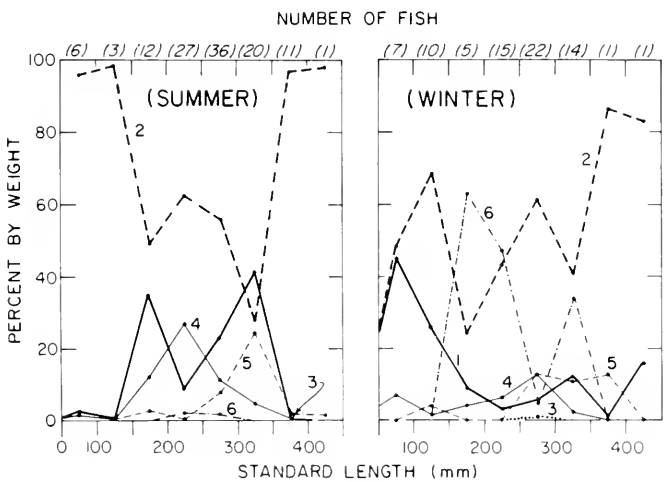

FIGURE 2.—The percent by wet weight of the major food taxa for different length groups of Dover sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, 5 = echinoderms, and 6 = coelenterates.

The largest difference between seasons was for coelenterates. Anemones and the feeding polyps of sea pens were unimportant constituents of the food during the summer (<2% of diet by weight) but were sometimes a major food (>30% by weight) during the winter. Anemones and sea pens are probably available as prey during both seasons but for some reason only consumed in significant quantities during the winter.

Seasonal differences in the intensity of feeding were also indicated by the higher frequency of empty stomachs in winter than in summer (Table 7). The number of principal prey occurring in the diet of Dover sole was consistently larger during summer than winter regardless of fish size. Although the smaller number of stomachs with contents during the winter reduces sample size, and hence the number of taxa found, the frequency of occurrence of many of the individual taxa of polychaetes, crustaceans, and mollusks (taxa listed in Table 5) was higher in summer than winter. Bertrand (1971) found no evidence for seasonal variations in the numbers or biomass of infauna sampled with grabs at these stations. Therefore a more diverse assemblage of prey was probably available to Dover sole during the summer or fish were usually less selective during the summer than during the winter. The summer is the season of most active growth of Dover sole (Demory 1972) when intraspecific and possibly interspecific competition for food may be most intense. Decreased prey selectivity is known to occur under conditions of low food abundance or availability (Ivlev 1961; Schoener 1971).

The number of principal prey taxa generally increased with size of Dover sole (Table 7). This trend may be related to sample size (number of stomachs with food) and to the ability of large fish to consume a larger range of prey sizes than small fish. The less diverse diet of small fish resulted from ingestion of only a few species of polychaetes.

TABLE 7.—Frequency of empty stomachs (no. empty stomachs/no. fish) and the number of principal taxa (occurring in 5% or more of at least 10 observations) of prey for different sizes of Dover sole collected during summer and winter seasons.

Standard length (mm)	Frequency of empty stomachs		Number of taxa	
	Summer	Winter	Summer	Winter
51-100	6/12	15/22	9	4
101-150	—	19/29	—	8
151-200	4/16	10/15	24	12
210-250	7/34	19/34	25	18
251-300	11/47	20/42	37	17
301-350	4/24	7/21	21	15
351-400	5/16	—	41	—

Those prey types eaten by a broad size range (50-400 mm SL) of Dover sole include: *Myrochele heeri*, *Typosyllis hyalina*, *Lumbrineris* sp., Glyceridae, gammarid amphipods, pelecypods, *Megacrenella columbiana*, ophiuroids, unidentified polychaetes, and unidentified crustaceans.

Annelids and crustaceans were the major food items for rex sole (Figure 3). (Most of the rex sole represented here are juveniles.) Annelids increased in importance with an increase in the sizes of rex sole, up to 150-250 mm. This increase was associated with a decrease in the proportion by weight of crustaceans, the dominant food item for small rex sole during both seasons. Euphausiids, decapod crab larvae, copepods, and ostracods were only found as principal prey of rex sole of <200 mm. Mollusks formed only a minor portion of the diet. Differences in the FO of principal prey were not pronounced. Some polychaetes (*Sternaspis fossor*, *Myriochele heerie*, *Nothria geophiliformis*, and *Choelia pinnata*) were found more frequently in large (220-300 mm SL) rex sole.

Some seasonal differences in the diet of rex sole were evident. Euphausiids were principal prey only during the summer. Cumaceans and *Oikopleura* were more common during the winter. Principal prey that were commonly ingested by all or most size groups during both seasons were: *Sternaspis fossor*, *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and uniden-

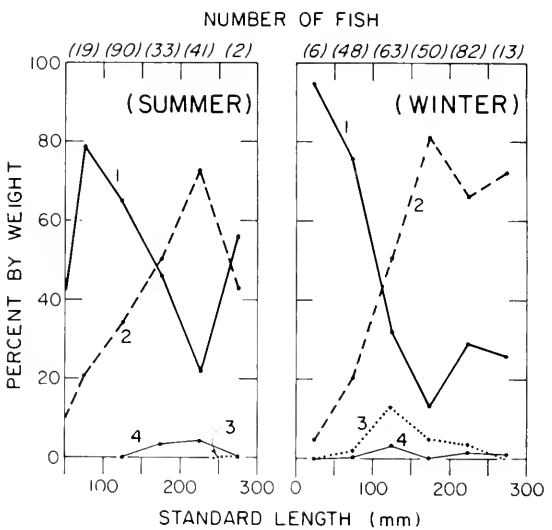

FIGURE 3.—The percent by wet weight of the major food taxa for different length groups of rex sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, and 4 = mollusks.

tified crustaceans. Kravitz et al. (1977) listed *Nothria* spp. as frequently occurring polychaetes and *Ampelisca macrocephala*, *Hippomedon wecomus*, *Paraphoxus epistomus*(?), and *P. obtusidens* as frequently occurring amphipod prey for rex sole.

Crustaceans composed the bulk of the diet of all sizes of slender sole during both seasons (Figure 4). Annelids and "other taxa" were most important in the diet of intermediate-sized (101-200 mm) slender sole during either summer or winter. Pelagic crustaceans such as copepods, euphausiids, and crab larvae occurred frequently in the diet of small (<150 mm) slender sole, whereas polychaetes, the shrimps *P. jordani* and *S. bispinosa*, and fishes were important for large slender sole (>150 mm). Again, a larger number of principal prey taxa occurred during the summer than winter.

Crustaceans also were the most important taxa in the diet of the Pacific sanddab, except for five 201-250 mm individuals during the summer, when fishes composed 95% of the food by weight (Figure 5). Kravitz et al. (1977) found that all *C. sordidus* (90-377 mm total length) collected in May off Oregon had been feeding intensively on northern anchovy. Barss (see footnote 4) reported

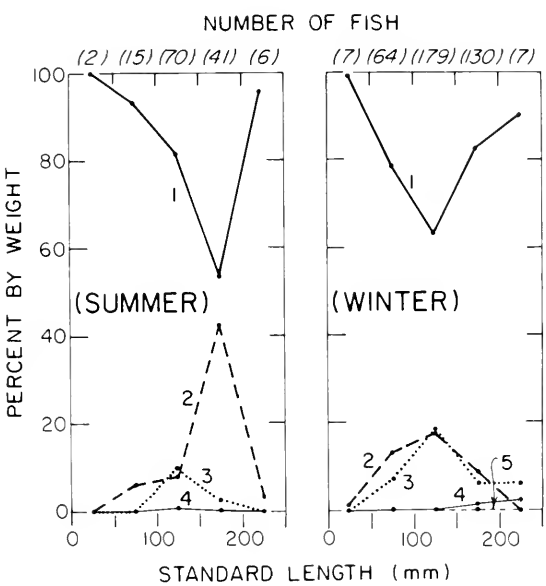

FIGURE 4.—The percent by wet weight of the major food taxa for different length groups of slender sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, and 5 = echinoderms.

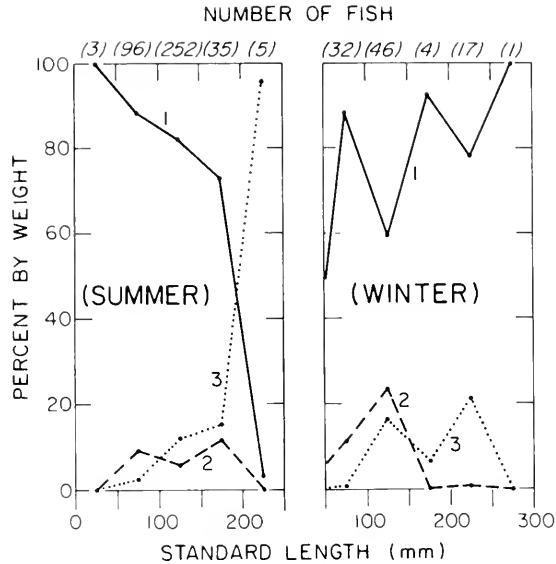

FIGURE 5.—The percent by wet weight of the major food taxa for different length groups of Pacific sanddab for summer and winter. 1 = crustaceans, 2 = annelids, and 3 = other taxa.

that sanddab eat small fishes, squids, and octopuses.

Crustaceans were the predominant prey during both seasons and for most sizes of sanddab. Euphausiids, copepods, and cumaceans occurred more frequently in small than large individuals. *Pandalus jordani*, crangonids, and fishes were most common in the diet of large Pacific sanddab.

DISCUSSION

The four common flatfishes caught in this study compose two generalized feeding types. Dover and rex soles feed almost exclusively on benthic invertebrates, mainly polychaetes and amphipods, while slender sole and Pacific sanddab prey mainly on pelagic crustaceans. The food habits of these two types are related to mouth structure and digestive morphology. Flatfishes that feed on benthos usually have asymmetrical jaws, small stomachs, and long intestines, whereas pelagic feeders have longer, symmetrical jaws with sharp teeth and long serrated gill rakers, adaptations for grasping and retaining animals that swim in midwater (Hatanaka et al. 1954; Groot 1971). Dover and rex soles belong to the benthos-feeding type and sanddab and slender sole to the pelagic-feeding type. Kravitz et al. (1977) also recognized these two feeding types among five flatfishes off

Oregon, and included rex sole as a benthophagus species and Pacific sanddab as a piscivorous-pelagic feeder.

Rae (1956, 1969) studied the feeding habits of the lemon sole, *Microstomus kitt*, and the witch, *Glyptocephalus cynoglossus*, off Scotland. Some of his results are remarkably similar to ours for the congeneric Dover sole, *M. pacificus*, and rex sole, *G. zachirus*. Both the witch and lemon sole, like the Dover and rex soles, feed predominantly on polychaetes. Crustaceans were next in importance followed by other phyla such as mollusks, echinoderms, and coelenterates. Ophiuroids and anthozoans were also eaten by both lemon sole and the witch. These similarities in diets indicate common feeding specializations within pleuronectid genera.

Although the major food of the lemon sole and witch were very similar, these two species, like the Dover and rex soles, preyed on different families or different genera of the same family so that food overlap, and presumably competition, are rare (Rae 1956, 1969). As pointed out by Rae, these differences in feeding habits reflect behaviorial differences of the fishes as well as differences in the composition of the benthic communities of which these fishes are a part. The habitats of the lemon sole and witch often differ, the lemon sole preferring hard, rocky bottoms, and the witch soft, muddy bottoms.

Both the lemon sole and witch fed most heavily during the summer. Regional differences were also marked. Polychaetes decreased in importance as prey for the witch in shallow water (<100 m), as they did in our study for Dover sole (Table 3). Rae (1939, 1956) also believed that differences in the types and quantities of food available between one area and another resulted in different growth rates of lemon sole. Sedentary polychaetes were most common as prey in areas of rapid growth.

One of the objectives of this study was to learn if differences in the availability of prey for flatfishes occurred and how it may be related to sediment types and water depth at our stations. The composition of prey of Dover sole clearly varies among stations. Polychaetes were the main food at the three deepest stations; echinoderms, coelenterates, and polychaetes were similar on a weight basis at the two 102-m stations; polychaetes, followed by mollusks, were most important at the 100-m station; and mollusks and crustaceans were most abundant at the 74-m station (Table 3). Based on the percentage by weight of major food taxa, higher similarities occurred among stations at similar depths rather than with similar sediment types: Stations 15 and 23 at 102 m and the deep stations 6, 2, and 8 at at 148-195 m (Table 4). Sediment texture at Stations 15 and 23 were dissimilar. (See Figure 1 for summary of depth and sediments for the stations.) Although Station 2 had an average sediment texture that differed from Stations 6 and 8, a thin layer of silt overlaid coarse sand at Station 2, hence the surface sediment of Stations 6, 2, and 8 were probably more similar than indicated in Figure 1.

The occurrence of individual species of polychaetes consumed by Dover sole is probably a more sensitive indicator of station differences than the biomass of major taxa. Stations 7, 15, and 23, at 100-102 m, but with different sediment types, were most similar in polychaete prey. Stations 2, 6, and 8 in deep water, at 148-195 m were again similar. Thus, these similarities in prey for these two groups of stations seem to be correlated with depth. However, polychaete prey at Station 2 (190 m) was similar to that of Station 7 (100 m), which had similar sediment type, as well as that at Stations 15 and 23 (102 m) with different sediments. Stations 22 and 15 with similar sediment types, but at different depths, had low similarity of polychaete prey.

Based on 82 species of mollusks, cumaceans, and ophiuroids sampled in 0.1-m^2 Smith-McIntyre grabs, Bertrand (1971) calculated the similarity of the fauna among the same seven stations included in this study. He also found that Stations 2, 6, and 8 formed a deep-water group of high similarity. Stations 7 and 23 (at 100-102 m) were similar, as were Stations 7 and 8, with different depths and sediment types. Gunther (1972) also calculated similarities among these same stations based on living benthic foraminifera and found that strong faunal affinities crossed depth and sediment boundaries. Again, Stations 2, 6, and 8 formed one group. Stations 2 and 7, and 15 and 22, station pairs based on sediments, were not very similar.

Similarities among the fishes caught were also strong among Stations 2, 6, and 8. The remaining stations (7, 15, 22, and 23) formed another group of high affiinity (Pearcy 1978). These two species associations agree with those described by Day and Pearcy (1968) for the continental shelf off central Oregon. They found a shallow (42-73 m) water association on a sand bottom dominated by Pacific sanddab and English sole, *Parophrys vetulus*, and an association at 119-159 m on a silty-

sand bottom dominated by slender sole and rex sole.

Shallow-water and deep-water associations are therefore evident at these stations, based on previous studies of benthic invertebrates and vertebrates, as well as the composition of the diet of Dover sole in this study. Because surface sediments were fairly similar at our three deep stations, sediment vs. depth effects could not be separated here. The lack of precise similarities of sediment types for station pairs also weakens this part of our study. Nevertheless, stations with the most similar sediment types often had low similarity of benthic fauna. We conclude that depth-related factors may have greater influence than sediment type on the composition of benthic fishes, fish food, and invertebrate fauna within the boundaries of our study area. This conclusion must be tempered, however, by the realization that other sediment parameters besides texture and percent organic matter may be important, and we simply did not study the proper sediment characteristics. We agree with Peterson (1918): "It is clear then that the character of the bottom is of fundamental importance for the presence or absence of epifauna. Nevertheless, the succession of the various types of epifauna and of the communities belonging to the level bottom cannot be explained by the character of the bottom alone."

Bertrand (1971) estimated the "edible" biomass of infauna (>1.0 mm) for demersal fishes (i.e., all infauna less holothurians, echinoids, echiurids, and burrowing anemones) at these stations from 0.1-m^2 Smith-McIntyre grab samples taken on the same cruises. He detected no seasonal variations in the wet or ash-free dry weight of this biomass fraction. The ash-free dry weights per square meter for polychaetes, mollusks, and crustaceans given by Bertrand for the seven stations are shown in Table 8. Crustacean biomass was consistently low at all stations, probably because of the ineffectiveness of the grab to sample epibenthic and motile amphipods, major food items of Dover and rex soles. There was no direct or consistent relationship between the biomass per square meter of "edible" fish food and the biomass of all fish or Dover sole. Stations with similar standing stocks of infaunal food had widely different standing stocks of benthic fishes.

TABLE 8.—Ash-free dry weights in grams per square meter of macro-infaunal fish food at the seven stations (from Bertrand 1971).

Taxa	Stn 22	7	23	15	6	2	8
Polychaetes	0.04	0.17	0.30	0.08	0.17	0.14	0.19
Mollusks	4.50	1.10	1.74	2.09	0.20	0.16	0.07
Crustaceans	0.006	0.005	0.001	0.004	0.008	0.004	0.003
Total	4.55	1.28	2.04	2.17	0.38	0.30	0.26

Station 22, the beach sand station—with the lowest organic carbon in the sediment of all stations—supported a fairly low biomass of fish, but the largest biomass of edible fish food, 4.55 g/m^2, and the largest biomass of invertebrate macrobenthos. Conversely, Wigley and McIntyre (1964) found the largest biomass in finer sediments off Massachusetts, and Lie and Kisker (1970) found that the shallow-water sand communities off Washington had a lower average standing stock of infauna than deeper communities on the shelf. The large biomass at Station 22 is composed primarily of the bivalves *Acila castrensis* and secondarily of *Tellina salmonea*. Both of these mollusks were principal prey of Dover sole only at Station 22 (Table 5). Although the frequency of occurrence of these two mollusks in Dover sole stomachs was only 10%, mollusks composed 58% by weight of the food of Dover sole at this station. Thus Dover sole are versatile predators, changing their diets opportunistically in response to changes of prey availability.

The dominant fish at Station 22 was Pacific sanddab, primarily a pelagic feeder. Mollusks were not principal prey. *Acila* and other burrowing animals are unavailable as food for fishes adapted for pelagic feeding, illustrating a basic reason for the lack of any direct relationships between edible fish food and fish biomass.

The average biomass of Dover sole was directly related to the biomass of their principal food, polychaetes, at the seven stations (Figure 6). Station 22, where Dover sole consumed principally mollusks, had the lowest biomass of both polychaetes and Dover sole; intermediate values of biomass of both fish and food are found at the three deep stations (2, 6, 8). The three stations at about 100 m (2, 7, and 15) differed markedly in standing stocks of both polychaetes and Dover sole. This positive correlation ($r = 0.73$) of standing stocks of predator and prey implies that Dover sole selected habitats within our study area where their prinicpal preferred food was most abundant regardless of depth and bottom type. Of more fundamental interest is the fact that standing stocks of polychaetes may indicate the amount of food available to Dover sole, and perhaps the production rates of polychaetes at the different stations. Similar direct relationships between standing

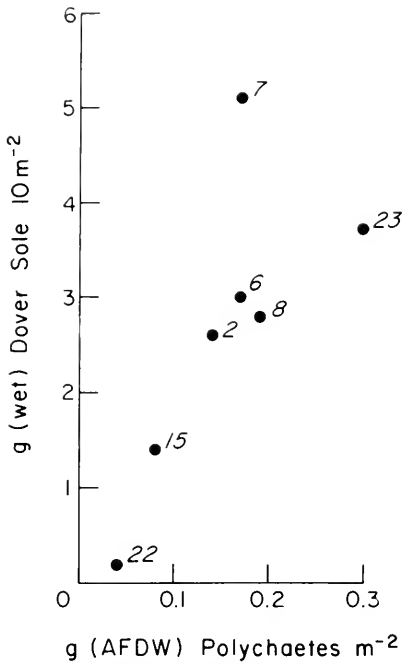

FIGURE 6.—The relationship between average standing stocks of prey (grams ash-free dry weight of polychaetes per square meter) and predator (grams wet weight of Dover sole per 10 m^2) at the seven stations.

stocks of predator and prey have been elucidated by Brocksen et al. (1970) for the biomass of phytoplankton and zooplankton and for zooplankton and sockeye salmon among ecosystems with different productivities. This is the first example, to our knowledge, of such a relationship for the marine benthos.

ACKNOWLEDGMENTS

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SKIPJACK TUNA, *KATSUWONUS PELAMIS*, HABITAT BASED ON TEMPERATURE AND OXYGEN REQUIREMENTS

RICHARD A. BARKLEY,[1] WILLIAM H. NEILL,[2] AND REGINALD M. GOODING[1]

ABSTRACT

The habitat of skipjack tuna, *Katsuwonus pelamis*, has generally been assumed to be the warm surface layers of tropical and subtropical ocean, where most of these fish are seen and caught. But experiments with captive Hawaiian skipjack tuna imply that their habitat is more restricted, with boundaries defined by both temperature and dissolved oxygen. The lower temperature limit appears to be about 18° C. The upper temperature limit apparently varies with size of the fish, from 30° C or more for small individuals to as little as 20° C for the largest. Skipjack tuna also require water with unusually high concentrations of dissolved oxygen, at least 3.0-3.5 ml/l (4-5 ppm), for long-term survival. If our Laboratory findings with captive skipjack tuna accurately define their natural habitat, only the smallest of these animals can inhabit the warm surface waters of the tropics; those larger than 4-5 kg must inhabit the thermocline. Our hypothesis, which can be tested, explains many features of the known distribution of skipjack tuna in the eastern and central Pacific Ocean.

For skipjack tuna, *Katsuwonus pelamis* (Linnaeus), the question "Where are the fish?" is particularly hard to answer. Their habitat is known only in the most general terms. These fish are found in tropical and subtropical waters of all oceans, at surface temperatures between 15° and 30° C. Because they are caught most frequently by methods such as trolling, purse seining, and pole-and-line fishing, it is generally assumed that skipjack tuna inhabit the surface mixed layer. Japanese longline gear, which fishes well below the sea surface, catches very few skipjack tuna, and then only on the hooks which fish nearest the surface (Yabe et al. 1963). In a review of the literature on this species, Matsumoto and Skillman[3] pointed out that the sea-surface temperature range where most skipjack tuna are caught varies from one fishery to another. Off Tasmania and southeast Australia, the range is 15° to 18° C. Off Japan and South America, the range appears to be 20° to 24° C, while the fishery off southern India operates in water of 28° to 29° C. The Hawaii fleet fishes skipjack tuna all year, in water with surface temperatures ranging from 23° to 27° C, with the majority of catches in the warm, summer months.

Because studies of the occurrence of wild skipjack tuna in relation to sea-surface temperature yield such disparate results from one area to another, and because the total temperature range, 15° to 30° C, includes more than half of the surface area of the world's oceans, we have worked with captive animals in a series of experiments intended to define more precisely their physiological requirements. Results of three of these studies (Neill et al. 1976; Dizon et al. 1977; Gooding and Neill[4]) provided information on the skipjack tuna's temperature and dissolved oxygen requirements which, taken together, appear to define the actual habitat of this species in nature.

We present here a summary of the physiological studies and their results, which suggest specific temperature and dissolved oxygen values that define the spatial limits of the skipjack tuna habitat. With the resultant temperature and dissolved oxygen values, we have mapped the habitat of the skipjack tuna using averaged oceanographic data from the eastern Pacific Ocean.

These habitat maps present our hypothesis in a testable form. If skipjack tuna in nature have the same requirements as those studied in captivity, their distribution should, on average, correspond

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with the habitat volume shown on the maps. If, under normal oceanographic conditions, they occur in significant numbers well outside of the mapped habitat volume the hypothesis is invalid, and we should look for evidence of adaptations (behavioral, physiological, and genetic) which were not evident in our work with captive fish. If the distribution of skipjack tuna is more restricted than our habitat maps would indicate, we should look for factors in addition to temperature and dissolved oxygen (e.g., turbidity) which might further limit the habitat. Salinity is not apt to be one of these factors, however, since captive skipjack tuna do not respond to rather drastic changes in this variable (Dizon 1977).

More immediate and definitive tests of the hypothesis can be made by tagging wild skipjack tuna of various sizes with tags capable of sensing and telemetering depth, temperature, and dissolved oxygen.

TEMPERATURE AND OXYGEN REQUIREMENTS

Lower Temperature Limit

Dizon et al. (1977) determined that 15° C was the lower lethal temperature limit for skipjack tuna. They subjected recently caught, apparently healthy individual fish to water temperatures which decreased 1° or 5° C/day, starting at ambient temperature (about 24° C), with other skipjack tuna held continuously at ambient temperature as controls. All seven of the test animals survived and fed until temperature had declined to 18° C; at 17° C all but one fish stopped eating, and one fish died. None of the fish survived 15° C for more than a few hours. Accordingly, we have selected 18° C as the lowest water temperature which Hawaii skipjack tuna can withstand for prolonged periods of time without significant increases in mortality.

This preliminary estimate of the lower temperature limit is essentially identical with the value obtained by Williams (1970) from a comparison of fishery catch data with sea-surface temperatures in the eastern Pacific. Williams found that most skipjack tuna were caught in water with temperatures between 29° and 20° C, with diminishing catches down to temperatures between 18° and 17° C, and no catches in colder waters.

Three large (ca. 70 cm) Hawaiian skipjack tuna released with tags that telemetered swimming depth were found to spend >85% of their time in water warmer than 20° C and <10% in water colder than 18° C (Dizon et al. in press).

In the western South Pacific, skipjack tuna have been caught in water near 15° C, off Tasmania (Robins 1952) and off eastern Australia (G. I. Murphy, Division of Fisheries and Oceanography, CSIRO, New South Wales, Australia, 1977, pers. commun.). These fish probably belong to a different subpopulation (Fujino 1972) than fish found in Hawaii.

Lower Dissolved Oxygen Limit

Gooding and Neill (see footnote 4) examined the effects of low dissolved oxygen concentrations on skipjack tuna. Their animals, habituated in open tanks with circulating, essentially saturated seawater (4.5 ml O_2/l, or 6.4 ppm), were transferred to tanks in which the concentration of dissolved oxygen could be maintained at a preselected constant subsaturation level. Temperatures in both sets of tanks were ambient, 23° to 24° C. Dissolved oxygen concentrations down to 1.0 ml/l (1.4 ppm) were used. Resistance times and swimming speeds were measured, and general behavior was observed for up to 4 h in each experiment. Under their experimental conditions, Gooding and Neill concluded that hypoxic stress was first manifest, through changes in swimming behavior and speed, at about 2.8 ml/l (4.0 ppm), a value fairly typical for fish. Lethal oxygen levels, leading to death in 4 h or less, were found to be higher than those for any other freshwater or marine fish thus far studied. Only one fish (out of six) survived 4 h at 2.5 ml/l (3.5 ppm), and none survived as long as 2 h at still lower concentrations. At higher oxygen values, above 2.5 ml/l, all skipjack tuna tested in this study survived at least 4 h.

Because we sought to estimate the lowest dissolved oxygen concentrations that skipjack tuna can tolerate indefinitely without significant stress, we have chosen a conservative value of 3.5 ml/l (5 ppm) as the lower limit to the skipjack tuna's habitat, where temperature and other variables are not limiting.

Upper Temperature Limit

The case for an upper temperature limit to the skipjack tuna's habitat is somewhat less direct. Three small (30-35 cm) individual skipjack tuna maintained in water warmed 1°C/day survived

until the temperature reached 33°C, when two died; the other lived until the water reached 34°C (Dizon et al. 1977). Skipjack tuna have a high metabolic rate and a countercurrent heat exchanger in their circulatory system which dramatically restricts heat loss through the gills. This accounts for the fact that freshly caught wild skipjack tuna can have red muscle core temperatures as high as 11°C above that of the surrounding water (Stevens and Fry 1971).

Temperature excesses of this magnitude could lead to dangerously high muscle temperatures if they occur in the warmer parts of the ocean. To examine this possibility we use a heat balance model developed for skipjack tuna by Neill et al. (1976) which yields an estimate of temperature excess in the red muscle core as a function of size and metabolic activity (Figure 1a). Actual muscle core temperatures are found by adding the values shown in this figure to the temperature of the surrounding water, for any given size fish. Clearly, large skipjack tuna in surface waters of the tropics must either tolerate high muscle core temperatures, or reduce their metabolic activity substantially below the 3 mg O_2 g^{-1} h^{-1} level.

But skipjack tuna appear to avoid heating their muscle tissue much above 35°C (Stevens and Fry 1971). This upper limit must place a similar upper limit on the water temperatures which skipjack tuna can inhabit, unless they can thermoregulate physiologically or behaviorally. In Figure 1b, 35°C is taken as the upper limit for the red muscle core, and temperature excesses of Figure 1a are subtracted from that value to arrive at an estimate of the upper temperature limits for the habitat of skipjack tuna, as a function of size. If the values thus obtained are valid, these fish should be able to live anywhere in the ocean when they are small, but they should be limited to lower and lower environmental temperatures as they grow. The largest known skipjack tuna, weighing approximately 16 kg, would—if active enough—be confined to water temperature near 18°C, which is also their approximate lower limit.

SKIPJACK TUNA HABITAT HYPOTHESIS

We hypothesize that skipjack tuna of the central and eastern Pacific Ocean occupy a primary habitat—a volume of water whose properties they can tolerate indefinitely—which is 18°C or warmer, but cooler than the upper limits for normally active animals shown in Figure 1b, provided that the dissolved oxygen concentration is at least 3.4 ml l^{-1} (5 ppm). Skipjack tuna can presumably

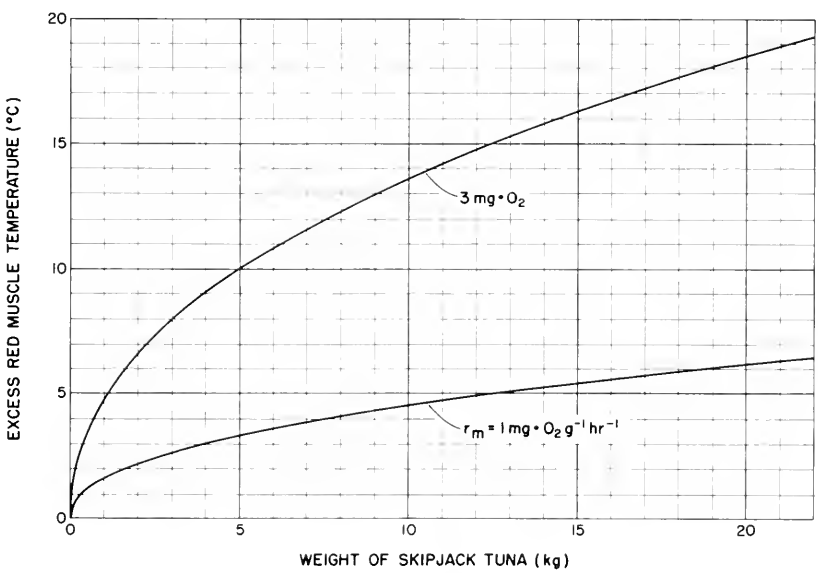

FIGURE 1a.—Calculated excess of internal temperature, over that of the surrounding water, in red muscle for skipjack tuna of all known sizes. Values are shown for a measured minimum (anesthetized) level of metabolic activity (lower line) and our estimate of the mean metabolic activity for normally active animals (upper line), triple the minimum level. (From Neill et al. 1976.)

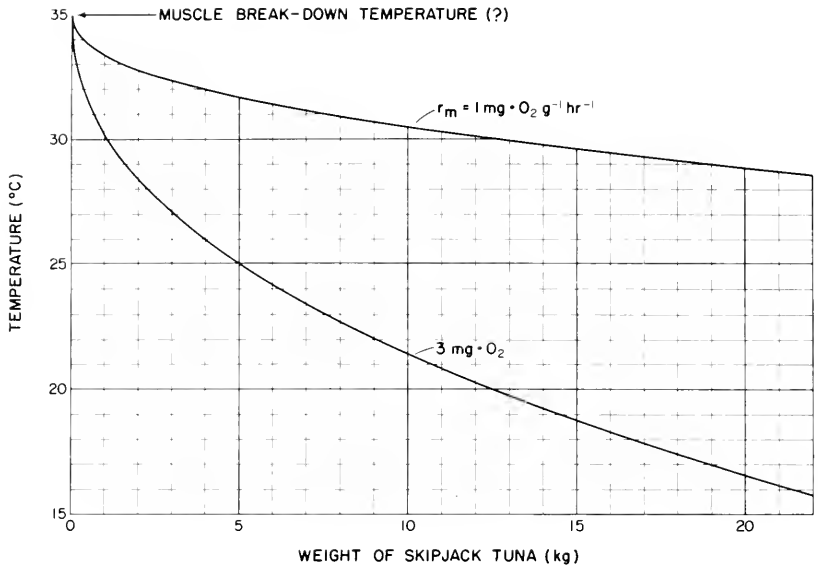

FIGURE 1b.—Maximum tolerable water temperature for skipjack tuna as a function of size for the same two rates of metabolic activity illustrated in Figure 1a. Based on calculated internal temperature excesses and the assumption that damage to red muscle tissue occurs above 35 C.

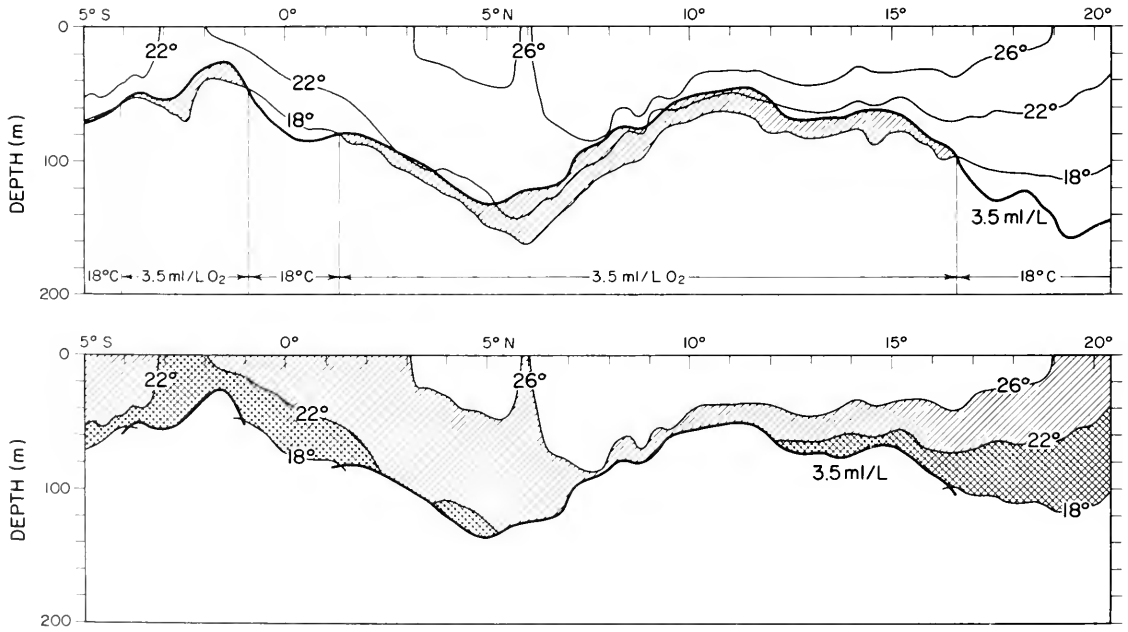

FIGURE 2.—Upper panel: Temperature and dissolved oxygen (selected isopleths only) along long. 119° W, eastern Pacific Ocean, August 1967 (Love 1972). Lower limits of the skipjack tuna habitat are assumed to be either 18°C or 3.5 ml/l dissolved oxygen, as indicated. The hatched layer should be warm enough for these fish, but oxygen deficient. Lower panel: Hypothesized habitat layers for skipjack tuna of two sizes, 4 kg (entire hatched area) and 9 kg (cross hatched area only) in the same section. Fish <4 kg could presumably live anywhere between the sea surface and the lower limits, 18°C or 3.5 ml/l of dissolved oxygen.

leave their primary habitat only for limited periods of time without suffering thermal or oxygen stress. Prolonged excursions to colder water would require increased activity and thus more dissolved oxygen and food. Skipjack tuna could stay in the warm upper layers only if they would reduce their physical activity, or tolerate overheating. Hypothetical consequences of these conditions are illustrated in Figure 2 which shows the hypothetical layers along long. 119° W for skipjack tuna of two sizes. The 4-kg fish are those most abundant in catches by the eastern Pacific fishery; 9-kg fish are the largest normally found there, and then only in certain areas such as the Revillagigedo Islands (ca. lat. 17° N, long. 112° W).

The deeper limit of the habitat should be the same for skipjack tuna of all sizes. The upper limit is deeper and more restrictive for larger fish, which find essentially no habitable water between lat. 5° and 12° N, a distance of more than 700 km or 400 n.mi. Larger fish also have much less continuous access to the sea surface than those weighing 4 kg. Only skipjack tuna of the smallest size commonly found in this area (<4 kg) could inhabit all of the water above the lower limits in Figure 2.

Figures 3 to 6 are maps of a hypothetical skipjack tuna habitat for the entire central and eastern Pacific Ocean, based on oceanographic station data used in preparing the Oceanographic Atlas of the Pacific Ocean (Barkley 1968). For these maps,

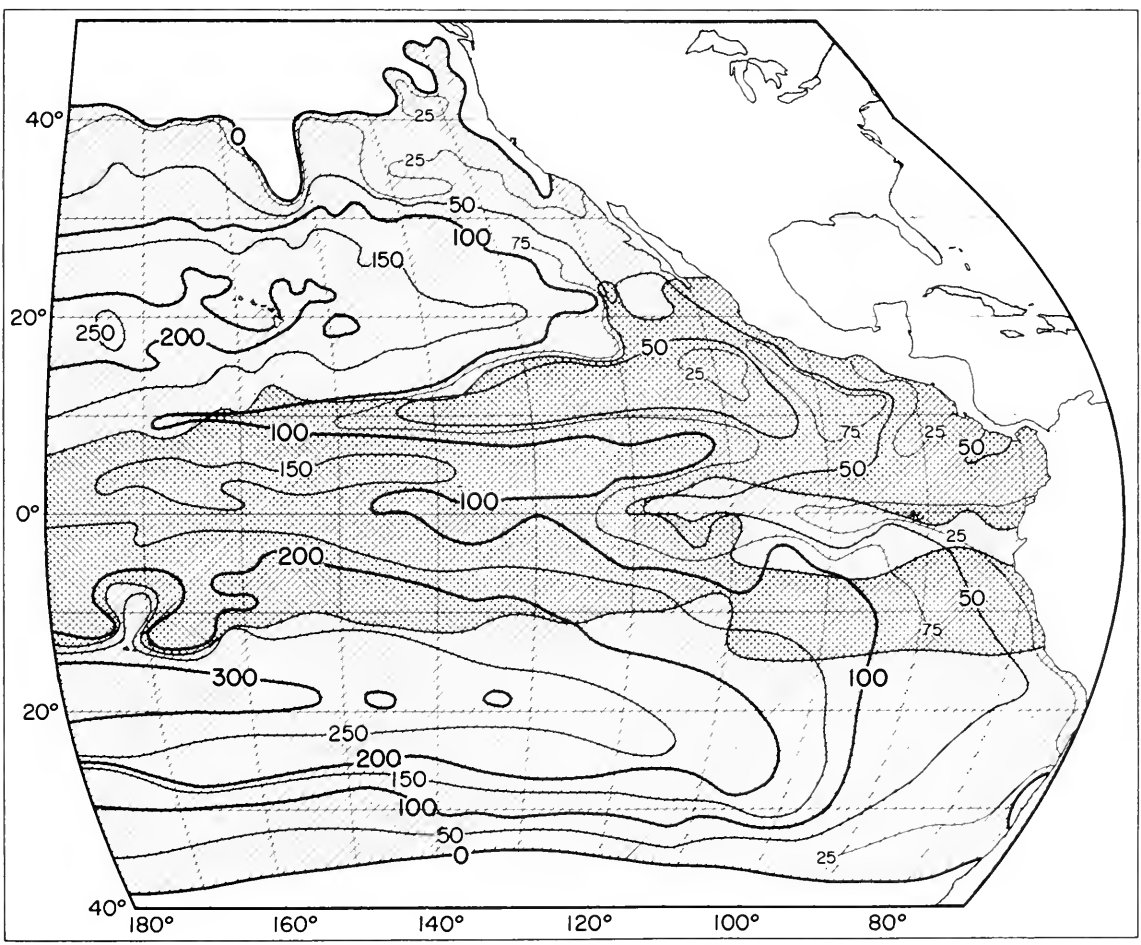

FIGURE 3.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml·l (5 ppm) isopleth of dissolved oxygen (cross hatched area). Contour interval is 50 m except for a few areas near the coast, where a 25-m contour interval is used.

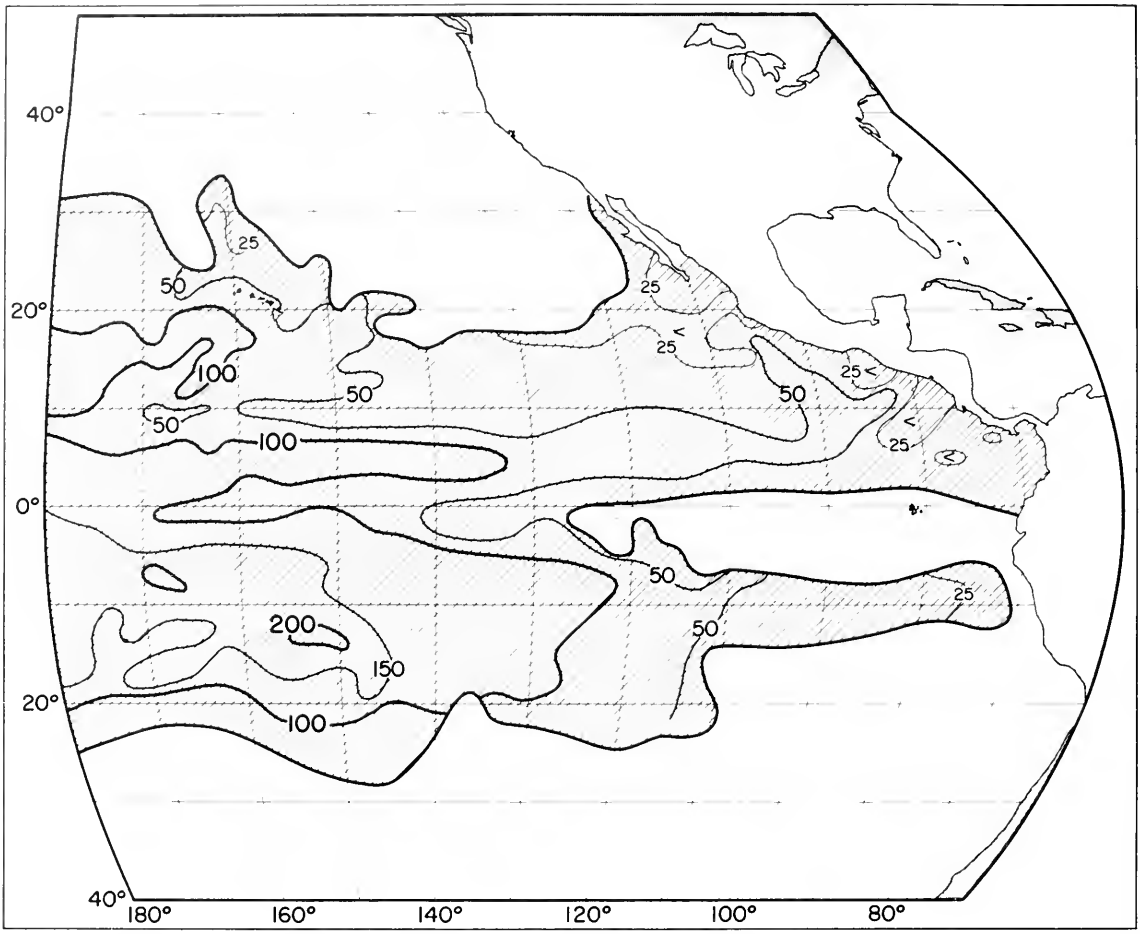

FIGURE 4.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of long. 180°, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24°C. Contours show the depth, in meters, of the 24°C isotherm.

station data were averaged within 2° areas of latitude and longitude, for all months, to approximate annual mean conditions.

Figure 3 shows the hypothetical "floor" of the skipjack tuna habitat, i.e., maximum depths (in meters) for this species. In Figure 3, the unhatched areas off the Pacific coast of the Americas, and at latitudes higher than about 40° in both hemispheres, indicate water which, at all depths, is colder on average than 18°C; presumably skipjack tuna would not normally be present.

Figure 4 shows the minimum habitat depth or ceiling for 6.5-kg fish. Outside of the hatched area annual mean surface temperatures are <24°C, and 6.5-kg fish would normally have access to all of the water column above the habitat floor (Figure 3), up to and including the sea surface.

Figure 5 shows the hypothesized habitat layer thickness for 6.5-kg skipjack tuna. In some areas, there is no water cooler than 24°C with more than 3.5 ml/l dissolved oxygen, so in these areas there is no habitat for 6.5-kg or larger fish; such areas are double hatched on Figure 5. Extensive regions around these areas have habitat layer thickness of 10 m or less, and large areas of the equatorial Pacific Ocean have <25 m of habitat layer thickness. This rather thin layer can lie beneath as much as 150 m of water warmer than 24°C (at lat. 4°N, long. 170°W, e.g.). North of the Hawaiian Islands, the opposite situation is present: a 150-m thick habitat layer lies under 25 to 50 m of water

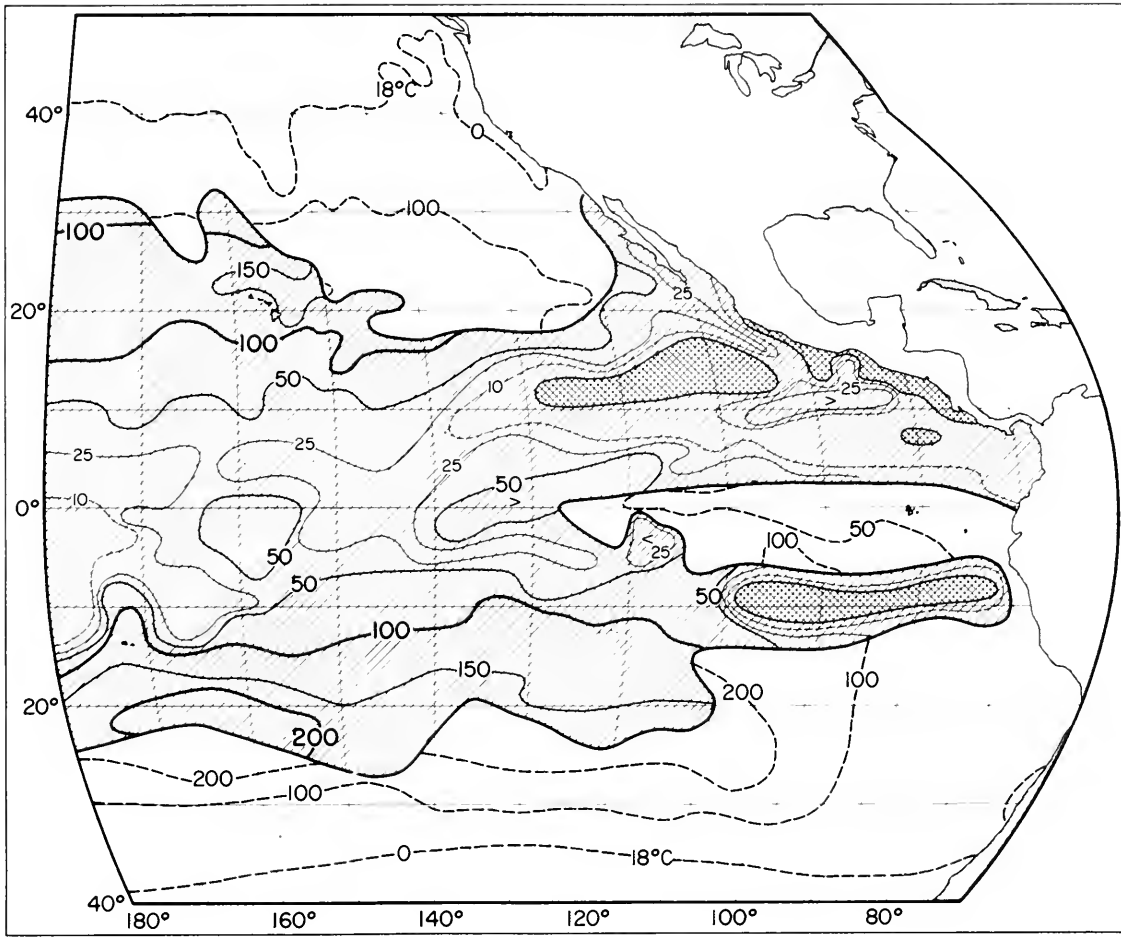

FIGURE 5.—Thickness of the hypothetical habitat layer (meters), for 6.5-kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Figure 4) from the lower one (Figure 3). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna.

warmer than 24°C. Clearly, the South Pacific Ocean offers the roomiest habitat to large skipjack tuna, and in fact some of the largest known individuals of this species were caught slightly south of Tahiti (lat. 17°S, long. 150°W), according to catch records of longline fishing boats (R. A. Skillman, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, 1977, pers. commun.).

An interesting feature of the habitat map for 6.5-kg fish (Figure 5) is a channel of relatively cool and adequately oxygenated water some 200 km off the coast of Mexico. This channel should allow skipjack tuna as large as 6.5 kg to pass from the Baja California fishery to the equatorial fishery, or vice versa, when fish as small as 4 kg would find stressful conditions for hundreds of kilometers on either side of that channel. Seasonal and year-to-year closure or shifting of this channel could readily explain puzzling variations in the distribution of skipjack tuna catches in the eastern Pacific.

Figure 6 shows areas of presumably stressful environment (zero habitat thickness) in the eastern tropical Pacific for fish of various sizes and therefore temperature limitations. Skipjack tuna >11 kg should find no habitat at all within the shaded area. Fish 4 kg in size would find no habitat within the smallest contour (temperatures above

26° C). Fish weighing <4 kg should find some thickness of habitable water, within and just below the upper mixed layer, everywhere in the eastern tropical Pacific.

DISCUSSION

Although we anticipate that temperature and dissolved oxygen will prove to be primary determinants of the habitat of skipjack tuna in all oceans, it is possible that limiting values of these variables may differ from one population or region to another. The lowest temperature (ca. 15° C) at which skipjack tuna are caught in Australian waters (Robins 1952) is considerably lower than in the eastern Pacific. The fish caught off Australia may also differ in their ability to tolerate warm or low-oxygen water.

The gross features of the distribution of skipjack tuna in the eastern tropical Pacific, where only small skipjack tuna are found in large numbers (Williams 1970), agree with the hypothesis. Those areas where large skipjack tuna do occur (Matsumoto 1975) are outside of the hatched area in Figure 6; the Revillagigedo Islands, e.g., are just north of the hatched area, and Tahiti is well south of it.

The hypothetical habitat proposed here explains why skipjack tuna leave the northern fishery of the eastern Pacific when they reach a certain size. To find cooler, better oxygenated water as they grow, these fish must move out of the eastern tropical Pacific toward higher latitudes in the central Pacific. Also, they must then spend less time at or near the sea surface, since the thermocline, where they live, is generally much deeper in the central Pacific, and the water above the thermocline is too warm to permit normal activity. This size-specific movement in response to the environment is consonant with Rothschild's (1965) migration model for the eastern Pacific skipjack tuna population. It also suggests a mechanism for the evolution of migratory processes, an important topic in marine ecology.

For several reasons, existing fishery data are inadequate for making a refined judgment of our skipjack tuna-habitat hypothesis: 1) Commercial fishery data generally include neither information

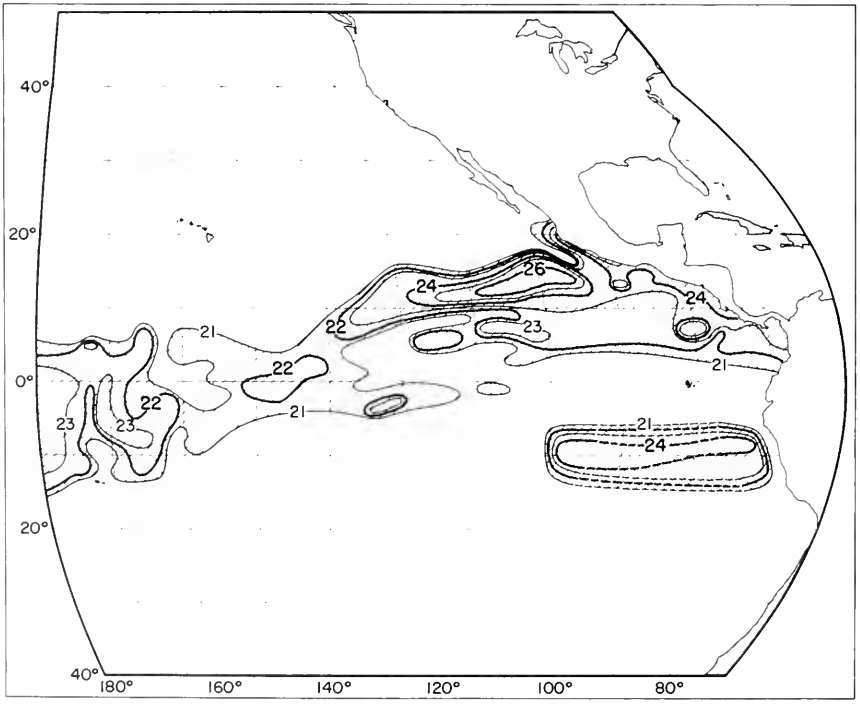

FIGURE 6.—Average water temperature in the eastern Pacific Ocean at those depths where the concentration of dissolved oxygen is 3.5 ml/l. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. See Figure 1b for the relationship between skipjack tuna size and upper temperature limits.

on individual sizes of skipjack tuna composing the catch nor synoptic information on the vertical distribution of temperature and dissolved oxygen in the fishing area. 2) The degree to which catch per unit effort measures fish abundance may vary greatly with gear type, fish size, and environmental conditions. For example, the habitat hypothesis implies that purse seines (which fish the upper 50 m or so of the water column) should be most effective in those parts of skipjack tuna habitat with a shallow floor. In fact, the eastern Pacific purse seine fishery operates almost entirely in waters with a skipjack tuna habitat-floor at depths of 50 m or less (c.f. our Figure 3 and fig. 1 of Matsumoto 1975). Efforts to catch skipjack tuna by purse seining in Hawaiian waters—where the habitat-floor lies at depths near 200 m (Figure 3)—have been ineffectual (Murphy and Niska 1953). Green (1967) reported strong positive correlations between the success of purse seining for eastern Pacific skipjack tuna and yellowfin tuna, *Thunnus albacares*, and the presence of shallow ($\leq$60 m to top), steep ($\geq$0.55°C cm^{-1}) thermoclines. 3) Commercial fishermen naturally fish only where they expect to find and catch fish; thus, fishing effort tends to be very unevenly distributed.

A partial test of the habitat hypothesis might be achieved through experimental fishing in and near the hatched areas of Figure 6; fishing effort, the sizes of captured skipjack tuna, and vertical distributions of temperature and dissolved oxygen would need to be measured at each fishing location. But, experimental fishing—even if conducted in a thorough and systematic fashion—might not yield a conclusive test of the hypothesis, because there would still be no guarantee that catch per unit effort accurately reflected fish abundance (reason 2 above).

We advocate, instead, the application of ultrasonic telemetry to test the skipjack tuna-habitat hypothesis. Because skipjack tuna tagged with ultrasonic transmitters tend to stay with their school (Yuen 1966) and because skipjack tuna schools tend to be homogeneous with respect to fish size (Brock 1954), the track of a single tagged fish could be taken as representative of a large number of normally behaving, similarly sized fish. Pressure-sensitive ultrasonic transmitters (like that described by Luke et al. 1973) would permit continuous monitoring of fish position in all three spatial dimensions through time. Spatial-temporal coordinates of fish could then be compared with synoptic data on vertical distributions of temperature and dissolved oxygen. A few dozens of such comparisons, for fish of various sizes in waters with diverse vertical distributions of temperature and dissolved oxygen, would constitute a valid and sufficient test of the habitat hypothesis. Toward this end, preliminary telemetry work is now underway at this Laboratory.

SUMMARY

Work with captive skipjack tuna at this Laboratory has yielded information on the temperature and dissolved oxygen requirements of this species. If these laboratory results apply to skipjack tuna in nature, they provide new insight into the evolution of migration in skipjack tuna populations, make it possible to account for the geographic distribution of skipjack tuna on the basis of environmental conditions, and provide means for predicting their movements in major fisheries such as those of the eastern tropical Pacific.

In particular, we suggest that only young skipjack tuna can inhabit tropical surface waters, and that the habitat of adult skipjack tuna in the tropics is the thermocline and not the warmer surface layer, as has generally been thought. Since the thermocline in many areas is too oxygen-poor to support these active fish and the well-oxygenated surface layer is too warm for adult skipjack tuna, only heat-tolerant young skipjack tuna can live in those areas. As they grow, these fish are forced to move into areas where well-oxygenated water of the proper temperature is more readily available.

Up to now, it has not been possible to trace the movements of migrating skipjack tuna largely because they move through areas of many millions of square miles, at unknown depths. Knowledge of their temperature and dissolved oxygen requirements dramatically reduces the scope of the problem: the fish should be in a well-defined layer of water, of directly and easily measured thickness, whose geographic extent can be sharply defined with either historical or current oceanographic observations.

ACKNOWLEDGMENTS

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HISTORICAL TRENDS AND STATISTICS OF THE SOUTHERN OSCILLATION, EL NINO, AND INDONESIAN DROUGHTS

WILLIAM H. QUINN, DAVID O. ZOPF, KENT S. SHORT, AND RICHARD T. W. KUO YANG[1]

ABSTRACT

A 116-yr Southern Oscillation index record was used in conjunction with environmental data and reports from various authors on disturbances to the anchoveta fishery, marine bird life, etc. off the Peruvian coast, to infer the occurrence of past El Niño type events and their intensities. The resulting long time history substantiates our earlier report that certain Southern Oscillation index features are excellent precursors of subsequent El Niño type events. We suggest that statistics derived from this time history could be useful in the management of the Peruvian anchoveta fishery and for providing long-range outlooks on El Niño type activity.

Anomalously heavy precipitation in the central and western equatorial Pacific and Indonesian droughts were closely associated with El Niño type events.

In recent years the world demand for fishmeal has continued to increase, as has the world population. The Peruvian anchoveta fishery, which ordinarily provides over half the world's supply of fishmeal, has become a critical resource; and anything that affects the output of this fishery is of world-wide significance. Johnson and Seckel (1977) reported that the catch in this fishery declined from a high of over 12 million tons (about 1/5 of the total world catch of all fish) in 1970 to about 2 million tons in 1973. Although overfishing in 1970-71 may have contributed heavily to this decrease in anchovy catch, the strong El Niño of 1972-73 was undoubtedly also a major cause for the precipitous decline in catch (Figure 1). However, the 1975 catch was still only about 25% of the record 1970 catch, the 1976 catch remained low, and the target for 1977 has now been reduced to 2 million tons of anchoveta and other fish such as sardines and hake. Apparently the unfavorable environmental conditions caused by the very weak event of early 1975 and the moderate El Niño of 1976-77 have not only contributed to the delay in recuperation of the fishery, but also are causing a further degradation of it. In early October 1977 the Fisheries Ministry of Peru said (according to a Reuters wire service report) that the stocks were believed to be so low that the anchoveta fishing, which was suspended in May 1977, would not resume until the second half of 1978.

Statistical information pertaining to the historical occurrence of El Niño type events is presented to: 1) aid in long-term fishery assessment (Peruvian anchoveta fishery); 2) provide a basis for speculative long-range outlooks on event occurrence (beyond a year in advance); and 3) guide long-range predictions (1-12 mo in advance). Relationships between El Niño type events, Southern Oscillation index trends, index component trends, and Indonesian droughts are shown and discussed.

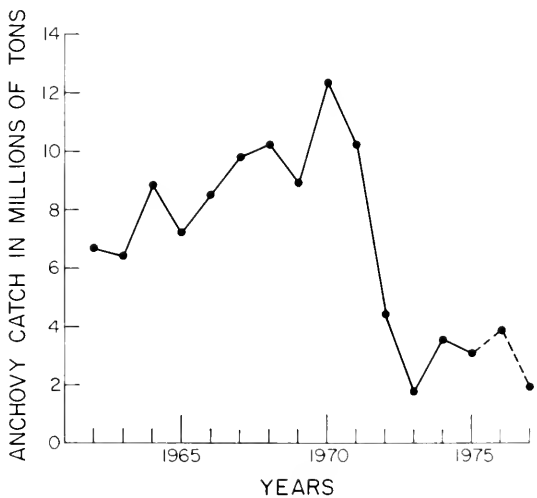

FIGURE 1.—The Peruvian anchovy catch for the period 1962-76 as obtained from the Industrial Fishery Products Market Review and Outlook for June 1977 (National Marine Fisheries Service 1977). The 1976 figure is a preliminary value. The 1977 figure is the Peruvian Fishery Ministry target value for anchovies and other species such as sardine and hake, as reported by Reuters wire service on 19 October 1977.

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Wooster (1960), Idyll (1973), Miller and Laurs (1975), and Caviedes (1975) furnished background information on El Niño; Quinn (1974) discussed monitoring and prediction; and Berlage (1957, 1966), Troup (1965), and Quinn (1971, 1976) provided background information on the Southern Oscillation and how it relates to phenomena discussed in this paper.

Definitions for terms frequently used in this paper follow: The Southern Oscillation was originally identified by Walker (1924). It was loosely defined by Berlage (1966) as a fluctuation in the intensity of the intertropical general atmospheric and hydrospheric circulation over the Indo-Pacific region. The fluctuation is dominated by an exchange of air between the South Pacific subtropical high and the Indonesian equatorial low. The differences in sea level atmospheric pressure between sites representing the South Pacific subtropical high and sites representing the Indonesian equatorial low are used as indices to represent the Southern Oscillation (Quinn 1974).

The El Niño type event refers to the appearance of anomalously warm sea surface temperatures and abnormally heavy rainfall in the equatorial Pacific and an invasion of anomalously warm surface water off the coast of Peru and southern Equador. This event, which is brought about by relaxation from a prolonged period of strong southeast trades, is represented by falling and low Southern Oscillation indices (Quinn 1974). The magnitude of the interannual relaxation and its timing with relation to the regular seasonal relaxation (Southern Hemisphere summer) appear to determine the strength of the El Niño invasion along the Peruvian coast. Heavy central and western equatorial Pacific precipitation usually starts a few or more months after El Niño initially sets in, but this may not always be the case. By using the term "El Niño type" we avoid arguments over what is and what is not an El Niño and can then account for events that evolve in a similar manner but vary in timing, intensity, and extent.

The anti-El Niño refers to the contrasting situation when a strengthening and strong southeast trade system prevails (represented by rapidly rising and high Southern Oscillation indices). At such times we can expect strong upwelling (due to the divergent equatorial flow under the influence of strong southeast trades and equatorial easterlies), anomalously low sea surface temperatures, and abnormally low amounts of rainfall over the equatorial Pacific. Also, off the coast of Peru, we find strong coastal upwelling, low sea surface temperatures, lower than average sea level, and generally favorable physical environmental conditions for biological productivity (due to the upwelling of nutrient-rich water from lower levels).

METHODS

Data Processing

Atmospheric pressure and much of the rainfall data before 1961 were obtained from the World Weather Records (Clayton 1927, 1934; Clayton and Clayton 1947; U.S. Department of Commerce 1959, 1968). Data for 1961-76 were obtained from Monthly Climatic Data for the World (U.S. Department of Commerce 1961-76). We were primarily interested in the large-scale interannual changes. Therefore, we eliminated regular oscillations from the data, such as the diurnal cycle, by using monthly mean values (or monthly amounts, for rainfall), and the seasonal or annual cycle by subtracting long-term average or normal monthly values from the actual monthly values. Data so processed show no particular regularity and no apparent cycle (Panofsky and Brier 1965). The filtered and unfiltered monthly anomalies were used to detect, identify, and evaluate any unusual changes that took place.

Our interests were focused on fluctuations of an intermediate scale (Southern Oscillation), with periods ranging between about 1 and 6 yr. The remaining short period fluctuations in the anomalies were eliminated by filtering with a low pass filter. At the other end of the time scale, there may be a gradual change of the variate over many years which is part of oscillations that are long compared with the record. These extremely long, gradual changes were not a factor in our study.

In earlier papers (e.g., Quinn 1974, 1976) the 12-mo running mean was applied directly to monthly values of pressure, pressure differences (indices), rainfall, etc. as a low pass filter. This filter not only smoothed the data to some extent but also eliminated the annual cycle. To more clearly define the interannual fluctuations (Southern Oscillation), we recently switched to the use of the triple 6-mo running mean filter on the monthly anomalies, which requires three successive passes of the 6-mo running mean over the data. It results in smoother plots and more clearly defined peaks and troughs, which are of particular assistance in establishing long-term trends. The

loss of 3 mo time with each application of the 6-mo running mean is a drawback to its use in forecasting, so we also use the 3-mo running mean and monthly plots of anomalies for locating inflection points and evaluating trends on a more immediate basis in support of forecasts.

Anomaly trends for several indices were maintained in time section plots (Figure 2a, b) to evaluate the Southern Oscillation and its expected effects on the southeast trade system. Although these limited records (25-30 yr) clearly showed the close association of low indices with El Niño type activity, and high indices with anti-El Niño conditions (Quinn 1974, 1976), it was essential to extend the study over a much longer period to determine how frequently these climatic extremes occurred

The World Weather Records were searched for the longest and most complete atmospheric pressure records which could be used to extend our study into the past. Madras, India (1841-1976); Bombay, India (1847-1976); Djakarta, Indonesia (1866-1974); and Darwin, Australia (1882-1976) were within the area noted by Berlage (1957, 1966) to reflect Southern Oscillation-related pressure changes in the Indonesian equatorial low pressure cell. Santiago, Chile (1861-1976) had the only long pressure record that could possibly represent Southern Oscillation-related pressure changes affecting the South Pacific subtropical high pressure cell. Although Santiago is generally to the east of the subtropical high, it does reflect these pressure changes (Berlage 1957, 1966).

Correlations were run between the Tahiti-Darwin index and the Santiago-Darwin index on data for 1935-76 to further substantiate use of the Santiago-Darwin index for representing the Southern Oscillation and related El Niño type activity. The Tahiti-Darwin index was used for this comparison since it and the Santiago-Darwin index showed similar amplitudes in their interannual fluctuations. The similarity was due to the fact that Tahiti and Santiago are separated by analogous distances from the usual core of activity in the subtropical high (see fig. 10 in Berlage 1957, or fig. 10 in Bjerknes 1969). At zero lag the correlation coefficient between the two indices was 0.88. The maximum correlation was 0.89 when the Tahiti-Darwin index led the Santiago-Darwin index by 1 mo.

Figure 3a-h shows the triple 6-mo running mean plots of pressure anomalies for Madras (1841-1976), Bombay (1847-1976), Djakarta (1866-1974), and Darwin (1882-1976). They also show similar plots of pressure index anomalies for Santiago-Bombay (1861-81) and Santiago-Darwin (1882-1976). The anomaly plots were used along with other data in the evaluation of El Niño type events reported over the past 135 yr.

Classification of Events

The classification of El Niño type events by intensity is highly subjective since no two cases are exactly alike with regard to time of onset, duration, areal extent, thermal departure, degree of devastation, etc. Determinations concerning event occurrence and intensity were primarily based on: 1) reported disruptions of the anchoveta fishery and marine bird life off the coast of Peru; 2) scientific reports which discussed events that affected the coastal regions of Peru and southern Ecuador [e.g., Eguiguren (1894), Frijlinck (1925), Murphy (1926), Hutchinson (1950), Sears (1954), Schweigger (1961)]; 3) hydrological data for the Peruvian coastal region; 4) sea-surface temperature data along the coasts of Peru and southern Ecuador; 5) rainfall at coastal stations in Peru and southern Ecuador; 6) height of preevent peaks and depth of relaxation troughs in Southern Oscillation index trends; 7) related indications from index component trends (when pressure components from only one core of the Southern Oscillation were available); 8) sea-surface temperatures over the equatorial Pacific; 9) rainfall data for islands in the central and western equatorial Pacific.

We categorized events as strong, moderate, weak, or very weak, depending on the intensity of the activity and the time of year that it occurred. The true El Niño sets in during the first half of the year. A symptom which is common to El Niños is the presence of anomalously high sea-surface temperatures off the coasts of southern Ecuador and Peru. Other frequently mentioned features include a southward coastal current, heavy rainfall, red tide (aguage), invasion by tropical nekton, and mass mortality of various marine organisms including guano birds, sometimes with subsequent decomposition and release of hydrogen sulfide (known as El Pintor) (Wooster 1960).

Strong El Niños are recognized as such by all investigators; they involve positive sea-surface temperature anomalies along the coast in excess of 3°C, they display most of the aforementioned features, and the anchoveta fishery is seriously

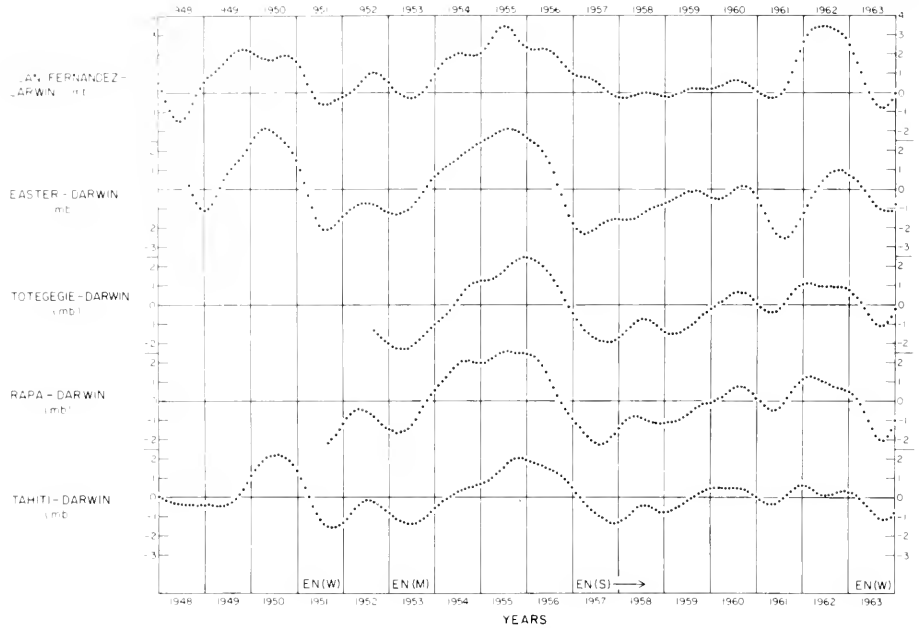


FIGURE 2a.—Triple 6-mo running mean plots of anomalies of the difference in sea level atmospheric pressure (millibars) between Juan Fernandez Is. (33°37′S, 78°50′W) and Darwin, Australia (12°26′S, 130°52′E), between Easter Is. (27°10′S, 109°26′W) and Darwin, between Totegegie (23°06′S, 134°52′W) (Gambier Is.) and Darwin, between Rapa (27°37′S, 144°20′W) (Austral Is.) and Darwin, and between Tahiti (17°33′S, 149°20′W) (Society Is.) and Darwin for 1948-63. El Niño type events (EN) are indicated in strong (S), moderate (M), and weak or very weak (W) intensity.

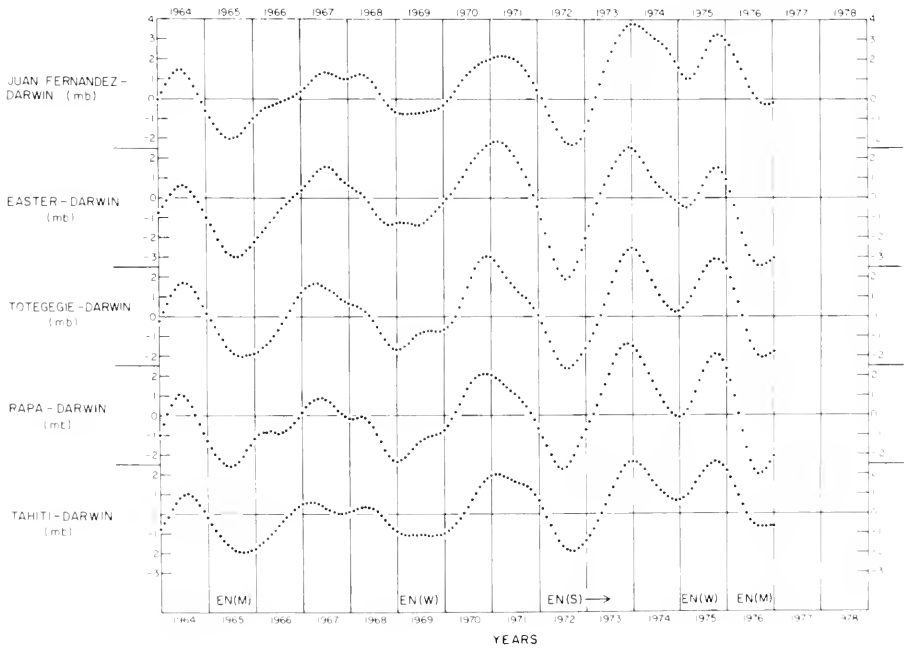


FIGURE 2b.—Triple 6-mo running mean plots of anomalies of the difference in sea level atmospheric pressure (millibars) between Juan Fernandez Is. and Darwin, between Easter Is. and Darwin, between Totegegie and Darwin, between Rapa and Darwin, and between Tahiti and Darwin for 1964-76. El Niño type events (EN) are indicated in strong (S), moderate (M), and weak or very weak (W) intensity.

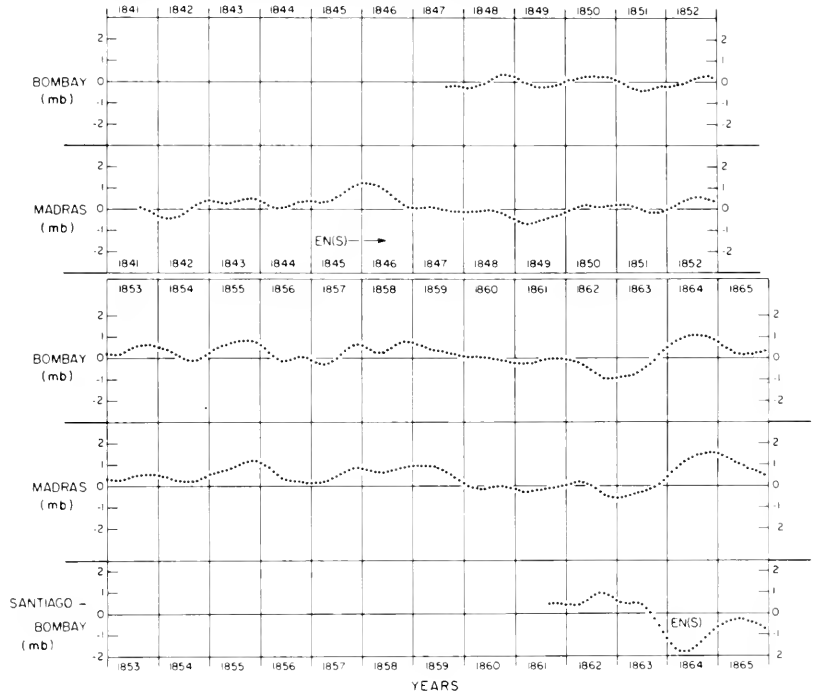


FIGURE 3a.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay (18°54′N, 72°49′E), India (1847-65) and for Madras (13°00′N, 80°11′E), India (1841-65); also triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago (33°27′S, 70°42′W), Chile and Bombay (1861-65). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

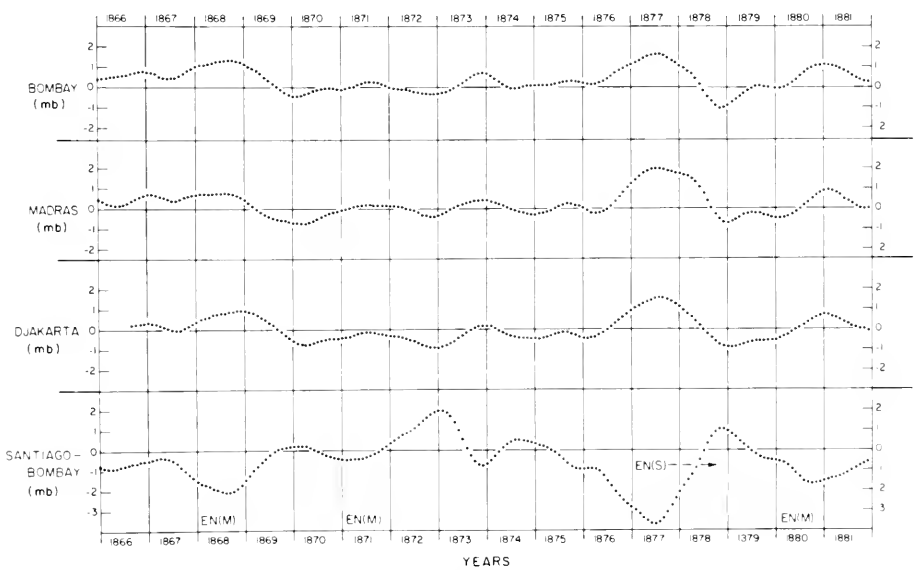


FIGURE 3b.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay and Madras, India, and Djakarta (06°11′S, 106°51′E), Indonesia (1866-81); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Bombay (1866-81). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

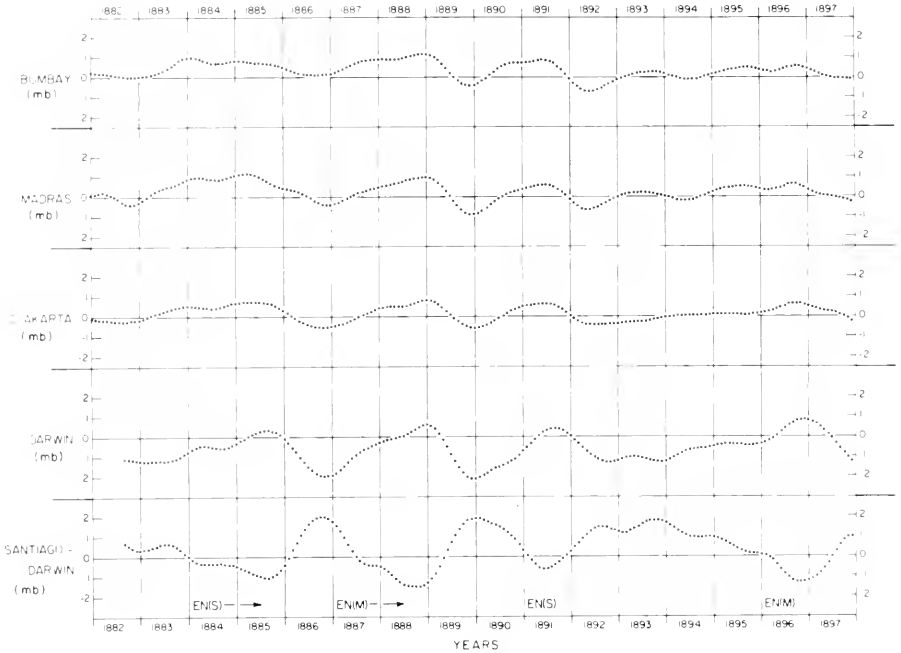


FIGURE 3c.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (12°26'S, 130°52'E), Australia (1882-97); also triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1882-97). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

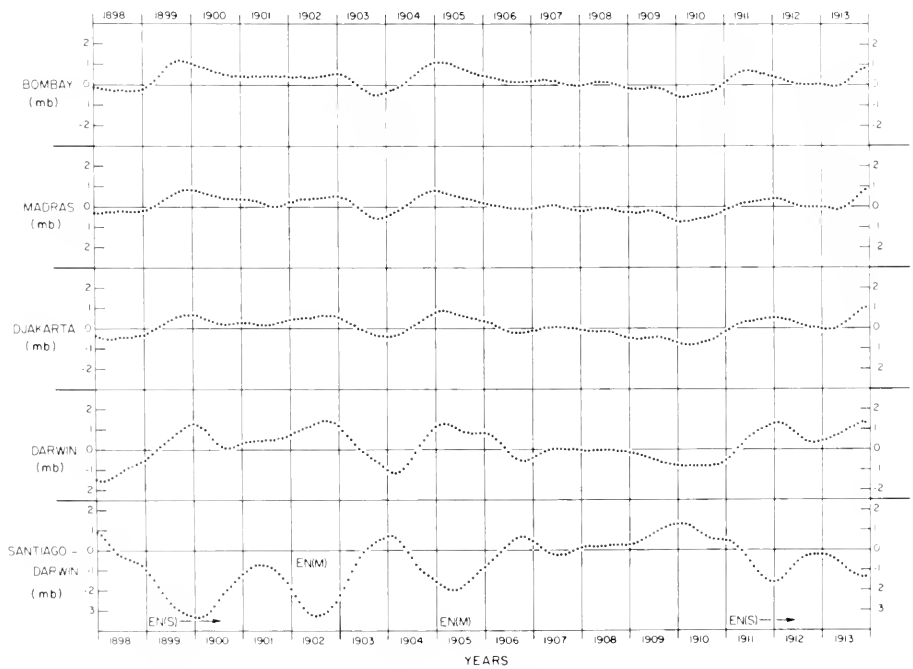


FIGURE 3d.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1898-1913); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1898-1913). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

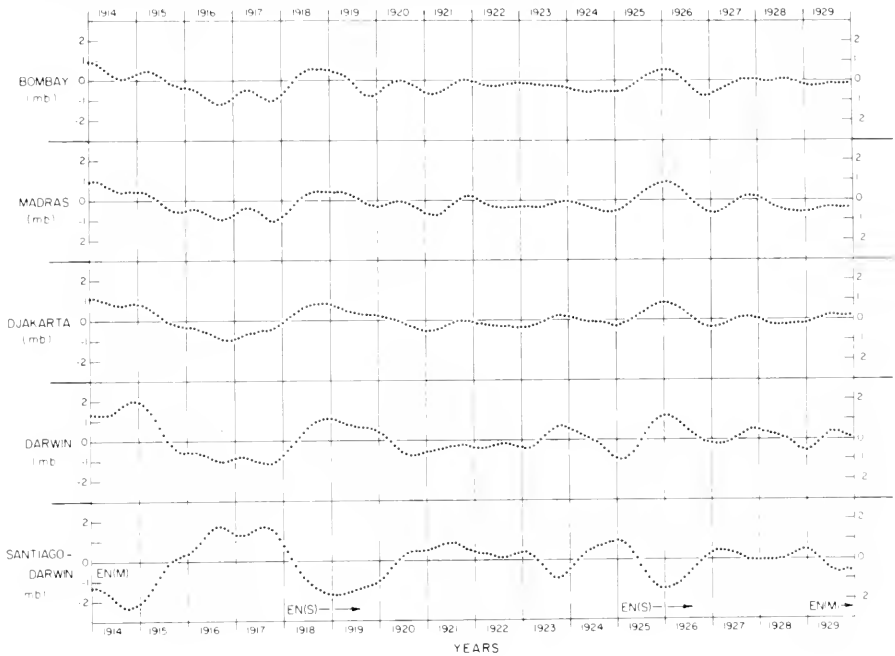


FIGURE 3e.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1914-29); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1914-29). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

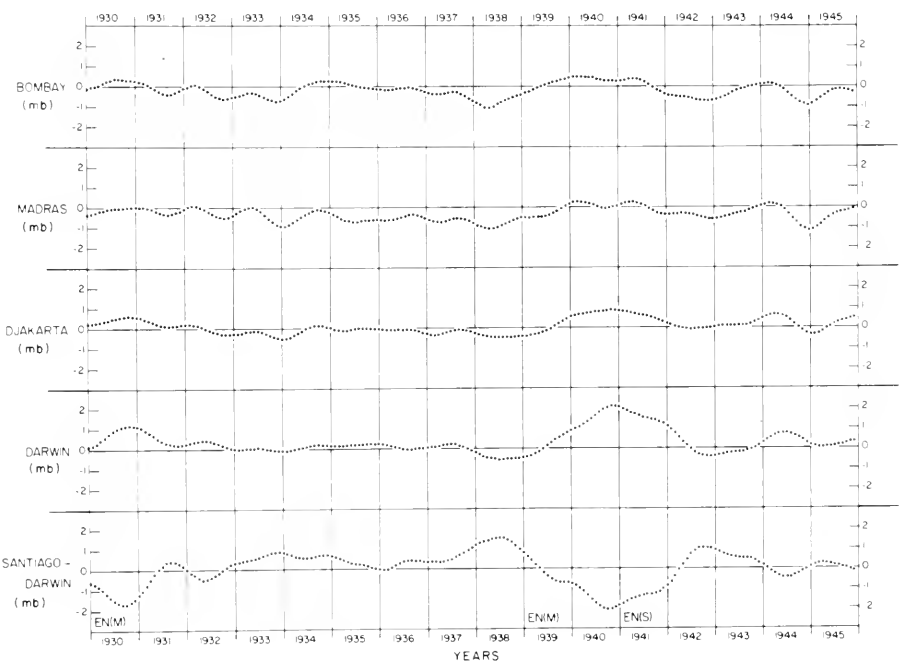


FIGURE 3f.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1930-45); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1930-45). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

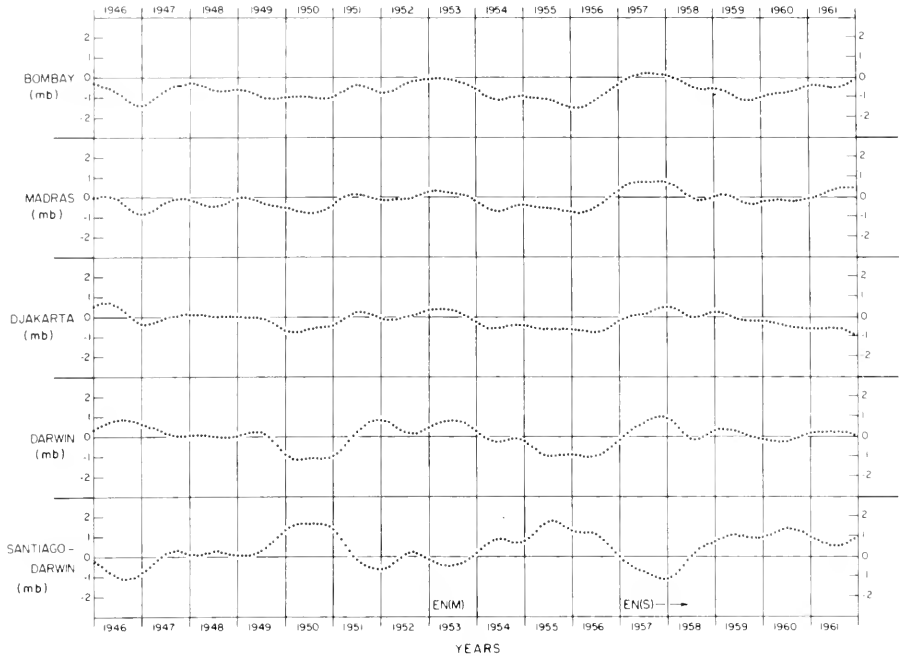


FIGURE 3g.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1946-61); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1946-61). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

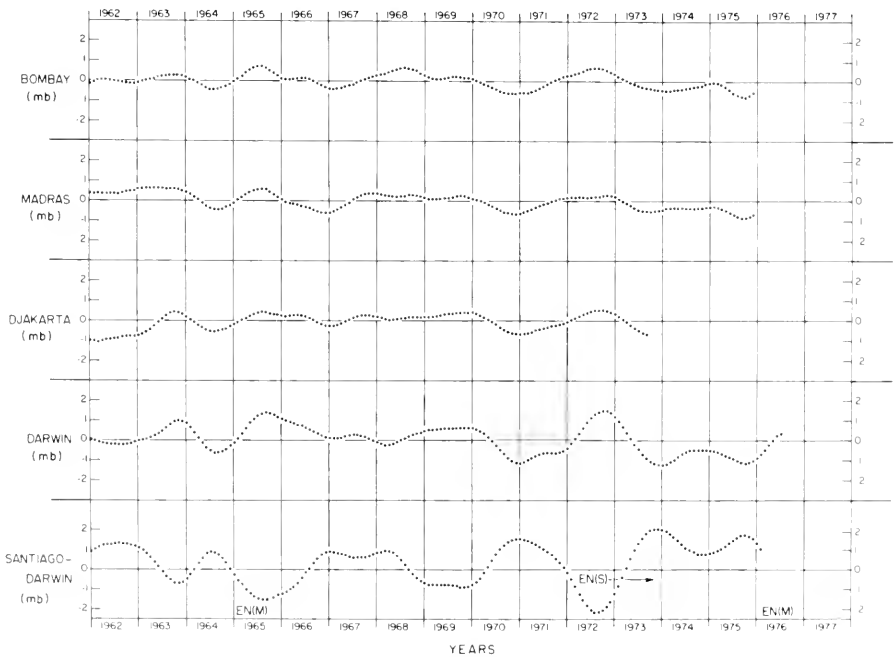


FIGURE 3h.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1962-76); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1962-76). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

affected (e.g., the 1957-58 and 1972-73 cases of recent years). Moderate cases are recognized as El Niños by most investigators, and display typical El Niño features to a lesser degree; maximum monthly sea-surface temperature anomalies along the coast usually peak in the 2.0°-3.5°C temperature range (e.g., the 1953, 1965-66, and 1976-77 cases of recent years). The effects of a moderate El Niño on the anchoveta fishery are considerable, but less serious than for the strong category.

Weak events may or may not be recognized as El Niños by investigators; maximum monthly sea-surface temperature anomalies along the coast usually peak in the 1.0°-2.5°C temperature range, but may appear relatively late in the year (e.g., the 1951 and 1969 cases of recent years). Very weak events are not considered to be El Niños; maximum sea-surface temperature anomalies, if they penetrate into the coast, are in the 0°-2°C range (e.g., the 1963 and 1975 events). The weak and very weak categories are included in this discussion because the difference between weaker and stronger events depends not only on the height of the preevent index anomaly peak and the subsequent degree of relaxation reflected in the southeast trade strength, but also on the timing of this interannual relaxation. If the timing is in phase with the regular annual relaxation (Southern Hemisphere summer and early fall), a moderate or strong event is likely to occur; if they are out of phase, a weak or very weak event is likely. Relaxation troughs that occur near the end of the year are usually associated with high Peruvian coastal sea temperature anomalies in the latter half of the year. The weak and very weak events may not be of significance to the Peruvian anchoveta fishery, but they do show up in the western equatorial Pacific rainfall and their larger scale aspects may be significant from the standpoint of associated global fluctuations. Figure 4 shows an example of how the recent events were reflected in the Tarawa rainfall.

The weaker events were included as EN(W) in Figure 2a, b, since we have a fairly large amount of evidence available from 1950 on. They were not included in Figure 3a-h due to the decreasing availability of evidence as we reach further back in time. However, these weaker events, ascertained to the best of our ability from available data

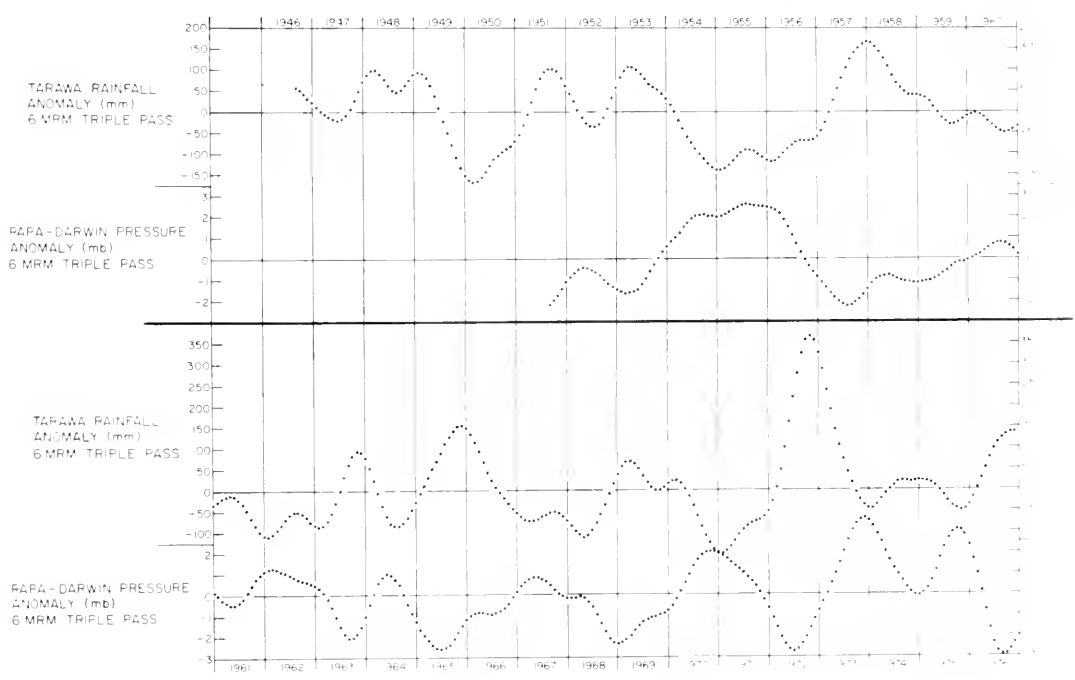


FIGURE 4.—Triple 6-mo running mean plot of anomalies of the difference in sea level atmospheric pressure (millibars) between Rapa (27°37'S, 144°20'W) (Austral Is.) and Darwin (12°26'S, 130°52'E), Australia compared with a similarly filtered plot of Tarawa (01°21'N, 172°55'E) (Gilbert Is.) rainfall anomalies (millimeters).

and literature, are included in Table 1; and, the typical index and index component trends associated with them can be noted in Figure 3a-h.

Eguiguren's (1894) data were evaluated to extend the record back even further. He classified rainfall at Piura, Peru (lat. 5°5'S, long. 80°38'W) into five categories: dry (0), light (1), moderate (2), good (3), and extra ordinary (4). Considering the distribution of events over the period 1891-1976 in relation to Eguiguren's rainfall category distribution for 1791-1890, it appeared that we could relate his category 4 to a strong El Niño, category 3 to a moderate El Niño, and categories 2 and 1 to weak and very weak events respectively. One must realize that for this Peruvian desert area long-term average rainfall values have little meaning, since averages combine data from the more-frequent drought years with data from the smaller number of event years when significant rainfall may occur. A year when an average amount of rain fell is likely to have been a year when an event occurred. Whereas the categories 3 and 4 rainfall situations were likely to have been associated with El Niño, there is no assurance that the categories 1 and 2 rainfalls were associated with the oceanic events.

A study of presumed event occurrences (based on Eguiguren's information) in relatiion to trends of the Southern Oscillation indices and index components for a period when overlapping data records were available (1841-90) showed a high degree of compatibility. Table 1 lists years in accordance with Eguiguren's rainfall classification as well as our interpretation of event intensity after considering his indications, the index and index component trends, and the various data and information sources listed early in this section.

After 1790 and prior to 1841, when no pressure records were available for a cross-check, we avoided the weak event category, but accepted Eguiguren's stronger categories 3 and 4 events. Events occurring prior to 1791, as reported by Frijlinck (1925), were considered to be of the strong variety. Sources for each event are listed in Table 1.

STATISTICAL STUDY OF EL NINO TYPE EVENTS

From a practical standpoint, we were concerned with the question of when the next event is likely to occur and what its intensity might be. Therefore, this study referred to the onset times for separate events and the interval between onset times. When the year immediately following the year of onset reflected an event of equal or lower intensity, it was assumed that the initial event extended into this next year or that the effects of the initial event held over into the early part of the next year; and, the whole situation was treated as a single event. However, when a weaker initial event preceded a stronger event in a following year they were treated as two separate events,

TABLE 1.—Year of onset of El Niño type events, 1726-1976, as classified according to event intensity by Eguiguren (1894), left, and the present authors, right (events below intensity 3 were not accepted prior to 1841 when pressure data became available). Numbers refer to event intensity: 1, very weak; 2, weak; 3, moderate; and 4, strong. Asterisks indicate onset of events considered separate (see text).

Year	Event intensity		Key to source	Year	Event intensity		Key to source	Year	Event intensity	Key to source	Year	Event intensity	Key to source
*1726		(3)	G	*1852	2	(2)	B, PC	*1896	(3)	PI, R	*1943	(2)	G, T, R
*1728		(4)	A, G	1854	2		B	*1899	(4)	D, PI, R	1944	(2)	PI, T
*1763		(4)	A	*1855		(2)	PC	1900	(3)	PI, R	*1946	(1)	PI, R
*1770		(4)	A	*1857	2	(2)	B, PC	*1902	(3)	PI, R	*1948	(1)	PI, T, R
*1791	4	(4)	A, B	1862	2		B	*1905	(3)	PI, R	*1951	(2)	G, PI, T
*1803	2		B	*1864	4	(4)	A, B, PI	*1911	(4)	F, E, PI	*1953	(3)	G, E, T
*1804	4	(4)	B	1866	2		B	1912	(3)	F, PI	*1957	(4)	G, L, PI
*1814	4	(4)	B	*1868	1	(3)	B, C, PI	*1914	(3)	G, PI, R	1958	(4)	G, L, PI
*1817	3	(3)	B	*1871	4	(3)	A, B, C	*1917	(2)	H	*1963	(1)	PI, R
*1819	3	(3)	B	*1873		(2)	PI	*1918	(4)	C, D, PI	*1965	(3)	M, PI, T
*1821	3	(3)	B	*1875	1	(1)	B, PC	1919	(3)	D, PI, R	*1969	(2)	PI, T, R
*1824	3	(3)	B	*1877	4	(4)	A, B, PI	*1923	(2)	H, PI	*1972	(4)	N, O, PI
*1828	4	(4)	A, B	1878	4	(4)	A, B, PI	*1925	(4)	D, E, PI	1973	(4)	N, O, T
1829	1		B	*1880	2	(3)	B, PI	1926	(4)	I, PI, T	*1975	(1)	P, PI, T
*1832	3	(3)	B	*1884	4	(4)	A, B, PI	*1929	(3)	G, I, PI	*1976	(3)	Q, PI, T
*1837	3	(3)	B	1885		(3)	PI	1930	(3)	G, PI, T			
*1844	3	(2)	B, PC	*1887	2	(3)	B, PI	*1932	(2)	E, I, J			
*1845	4	(4)	B, C, PC	1888	2	(3)	B, PI	*1939	(3)	E, J, T			
1846	2	(3)	B, PC	1889	1	(1)	B, PI	1940	(2)	C, PI, T			
*1850	2	(2)	B, PC	*1891		(4)	D, E, PI	*1941	(4)	E, K, T			

Key	Source
A	Frijlinck (1925)
B	Eguiguren (1894)
C	Hutchinson (1950)
D	Murphy (1923, 1926)
E	Sears (1954)
F	Forbes (1914)
G	Schweigger (1961)
H	Lavalle (1917, 1924)
I	Shepard (1930, 1933)
J	Mears (1944)
K	Lobell (1942)
L	Wooster (1960)
M	Guillén (1967)
N	Idyll (1973)
O	Caviedes (1975)
P	Wyrtki et al. (1976)
Q	Quinn (1976)
R	Rainfall (equatorial and/or Peruvian)
T	Sea-surface temperature off Peru
PC	Pressure component of Southern Oscillation index
PI	Southern Oscillation pressure index

since an additional contribution was introduced in the following year. The foregoing assumptions were based on findings from a study of the Southern Oscillation index trends and associated events over recent decades when more data were available for case history studies.

Our study of strong events was limited to the period 1763-present (Table 2, Figure 5), since the break of 35 yr between 1728 and 1763 was 14 yr longer than the longest subsequent break between events, and there was no way of eliminating the possibility that one or more strong events might have gone unreported over the 35-yr gap. These data indicate that given a strong El Niño, there is a 35% probability of having another strong event in 7-8 yr, and an 82% probability of having one within the next 15-16 yr. Considering all available data, the time between onsets of separate strong events was never <7 yr.

For strong and moderate events (Table 3, Figure 5) the record was limited to the period 1791-present when data for both categories were available. For strong, moderate, and weak events (Table 4, Figure 5) the record was limited to 1842-present, so we would have at least one index component trend available for cross-checking the less prominent weak events. (Madras pressure data became available in 1841.) With the addition of very weak events (Table 5, Figure 5), we limited our record to 1862-present in order to have an index trend available for cross-checking the more obscure very weak events. (The Santiago-Bombay index became available in 1861.)

Cases were noted where relaxation from a large preevent index anomaly peak appeared to be a two or more stage process. [This type development was

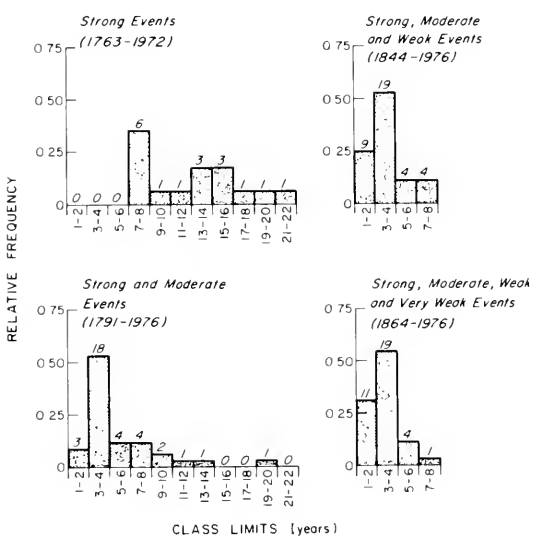


FIGURE 5.—Histograms of frequency distributions for El Niño type events by intensity. Number of occurrences within class intervals is indicated.

TABLE 2.—Strong El Niños, with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1763	1770	7	1884	1891	7
1770	1791	21	1891	1899	8
1791	1804	13	1899	1911	12
1804	1814	10	1911	1918	7
1814	1828	14	1918	1925	7
1828	1845	17	1925	1941	16
1845	1864	19	1941	1957	16
1864	1877	13	1957	1972	15
1877	1884	7			

209 (cumulative years between onsets) ÷ 17 (number of intervals) = 12.3 yr, average time interval between onsets of strong El Niños

TABLE 3.—Strong and moderate El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1791	1804	13	1887	1891	4
1804	1814	10	1891	1896	5
1814	1817	3	1896	1899	3
1817	1819	2	1899	1902	3
1819	1821	2	1902	1905	3
1821	1824	3	1905	1911	6
1824	1828	4	1911	1914	3
1828	1832	4	1914	1918	4
1832	1837	5	1918	1925	7
1837	1845	8	1925	1929	4
1845	1864	19	1929	1939	10
1864	1868	4	1939	1941	2
1868	1871	3	1941	1953	12
1871	1877	6	1953	1957	4
1877	1880	3	1957	1965	8
1880	1884	4	1965	1972	7
1884	1887	3	1972	1976	4

185 (cumulative years between onsets) ÷ 34 (number of intervals) = 5.4 yr, average time interval between onsets.

TABLE 4.—Strong, moderate, and weak El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1844	1845	1	1905	1911	6
1845	1850	5	1911	1914	3
1850	1852	2	1914	1917	3
1852	1855	3	1917	1918	1
1855	1857	2	1918	1923	5
1857	1864	7	1923	1925	2
1864	1868	4	1925	1929	4
1868	1871	3	1929	1932	3
1871	1873	2	1932	1939	7
1873	1877	4	1939	1941	2
1877	1880	3	1941	1943	2
1880	1884	4	1943	1951	8
1884	1887	3	1951	1953	2
1887	1891	4	1953	1957	4
1891	1896	5	1957	1965	8
1896	1899	3	1965	1969	4
1899	1902	3	1969	1972	3
1902	1905	3	1972	1976	4

132 (cumulative years between onsets) ÷ 36 (number of intervals) = 3.7 yr, average time interval between onsets

TABLE 5.—Strong, moderate, weak, and very weak El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1864	1868	4	1923	1925	2
1868	1871	3	1925	1929	4
1871	1873	2	1929	1932	3
1873	1875	2	1932	1939	7
1875	1877	2	1939	1941	2
1877	1880	3	1941	1943	2
1880	1884	4	1943	1946	3
1884	1887	3	1946	1948	2
1887	1891	4	1948	1951	3
1891	1896	5	1951	1953	2
1896	1899	3	1953	1957	4
1899	1902	3	1957	1963	6
1902	1905	3	1963	1965	2
1905	1911	6	1965	1969	4
1911	1914	3	1969	1972	3
1914	1917	3	1972	1975	3
1917	1918	1	1975	1976	1
1918	1923	5			
112 (cumulative years between onsets)			35 (number of intervals)		3.2 yr.
average time interval between onsets					

first mentioned in Quinn and Zopf (1975).] In some cases there was an initial fall from a large preevent (primary) peak which was not fully in phase with the seasonal relaxation (Southern Hemisphere summer and early fall) and the result was a relatively weak event; then, there was the rise to a smaller secondary peak followed by relaxation to a secondary trough which was in phase with the seasonal relaxation and resulted in a stronger event. The length of time between the two troughs was generally 18-22 mo and it is our opinion that situations of this type may account for many of the event-to-event intervals that fall in the short 1-2 yr category. Examples of such developments can be noted in 1950-53, 1962-65, and 1973-76 (Figure 2a, b). Preevent peaks occurred in 1950, 1962, and late 1973-early 1974. The first relaxation troughs following these peaks occurred in late 1951, late 1963, and late 1974-early 1975, and weak or very weak events resulted in all three cases. Then, there were rises to secondary peaks by mid-1952, mid-1964, and late 1975, followed by falls to troughs by early to mid-1953, mid-1965, and mid-1976, resulting in moderate El Niños for these latter years. We must be aware that these situations can arise and should be particularly wary when a large preevent peak is followed prematurely by a weak or very weak event. (One must not lose sight of the fact that these interannual fluctuations in the index anomaly trends were used to represent the interannual fluctuations in southeast trade and equatorial easterly strength as affected by the Southern Oscillation.) Figure 6 demonstrates the similarity of the three two-stage developments discussed above; a particularly obvious index trend was selected to represent each case.

The index trend between late 1872 and 1877 indicates a possible three stage development (Figure 3b), with a weak event in 1873, a very weak event in 1875, and a strong event in 1877 (Table 1). It is noteworthy that Indonesian droughts, which are usually associated with El Niño, occurred in 1873, 1875, and 1877 (Berlage 1957).

The preevent index anomaly peak has been reported to be a reliable indicator for subsequent El Niño type activity, and our long index record substantiates this viewpoint. We compiled statistics on the climb time from trough to peak and fall time from peak to trough from our long index anomaly record to provide some general guidance for event predictions. Figure 7 shows the applicable statistics. Events usually set in while the index is falling and prior to the index trough inflection point. Therefore, the contents of Table 6 and Figure 8, which pertain to time between index peak and subsequent event onset, can be used to further refine event predictions. We assumed a March onset time for all cases in arriving at values in the column headed "Peak to event onset" (Table 6). This assumption was made since month of onset was not available for most of the early cases, and a study of recent cases showed onset times to range from January to May.

INDONESIAN DROUGHTS

What happens over Indonesia relates to the Southern Oscillation (Berlage 1957) and is, therefore, an integral part of the activity affecting the

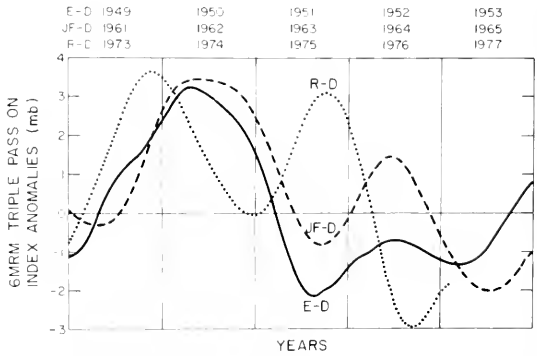


FIGURE 6.—Recent examples of two stage developments using triple 6-mo running mean plots of: 1) Easter-Darwin (E-D) index anomalies (1949-53); 2) Juan Fernandez-Darwin (JF-D) index anomalies (1961-65); 3) Rapa-Darwin (R-D) index anomalies (1973-77).

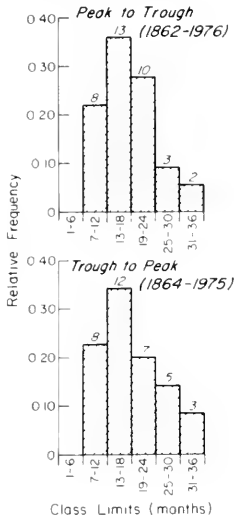


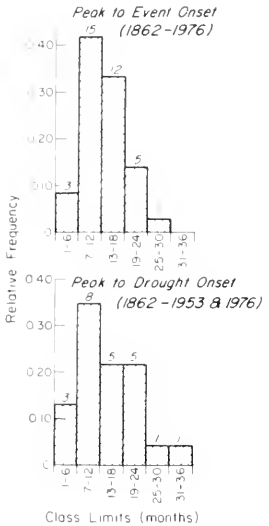
FIGURE 7.—Frequency distributions of rise time from trough to peak and fall time from peak to trough (in months) for the triple 6-mo running mean plots of Southern Oscillation index anomalies (see text). The number of cases falling within a class interval is entered at the top of the relevant histogram element.

equatorial Pacific and the oceanic region off northwestern South America. In general, years when the index is low and El Niño type activity occurs are also years of drought in Indonesia (particularly during the east monsoon season, May-October).

Using sea salt production on the Island of Madura (near Java), which is a very sensitive indicator of drought and precipitation, as well as some administration reports from Java estates, compiled by Van Bemmelen (1916), Berlage (1957) drew up a complete series of east monsoons drier than normal, from 1830 to 1953. Although 93% of the drought periods occurred during years when El Niño type events were under way (Table 7), only 77% of the periods when El Niño type events were underway were also designated as periods of east monsoon drought (Table 8). Nevertheless, the association between occurrences of these two phenomena and changes in the Southern Oscillation index trends are close enough in either case to indicate common relationships with the large-scale ocean-atmosphere changes over the Indo-

TABLE 6.—Time (in months) between index peak and El Niño type event onset (assuming onset is in March of indicated year), and time between index peak and associated Indonesian drought onset (assuming onset is in May of associated year). Pressure indices (see text) used to determine time of preevent peak were: S-B, Santiago-Bombay; S-D, Santiago-Darwin; JF-D, Juan Fernandez-Darwin; E-D, Easter-Darwin; T-D, Totegegie-Darwin; and R-D, Rapa-Darwin. In last column ND indicates no associated drought.

El Niño type event	Preevent index peak		Peak to event onset	Peak to drought onset
Year of onset	Month of peak	Index used	No. of Months	No. of months
1864	Aug.-Sept. 1862	S-B	18.5	20.5
1868	Mar.-Apr. 1867	S-B	11.5	ND
1871	Jan.-Feb. 1870	S-B	13.5	ND
1873	Jan. 1873	S-B	2.0	4.0
1875	Aug.-Sept. 1874	S-B	6.5	8.5
1877	Feb. 1876	S-B	13.0	15.0
1880	Nov. 1878	S-B	16.0	30.0
1884	May 1882	S-B	22.0	12.0
1887	July-Aug. 1886	S-B	7.5	21.5
1891	Nov.-Dec. 1889	S-B	15.5	17.5
1896	Oct. 1893	S-D	29.0	31.0
1899	Nov.-Dec. 1897	S-D	15.5	ND
1902	May 1901	S-D	10.0	12.0
1905	Sept.-Oct. 1903	S-D	14.5	16.5
1911	Jan.-Feb. 1910	S-D	13.5	ND
1914	Sept.-Oct. 1912	JF-D	17.5	7.5
1917	Aug.-Sept. 1916	S-B	6.5	ND
1918	Aug.-Sept. 1917	S-D	6.5	8.5
1923	Aug. 1921	JF-D	19.0	21.0
1925	May-June 1924	S-B	9.5	11.5
1929	Dec.-Jan. 1928 29	JF-D	2.5	4.5
1932	Aug.-Sept. 1931	S-D	6.5	8.5
1939	June-July 1938	JF-D	8.5	22.5
1941	Jan.-Feb. 1940	JF-D	13.5	15.5
1943	July-Aug. 1942	JF-D	7.5	21.5
1946	Dec.-Jan. 1944 45	S-B	14.5	4.5
1948	Aug. 1947	JF-D	7.0	ND
1951	Apr.-May 1950	E-D	10.5	ND
1953	Apr.-May 1952	R-D	10.5	12.5
1957	July-Aug. 1955	E-D	19.5	↑
1963	May 1962	JF-D	10.0	↑
1965	June 1964	JF-D	9.0	Data not
1969	Mar.-Apr. 1967	T-D	23.5	available
1972	Oct.-Nov. 1970	R-D	16.5	↓
1975	Nov.-Dec. 1973	R-D	15.5	↓
1976	Sept.-Oct. 1975	R-D	5.5	7.0



Pacific region. Based on the association between El Niño type events, drought years and index features, and also an assumption that the drought will set in during May of involved drought years, we arrived at values in the column headed "Peak to drought onset" (Table 6). Figure 8 shows the resulting statistics which could be applied to Indonesian drought predictions.

FIGURE 8.—Frequency distributions of time (in months) between preevent peaks in triple 6-mo running mean plots of Southern Oscillation index anomalies (see text) and: 1) the onset of subsequent El Niño type events (assuming onset is in March of involved years); 2) the onset of associated Indonesian droughts (assuming onset is in May of involved years). The number of cases falling within a class interval is entered at the top of the relevant histogram event.

TABLE 7.—Association of east monsoon droughts in Java with El Niño type events.

Drought years	El Niño type event years	Notes	Drought years	El Niño type event years	Notes
1844	1844		1913	1914	
1845	1845-46		1914		
1850	1850		1918	1918-19	
1853	None	Event in 1852	1919		
1855	1855		1923	1923	
1857	1857		1925	1925-26	
1864	1864		1926		
1873	1873		1929	1929-30	
1875	1875		1932	1932	
1877	1877-78		1935	None	Slight lowering of index
1881	1880	Index low 1880-81	1940	1939-40	
1883			1941	1941	
1884	1884-85		1944	1943-44	
1885			1945	1946	
1888	1887-89		1946		
1891	1891		1953	1953	
1896	1896		Drought data unavailable 1954-75		
1902	1902		1976	1976	
1905	1905				

28 (separate events) ÷ 30 (east monsoon drought situations) = 0.93

93% of east monsoon droughts can be associated with El Niño type events

TABLE 8.—Association of El Niño type events with east monsoon droughts in Java.

El Niño type event years	Drought years	Notes	El Niño type event years	Drought years
1844	1844		1905	1905
1845-46	1845		1911-12	None
1850	1850		1914	1913-14
1852	None	Drought in 1853	1917	None
1855	1855		1918-19	1918-19
1857	1857		1923	1923
1864	1864		1925-26	1925-26
1868	None		1929-30	1929
1871	None		1932	1932
1873	1873		1939-40	1940
1875	1875		1941	1941
1877-78	1877		1943-44	1944
1880	1881	Index low 1880-81	1946	1945-46
1884-85	1883-85		1948	None
1887-89	1888		1951	None
1891	1891		1953	1953
1896	1896		Drought data unavailable 1954-75	
1899-1900	None		1976	1976
1902	1902			

28 (east monsoon drought situations) ÷ 36 (separate events) = 0.78

78% of El Niño type events can be associated with east monsoon droughts

DISCUSSION

Over the past 116 yr (1861-1976), for which we have adequate data on the occurrence of El Niño type events of weaker intensity, there were decades of minimal activity (e.g., 1901-10, 1931-40, 1961-70), but no decade without such activity. There is no reason to expect any significant change in the amount of El Niño activity in the foreseeable future over that experienced in the past century. Therefore, it would appear that our data (e.g., Tables 2-5) might eventually be used in conjunction with associated catch data and biological findings for effective long-range planning in the management of the anchoveta fishery. For example, assessment of maximum sustainable yields under various environmental conditions ranging from the favorable extended anti-El Niño condition (when there are two or more consecutive years with high Southern Oscillation indices) to the El Niño situation (when there are rapidly falling and low Southern Oscillation indices) might prove useful for determining the optimum size and flexibility of the fishing fleet and fish processing facilities. A key element to such assessments will be a knowledge of the required biological recuperation time following cessation of an unfavorable physical environmental condition.

Such data could also be used for speculative long-range outlooks. For example, if we had just experienced a strong El Niño, our results suggest that there is a near-zero probability that we would experience another strong event in <7 yr after the onset of the recent situation. However, there would be an 86% probability that an event in the very weak, weak, or moderate category would occur within 3-4 yr after the strong El Niño onset. Considering the current situation, and recognizing that a moderate event set in during 1976 and held over into early 1977, there is a 54% probability (based on our data) that another event of unknown intensity would set in during 1980. It would not be reasonable to go beyond statistical estimates until we find we are approaching a peak in the Southern Oscillation index anomalies.

When we are nearing a preevent peak and can assess its height and time of occurrence, then we can use peak to trough statistics (e.g., Figure 7) to advantage in forecasting onset time and likely intensity of the coming El Niño type event. The intensity would be based on the height of the index anomaly peak and the time of year when the subsequent trough was expected to occur. Event onset time can be further refined by considering Figure 8 statistics. It is also essential in the prediction procedure to realize that some developments may involve two or more stages. In cases of this type, forecast lead times for the separate stages will often be greatly reduced (to 1-6 mo in advance), unless historical analogies lead to pattern recognition as the situation evolves.

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THE PRECISION OF SIMULATED TRANSECT SURVEYS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SCHOOL GROUPS

PAUL C. FIEDLER[1]

ABSTRACT

Simulated transect surveys of model anchovy populations were compared in terms of precision and efficiency. The precision of systematic surveys varies inversely with the distance between transects. Systematic surveys give more precise population estimates than random surveys, due to the large positive correlation between closely spaced transects. The precision of stratified systematic surveys is not significantly different from that of the unstratified surveys when the school groups are randomly distributed in the survey area. However, stratified systematic surveys are more precise when the school groups are clumped in one end of the survey area. The results of the simulations show that the patchy distribution of anchovy schools can be a major source of error in population estimates.

Any sampling program intended to estimate the size of a population is subject to a variety of errors which may reduce the accuracy or precision of the estimate. Precision is the reciprocal of the variation of replicate estimates. Successful management of a northern anchovy fishery in California will require the monitoring of changes in the population size. Acoustic survey techniques are currently being developed to obtain population and biomass estimates independent of the fishery (Hewitt et al. 1976). As in the study of any biological population, it will be important to avoid confusing the variation of a series of estimates due to sampling error with true fluctuations in the population size.

Precision may be affected by 1) the manner in which the sampled population is distributed in space, and 2) variations within the sampling method itself. Several studies have shown that the patchy distribution of individuals in a population may cause considerable variation in replicate population estimates and that the variation is related to sample design. Winsor and Clarke (1940) studied the variation of catches in series of plankton net tows. Although they did not separate the components of between-tow variation due to factors (1) and (2), it was observed that oblique tows were more precise than vertical or horizontal tows. Barnes and Marshall (1951) took an extensive series of replicate pump samples and attributed the considerable variation observed to the nonrandom distribution of the zooplankton since the volumes filtered were known accurately. Taft (1960) analyzed the variance of sardine egg counts in a grid of closely spaced stations. The distribution of eggs was extremely patchy (the densities between samples ranged over more than four orders of magnitude) and the relative 95% confidence limits for an estimate of the egg population in the area of the grid from a single sample were represented by a factor of 62. A simulation study by Wiebe (1971) showed that the precision of zooplankton population estimates depends both on the sampling design (net size and tow length) and the distribution of the population (size and location of patches).

Similar studies have investigated the precision of sampling fish populations. Taylor (1953) discussed the implications of the patchy distribution of fish for the optimum design of trawl surveys to estimate population size. Cram and Hampton (1976) demonstrated that the patchy distribution of pilchard schools can cause imprecision sufficient to render a population estimate useless for management.

The anchovy population is patchy on two levels: individual fish are aggregated in schools and schools themselves tend to be aggregated in school groups. This patchiness, or nonrandomness, is expected to be a major source of variation in population estimates. The present study simulated surveys of model anchovy populations to determine the effect of patchiness on the precision of population estimates. Three transect survey designs were compared: systematic, random, and stratified systematic. These are merely different

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methods of selecting transects, or allocating sampling effort. The three types of simulated survey, with a range of sample sizes (numbers of transects), were run on 15 model anchovy populations.

METHODS

Anchovy populations were modeled as arrays with each element representing 1 n.mi.^{2}. The array dimensions were 180 × 75, approximately the dimensions, in miles, of the Los Angeles Bight. Since a school is the population unit detected in an acoustic or aerial survey, the units of the model populations were schools. One hundred fifty thousand schools were distributed in the array resulting in a mean density of 11.1 schools mi^2. Four acoustic surveys by the California Department of Fish and Game[2] in 1975 and 1976 yielded estimates ranging from 88,887 to 319,878 anchovy schools off southern California in the area of the bight. Mais (1974) gave a range of 21,920-343,070 ($\bar{x}$ = 150,996) schools off southern California and northern Baja California, most of which were within the bight.

The schools were placed in circular school groups located at random. Schools were distributed uniformly within a school group. School group radii and densities were chosen randomly and independently from log-normal approximations of observed frequency distributions based on 52 school groups from six California Department of Fish and Game Sea Survey acoustic surveys (MacCall et al.[3]) (Figure 1). There was no significant correlation between the density of schools within a school group and the size of the school group in these observations. Where school groups overlapped, the densities were simply added together, although this effectively increased both the mean radius and density. In one model population illustrated in Figure 2, 16 school groups containing 150,303 schools covered about 14% of the survey area. Fifteen model populations were used, each with the same total number of schools, but different locations, sizes, and densities of school groups.

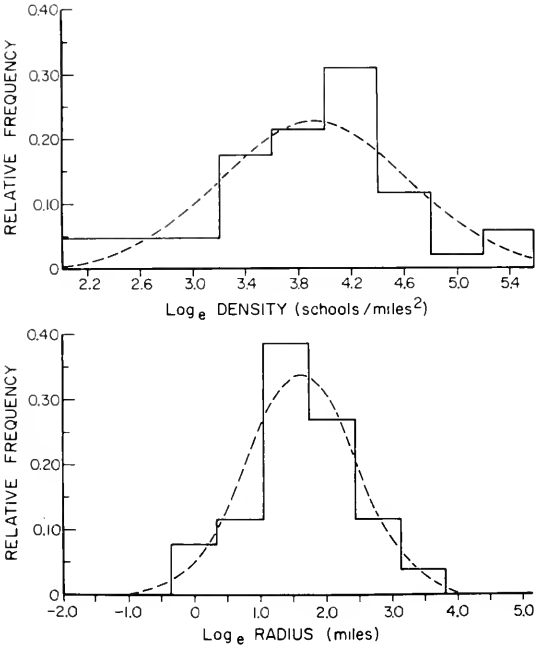

FIGURE 1.—Comparison of distributions of northern anchovy school group density and size observed in the California Current during California Department Fish and Game surveys (solid lines) to log-normal approximations used in simulations (dashed lines).

A simulated survey consisted of a series of transects across the survey area. There were 180 possible transects, each 1 mi wide. Acoustic surveys currently run by the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, used a transect width of 0.14 mi (250 m). Aerial transect widths were typically 0.2 to 0.5 mi. A larger transect width was used in the simulations to hold the model population array down to a reasonable size. We assumed that the general results of the simulations would not change by using a smaller transect width. Since all schools were counted within a transect, the only source of error in the survey estimate was the large variance in the number of schools per transect. For instance, in the model population in Figure 2, the mean number of schools per transect was 835.0, while SD was 920.4 (variance = 8.47 $\times 10^5$).

Systematic surveys were simulated by counting the schools within a series of transects separated by a constant transect interval. A population estimate was calculated simply by dividing the survey count by the fraction of the survey area covered by the transects. Transect intervals of 2, 3,

[2]S. J. Crooke. 1975. Cruise reports 75-A-1 and 75-A-6. K. F. Mais. 1976. Cruise reports 76-A-3 and 76-A-9. State of California - The Resources Agency, Department of Fish and Game, Marine Resources Region, Long Beach, CA 90802.

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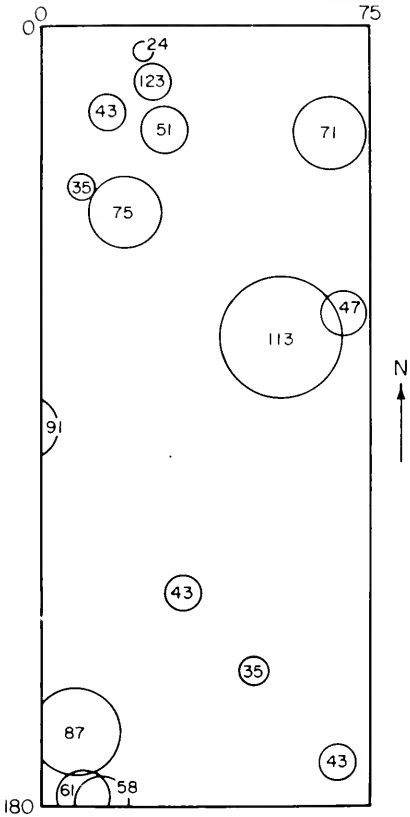

FIGURE 2.—A model northern anchovy population. Densities of school groups in schools per square mile. Simulated survey transects are oriented horizontally. The numbers on the axes are the coordinates of the array and the dimensions, in miles, of the survey area it represents.

4, 5, 7, 10, 12, 15, 20, 25, 30, and 40 mi were used. A survey with a transect interval of d miles consisted of 180 d transects. For each transect interval, 20 replicate surveys were run by randomly choosing the initial transect from the first d transects in the survey area. The replicate survey estimates were used to calculate an unbiased mean population estimate and a coefficient of variation (standard deviation of the replicate estimates divided by the mean), which is a measure of the precision of the estimate (Wiebe 1971). This procedure was repeated on the 15 different model populations.

Random surveys were simluated in an analogous manner to allow a direct comparison of sampling errors. For each of the transect intervals (d) of the systematic surveys, 20 replicate surveys were run consisting of 180 d transects chosen at random without replacement (a transect was not repeated within a survey). Coefficients of variation were calculated as a measure of precision.

Stratified systematic surveys were simulated after dividing each of the model populations into four 45-mi wide strata. The schools along three transects in each of the four strata were counted to obtain a preliminary estimate of relative population sizes. Then a total of 60, 36, 18, 12, 9, 7, or 6 transects were divided among the strata according to the estimated population fractions. For example, if a stratum contained one-half of the schools counted in the preliminary survey, one-half of the total number of transects was allocated to that stratum for the stratified survey. At least one transect was allocated to each stratum to avoid biasing the final population estimate. For each total number of transects, 20 replicate systematic surveys were run by randomly choosing the initial transect and simulating a systematic survey within each stratum with the allocated number of transects. Once again, coefficients of variation of the replicate population estimates were calculated for each of the 15 model populations.

RESULTS

The results of the systematic survey simulations indicate that the sampling error represented

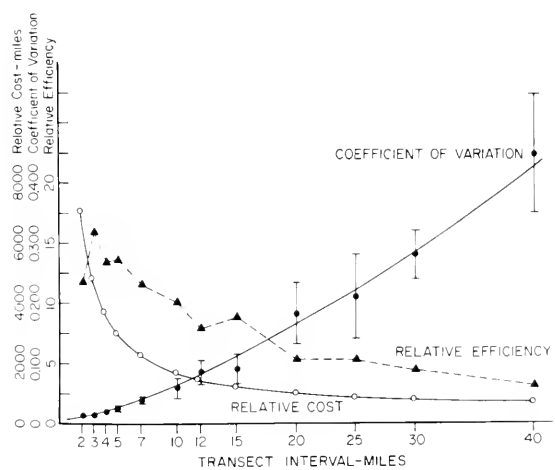

FIGURE 3.—Results of the simulations of systematic surveys of the 15 models for northern anchovy populations. Relative efficiency is proportional to precision (the reciprocal of the coefficient of variation) divided by relative cost (see text). Averages and 95% confidence limits are given for coefficients of variation.

by the coefficient of variation increased as the transect interval increased and sample size decreased (Figure 3). The cost of a survey was assumed to be proportional to the distance covered along the transects plus 360 mi to and from port. Relative efficiency was 10^3 times the reciprocal of the product of the coefficient of variation (C.V.) and relative cost, i.e., precision divided by cost. Efficiency generally decreased as the transect interval increased, but peak efficiency was obtained at a transect interval of 3 mi. By interpolation, it can be seen that a population estimate may range 10 and 25% (2 × C.V.) from the true population size when surveys are run with transect intervals of 8.5 and 16 mi, respectively.

Systematic sampling gave a consistently lower coefficient of variation, or greater precision than random sampling (Figure 4). The variability between model populations, indicated by the confidence limits on the mean coefficient of variation, was greater for the random sampling error ($F_{(14,14)} \geq 5.44, P<0.05$ 12) for 8 of the 12 sample sizes. Also represented in Figure 4 are the expected coefficients of variation for random sampling calculated from the model population parameters (σ^2 and μ) by the following equation with a finite population correction:

$$\text{C.V.} = \frac{1}{\mu}\sqrt{\frac{\sigma^2}{n}\left(\frac{N-n}{N}\right)}$$

where σ^2 = the average variance of the number of schools per transect in the 15 model populations = 1,154,636

μ = the mean number of schools per transect = 835.3

n = the number of transects in the survey

N = total number of transects in the survey area = 180.

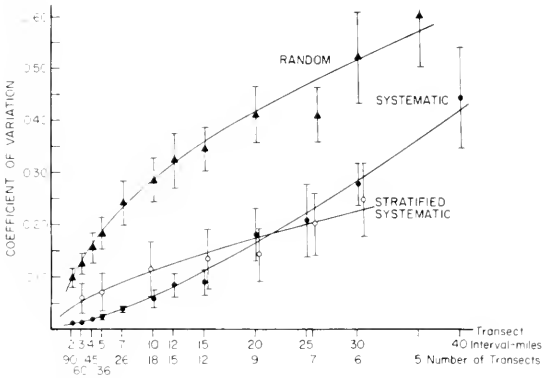

FIGURE 4.—Comparison of the results of the simulations of random, systematic, and stratified systematic surveys. For random surveys, the curve represents the expected coefficients of variation calculated from the parametric variance of the model populations (see text).

For 11 of the 12 sample sizes, the expected value was within 95% confidence limits of the mean observed coefficient of variation. This close agreement supports the validity of the method used to obtain the coefficients of variation in the simulations. There was apparently no significant difference between the coefficients of variation of the systematic and stratified systematic surveys (Figure 4). This was confirmed by analysis of variance (Table 1, $P>0.25$ that there was no added variance due to survey design). However, there were significant interaction effects between survey design and model population ($P<0.01$ that there was no added variance from this source) and between survey design and the number of transects ($P<0.05$).

An attempt was made to elucidate the interactions involving survey design by performing analyses of variance on subsets of the data. It was found that for large sample sizes (transect interval ≤15 mi, or number of transects ≥12) unstratified

TABLE 1.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations. This is a mixed model analysis of variance (Sokal and Rohlf 1969); survey design and number of transects are fixed treatment effects and model population is a random effect.

Source of variation	SS	df	MS	Significance level
Main effects				
Survey design	0 0157	1	0 0157	$F_{(1,14)} = 0.908, P > 0.25$
Number of transects	1 2872	6	0 2145	$F_{(6,84)} = 56\,681, P << 0.001$
Model population	0 5270	14	0.0376	$F_{(14,84)} = 8\,000$ P 0 001
Interactions				
Design-number of transects	0 0748	6	0 0125	$F_{(6,84)} = 2.627, P$ 0 05
Design-population	0 2418	14	0 0173	$F_{(14,84)} = 3\,681$ P 0 001
Number of transects-population	0 3179	84	0 0038	$F_{(84,84)} = 0.819, P$ 0 50
Error	0 3988	84	0 0047	
Total	2 8633	209		

systematic surveys were significantly more precise than stratified systematic surveys ($P < 0.025$), although there is still a significant interaction between survey design and model population ($P < 0.001$). For smaller sample sizes, there was no significant difference between the precision of the two designs.

In the model populations, school groups were located randomly within the survey area. However, the distribution of schools between strata was never random because of the wide range of school group sizes and the small number of school groups in a population. The 15 model populations were divided into three groups (low, intermediate, and high nonrandomness) based on the index of dispersion of the number of schools per stratum. Analysis of variance revealed that for highly nonrandom populations, stratified systematic surveys were significantly more precise than unstratified surveys ($P < 0.025$). On the other hand, there was no significant difference between the survey designs for populations of intermediate or low nonrandomness. The effect of the nonrandomness of the populations, in the limited sense used here, is illustrated more dramatically below.

In summary, these results indicate that both the number of transects and the spatial distribution of the population can affect the precision of a survey estimate. The effect of survey design involves complex interactions with the other two factors. These factors should be considered, if possible, when choosing the optimum design for a survey.

DISCUSSION

In general, systematic sampling may result in considerable gains or losses in precision compared with simple random sampling. The greatest increase in precision occurs when there is a high degree of correlation between adjacent sampling units and the correlation decreases as the interval between units increases. In this situation, systematic sampling resembles stratified sampling. On the other hand, precision may be greatly reduced when there is a periodic variation in the population and the sampling interval is equal to this period or a multiple of it (Hansen et al. 1953).

Correlograms between sampling units (transects) in five of the model anchovy populations indicated that transects <10 mi apart had a high positive correlation, while the correlation tended to be slightly negative at distances >20 mi (Figure 5). This autocorrelation structure was due to the frequency distribution of school group sizes. The mean distance at which the autocorrelation function passed through zero was 15.0 mi, while the mean diameter of the individual school groups in the five model populations was 11.8 mi. Distribution of school groups within the model populations was random. However, real populations are likely to be nonrandom in this respect and additional correlations would be expected from this factor. The strong positive correlation between transects separated by short distances explains why systematic surveys with small transect intervals were more precise than random surveys with an equivalent number of transects. As the transect interval increased, the correlation between transects decreased to near zero and the imprecision of systematic sampling approached that of random sampling (Figure 4).

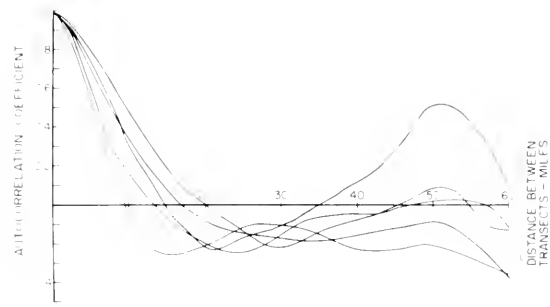

FIGURE 5.—Autocorrelation of transect counts in five model northern anchovy populations.

In order to reduce total sampling error, a common strategy is to allocate effort proportional to the sampling error within parts of a sampling program. The variation observed in the population estimates of the simulated surveys was caused by the large variance in the number of schools per transect. It can be shown in the model populations, as in many biological populations, that the standard deviation was positively correlated with the mean number of schools per transect in a stratum. Therefore, it was thought that the stratified systematic surveys would reduce the total sampling error by allocating more transects where the variance was large. The simulations failed to show any gains in precision from this strategy. This result was not expected, but is possibly due to the random distribution of school groups. The model populations may have been ideal in this sense, but we had relatively little information on the distribution of school groups within the range of the

northern anchovy. As stated above, stratified systematic surveys were significantly more precise than unstratified surveys for the five model populations with the most nonrandom distribution of schools between strata. If the school groups themselves are aggregated, it is reasonable to expect an increase in precision by stratifying the survey.

To test this possibility, the simulations were repeated on model populations in which the school groups were limited to only one-half of the survey area. An analysis of variance (Table 2) indicated in this case that the stratified systematic surveys were more precise than the unstratified systematic surveys ($P<0.005$ that there was no added variance due to survey design). The overall mean coefficients of variation were 0.095 and 0.133, respectively. However, there were significant interaction effects involving survey design, indicating that the advantage of stratifying the survey will depend on the number of transects and the spatial distribution of the population. The additional cost of the preliminary survey in the stratified design must also be considered when comparing it with the unstratified design.

The results of the simulated systematic surveys showed that the patchy distribution of schools was an important source of error in estimates of the anchovy population size. Acoustic surveys run by the Southwest Fisheries Center have used transect intervals of 6.6 and 40 mi. The simulations gave evidence that the population estimates from these surveys could be expected to range at least 8 and 90% (2 × C.V.), respectively, from the true population size. The most efficient simulated sampling, in terms of precision per unit cost, occurred at a transect interval of 3 mi. This would require a cruise grid of 4,860 mi, equivalent to a 34-day acoustic survey at 12 kn and 12 h per day, to reduce the coefficient of variation (due to the patchy distribution of schools) to 1.4%. Maximizing efficiency is not a valid goal, however, when the precision gained is greater than that required for the problem of managing the fishery, when other sources of error become more important, and when there are absolute limits on cost. Anchovy population estimates within 25% of the true value might be considered sufficient for management, at least to allow confidence that a consistent change observed over several years is real (pers. commun., P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., Oct. 1977).

As stated before, the anchovy population is patchy on two levels: individuals are aggregated into schools and schools are aggregated into school groups. The simulations have quantified the sampling error due to the second level of patchiness only. Although little is known about the distribution of anchovy school groups, it was also demonstrated that their aggregation is potentially an important consideration in designing a survey. The acoustic survey methods currently used by the National Marine Fisheries Service and the California Department of Fish and Game do little more than count the number of anchovy schools (Hewitt et al. 1976; Mais 1974). The Department of Fish and Game calculates a biomass estimate by multiplying the observed school area by a constant factor thought to represent an average biomass per unit area. More sophisticated methods of estimating biomass from the acoustic signal received from a school are now being explored at the Southwest Fisheries Center. For these reasons, the problem of sampling error due to a varying number of fish per school (the first level of patchiness) was not addressed here.

Many sources of error may be involved in an anchovy biomass estimate. Patchiness is important in any type of sampling program. Other sources of error that may be important in an

TABLE 2.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations when the model population school groups are clumped in one-half of the survey area.

Source of variation	SS	df	MS	Significance level
Main effects				
Survey design	0.0732	1	0.0732	$F_{(1,14)} = 12.908$, $P<0.005$
Number of transects	1.4995	6	0.2499	$F_{(6,84)} = 119.403$, $P<<0.001$
Model population	0.1327	14	0.0095	$F_{(14,84)} = 4.318$, $P<0.001$
Interactions				
Design-number of transects	0.0476	6	0.0079	$F_{(6,84)} = 3.589$, $P<0.005$
Design-population	0.0794	14	0.0057	$F_{(14,84)} = 2.591$, $P<0.01$
Number of transects-population	0.1758	84	0.0021	$F_{(84,84)} = 0.955$, $P>0.50$
Error	0.1858	84	0.0022	
Total	2.1941	209		

acoustic survey are as follows (Instituto del Mar del Peru 1974; Cram and Hampton 1976; P. E. Smith pers. commun.):

1) Failure to discriminate between anchovy schools and other acoustic targets.
2) Unschooled fish and small schools not detected.
3) Vessel avoidance.
4) Inability to survey in shallow inshore waters.
5) Movement of school groups relative to the survey grid.
6) Fish in the top surface layer missed by the acoustic beam.
7) Errors in the factor for conversion of the acoustic signal information to a biomass estimate.
8) Effect of varying hydrographic conditions on the acoustic signal.
9) Blocking of signal to and from fish far from the ship by fish nearer to the ship.

The magnitude of the error caused by these factors can now only be roughly estimated. They may affect either or both the precision and accuracy of a population estimate. Corrections to reduce the biases are conceivable. The present study has demonstrated the magnitude of the error associated with the patchiness of the anchovy population. Although the model population distributions may be crude approximations to the real distribution, the general conclusions reached here are not likely to be changed by adding further levels of complexity to the model. The sampling error due to patchiness can be reduced by properly designing a survey, but never eliminated. Temporal and spatial differences in population estimates must be interpreted with an awareness that the error exists.

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INTERSEX ANOMALIES IN SHRIMP OF THE GENUS *PENAEOPSIS* (CRUSTACEA: PENAEIDAE)

While examining a relatively large collection of *Penaeopsis* (40 lots containing 196 specimens) taken by the U.S. steamer *Albatross* during the Philippine Expedition, 1907-10, I found three specimens having external characteristics of both males and females. Each specimen had a fully developed thelycum, a moderately well-developed petasma (about two-thirds the length of the petasma of males of corresponding size), small appendices masculinae, and genital apertures on the coxae of the fifth pair of pereopods. The shrimps were poorly preserved—the exoskeletons were soft, rostrums and telsons broken, and internal organs macerated; however, most of the features of the carapace were clearly distinct and the external genitalia intact.

The discovery of these shrimp elicits several questions: to which species do they belong? What is their functional sex? Do they represent a transitional stage in a protandrous hermaphroditic species? If not, have their intersex-appearing anomalies resulted from parasitism? Although none of these questions is answered definitively, all are discussed following a brief description of the external genitalia of the shrimp.

The specimens are deposited at the National Museum of Natural History: USNM 170581, 23 mm cl (carapace length), Bohol Strait, between Bohol and Cebu, 291 m, 25 March 1909, *Albatross* stn 5418. USNM 170582, 24.5 mm cl, Bohol Strait, 320 m, 25 March 1909, *Albatross* stn 5419. USNM 170583, 19 mm cl, Gulf of Davao, SE Mindanao, 247 m, 18 May 1908, *Albatross* stn 5247.

Description

Petasma (Figure 1B-C) with length about two-thirds that of petasma of males of *P. rectacuta* of comparable size, and twice as long as endopod of first pair of pleopods in females of *P. rectacuta* (Figure 1A) and all other congeners. Dorsomedian lobule with distinct distomedian projection and well-formed proximal plate. Dorsolateral lobule with supporting rib (in two of three specimens) ending proximally in subelliptical process. Ventral costa tapering distally, forming free, inwardly excavate, blunt projection directed dorsomesially at broadly obtuse angle with shaft of petasma.

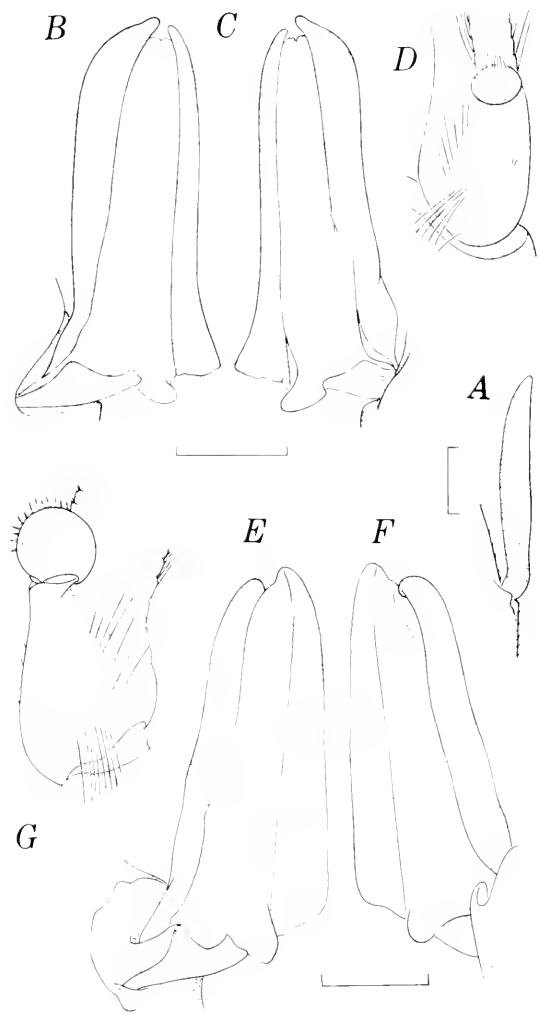

FIGURE 1.—A, *Penaeopsis rectacuta*, USNM 170586, ♀ 23.5 mm cl (carapace length), off Palompon, Leyte, Philippines, endopod of left first pereopod, dorsal view. B, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419, petasma, dorsal view of left half. C, Ventral view of same. D, Left appendix masculina, dorsal view, same specimen. E, *Penaeopsis rectacuta*, USNM 170587, ♂ 13 mm cl, off Mindanao, Philippines, *Albatross* stn 5518, petasma, dorsal view of left half. F, Ventral view of same. G, Right appendix masculina, dorsal view, same specimen. 0.5 mm indicated.

Appendix masculina (Figure 1D) minute, somewhat oval, bearing distal patch of setae; thickening at its base, inconspicuous.

Thelycum (Figure 2A-C) with anterolateral borders of plate of sternite XIV varying from slightly concave to convex, and separated by posteromedian projection of sternite XIII; plate strongly slanting dorsomesially, its surface flat or each side biconvex ventrally. Lateral borders slightly concave, strongly converging posteriorly, not reaching posterior ridge but separated from it by deep depression, latter extending anteriorly adjacent to median rib and merging with anteromedian depression; median rib broadest basally, gently tapering toward, but not reaching, posteromedian projection of sternite XIII. Median plate of XIII trilobed to cordiform, slightly to pronouncedly elongate, covered with setae (most lost in specimen illustrated in Figure 2C) except for naked central concavity, setae directed anteriorly except on base of posteromedian projection where directed caudally; posteromedian projection short, with caudal margin straight or shallowly emarginate. Sternite XII bearing small posteromedian tooth and pair of sharp ridges, extending posterolaterally from base of tooth.

Discussion

In several features the three specimens are markedly similar to members of *P. rectacuta* (Bate 1881). The rostrum (Figure 3) is straight and its second tooth is located in line with the orbital margin, the anteroventral angle of the carapace is approximately 90°, and the moderately long branchiocardiac carina is conspicuous, its anterior extremity not nearly reaching the posterior end of the hepatic sulcus. Also the relative length of the pereopods and—in the two smaller animals—the shape of the median plate of sternite XIII are similar to those in *P. rectacuta*. Furthermore, the three shrimps were collected together with specimens of the latter species, all three in localities where the only other *Penaeopsis* occurring in the area (*P. eduardoi* Pérez Farfante 1977) was not taken—another indication that these shrimp probably belong to *P. rectacuta*.

The petasma and the thelycum of these shrimp are different from those of other species of *Penaeopsis*, including those of *P. rectacuta*. The ventral costae of the petasma (Figure 1B-C), tapering distally into a short projection disposed at an obtuse angle to the shaft, differ from those of adult males of *P. rectacuta* in which the ventral costae turn abruptly at right angles and bear a thin marginal border that is bent inward. In the three specimens the petasma somewhat resembles that of large juveniles (with a carapace length of about 13 mm) of *P. rectacuta* (Figure 1E-F); however, in the latter the distomedian projections are less distinct than they are in my specimens or in adult *P. rectacuta*. Also, in juveniles of *P. rectacuta* the ventral costae do not taper distally into free projections, instead the tips are broad and turned

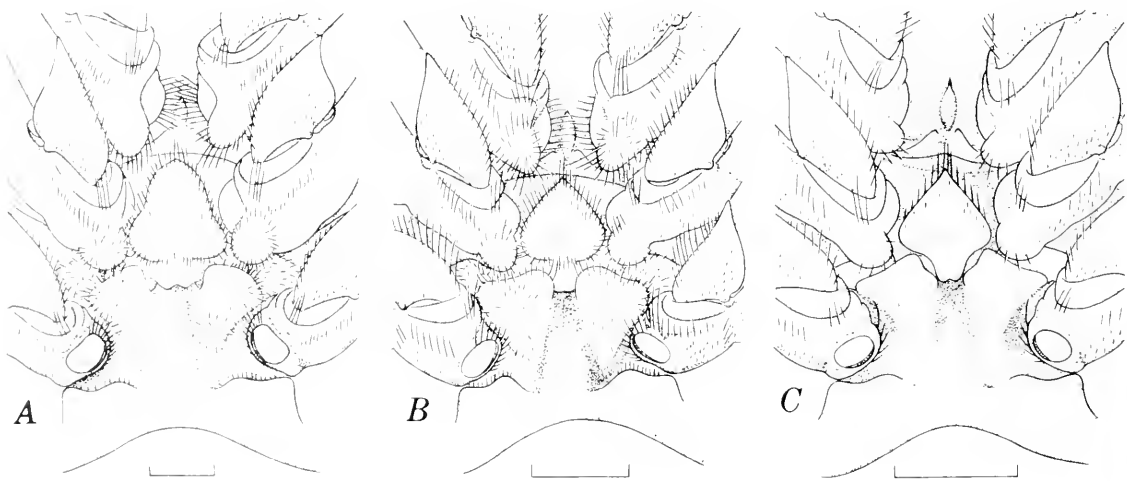

FIGURE 2.—*Penaeopsis* sp. Thelyca. A, USNM 170582, 24.5 mm cl, Bohol Strait, *Albatross* stn 5419. B, USNM 170581, 23 mm cl, Bohol Strait, *Albatross* stn 5418. C, USNM 170580, 19 mm cl, Gulf of Davao, Mindanao, Philippines, *Albatross* stn 5247. 2 mm indicated.

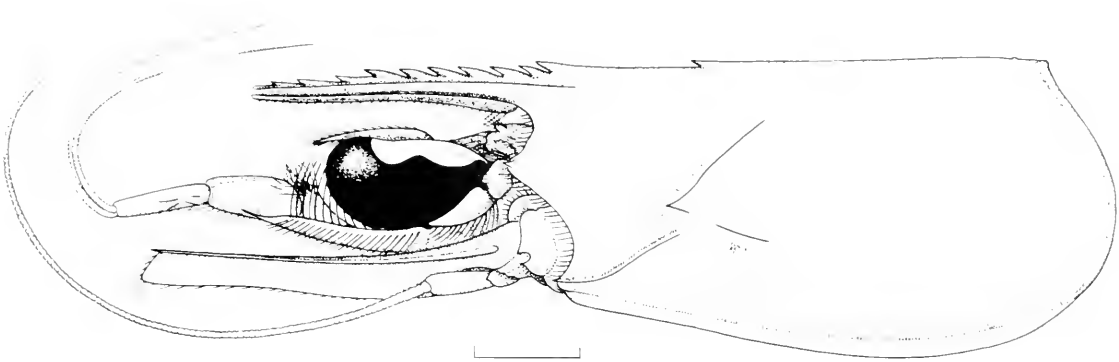

FIGURE 3.—*Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. Cephalothorax, lateral view. 5 mm indicated.

at right angles to the shaft. The appendices masculinae (Figure 1D) are considerably less well developed in the present specimens than in juvenile males of *P. rectacuta*, in which they are circular (Figure 1G), and bear only marginal setae. The thelyca of the three specimens differ from those of *P. rectacuta* in that the lateral borders of the plate of sternite XIV converge strongly (rather than gradually) toward the posterior thoracic ridge and are separated from the ridge by a deep groove, a unique characteristic; the median plate of sternite XIII, although trilobed in one specimen, is cordiform in the other two, the latter resembling that of *P. rectacuta*.

The functional sex of the three specimens cannot be ascertained because their gonads had disintegrated. It is unlikely that they were hermaphrodites for each bears only one pair of gonopores. Because they have a completely developed thelycum one would expect ovipores to occur on the coxae of the third pair of pereopods, but whereas these coxae are similar in outline to those of female *P. rectacuta*, they lack openings and are covered by a hardened cuticle (Figure 2A-C) like those of males; instead, the coxae of the fifth pair of pereopods exhibit a membraneous cuticle with an opening on the proximomesial border. Although the latter aperture is situated on the last pereopod, it occurs on the coxa (Figure 4A) rather than on the bulging articular membrane as it does in typical males (Figure 4B). Furthermore, no terminal ampullae—the ectal muscular region of the vasa deferentia—appear to have been present, even though the skeletal muscles are rather well preserved.

Many anomalies of the secondary sexual characters of decapod crustaceans have been recorded, e.g. in lobsters (Chace and Moore 1959, among others) and crayfishes (Turner 1924, 1929, 1935). Recently Zongker (1961) described many sexually aberrant individuals within a population of *Cambarus montanus acuminatus* Faxon 1884. Among the aberrant individuals she found were females (sex identified by examination of the gonads) lacking ovipores on the coxae of the third pair of pereopods, but with "male openings" on those of the fifth, an anomaly similar to that exhibited by my specimens. In these shrimp, the apertures are not typical of penaeoid males because of their location on the coxae rather than on the articular membranes. Being present on the coxae, they resemble female openings; however, ovipores are typically subcircular rather than slitlike and, furthermore, they are characteristically situated on the mesial surface of the coxa, dorsal to the coxal plate, instead of on the ventral face as in my specimens.

Individuals of the superfamily Penaeoidea bearing both a thelycum and a petasma have not been recorded previously in the literature. Based on size distribution and characters of the endopod of the first pair of pleopods in females, Heegaard (1967, 1971, 1972) suggested the possibility that protandrous hermaphroditism occurs in *Solenocera membranacea* (Risso 1816) and also in *Penaeus kerathurus* (Forskål 1977), but no individuals with both petasma and thelycum were found by him. The external genitalia in my three specimens causes one to suspect that they might be transitional forms and that therefore at least some members of the genus *Penaeopsis* exhibit protandrous hermaphroditism (protandrous because at their size the thelyca are fully developed whereas the petasmata are relatively small). Their rather

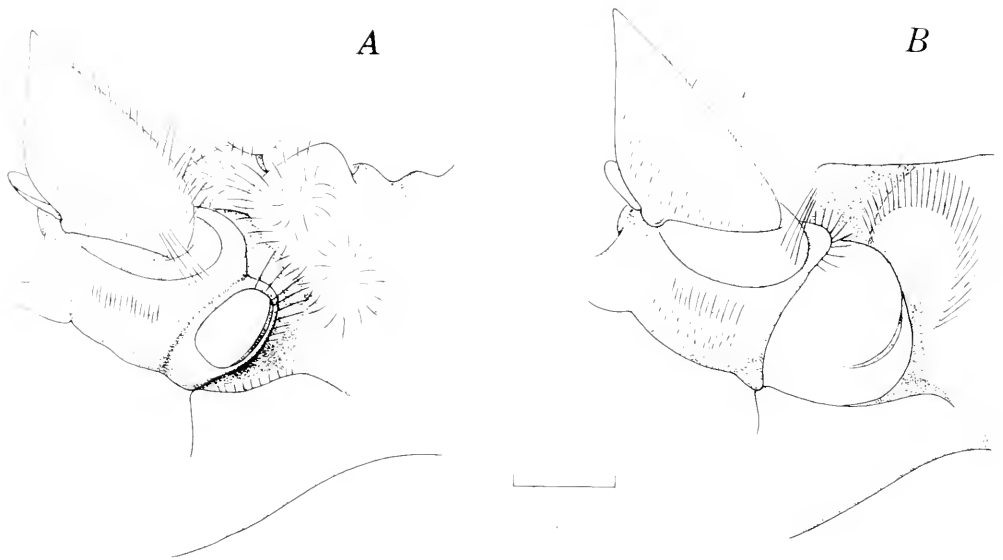

FIGURE 4.—Right fifth pereopod. A, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. B, *Penaeopsis rectacuta*, USNM 170586, ♂ 24.5 mm cl, off Palompon, Leyte, Philippines, *Albatross* stn 5403. 1 mm indicated.

large size, however, makes it unlikely that they are in a transitional stage. Furthermore, hermaphroditism has not been recorded in any species of the genus *Penaeopsis*, consequently its occurrence in these specimens would be exceptional.

Effects of parasitism in a species of *Metapenaeopsis*, a genus closely allied to *Penaeopsis*, were reported by Hiraiwa and Sato (1939). These authors observed conspicuous changes in the petasmata of males and the gonopores of males and females in the shrimp *Penaeopsis akayebi* Rathbun 1902 (= *Metapenaeopsis barbata* de Haan 1850) parasitized by the bopyrid isopod *Epipenaeon japonica* Thielemann 1910. In males, the petasmata were considerably smaller than those in normal individuals of corresponding size and their two parts were unjoined; the gonopores were barely noticeable, and the papillae, at the tips of which the gonopores are situated in normal individuals, were lacking. In the females, the ovipores were obscured, but the thelycum was not apparently affected by the presence of the parasite. In the extensive material examined, however, none of the specimens bore both a petasma and a thelycum. Among the specimens of *P. rectacuta* collected in the waters of the Phillippines, I found a few that were parasitized by bopyrids (one of them was taken at Bohol Strait, in a locality near those at which two of my three individuals were obtained). The parasitized specimens had normal external genitalia, thus lending no support to an assumption that the anomalies in the genitalia of these three individuals were induced by a bopyrid parasite. Nevertheless, parasitism offers the only clue as to the possible origin of the anomalies present in these shrimp.

Acknowledgments

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ON THE ROLE OF THE DIFFERENT FIBRE TYPES IN FISH MYOTOMES AT INTERMEDIATE SWIMMING SPEEDS

In most fishes the myotomal locomotor musculature is made up of two main fibre types: a superficial layer of red fibres overlies the white fibres which form the main mass of the myotome. A spectrum of such differences as mitochondrial content, enzyme activities, blood supply, and innervation (as well as color) distinguishes these two fibre types.The electrophysiogical properties of the two fibre types have only been investigated in a few species, but in all of these the white fibres have been found to propagate muscle action potential, whereas only local nonpropagated activity is seen from red fibres (which are invariably multiply innervated). In many (but not all) fishes, there are also other less abundant fibre types in the myotomes, in some respects intermediate between the red and the white fibres (e.g., Patterson et al. 1975).

There is general agreement that at low sustained swimming speeds only the red fibres are employed and that the white fibres are active during short bursts of maximum speed, which cannot be long sustained. However, agreement has not yet been reached about which fibres are active during sustained swimming at speeds above the minimum cruising speed. Indirect evidence from a number of teleost species (e.g., Greer Walker and Pull 1973) indicated that the white fibres are active at these intermediate swimming speeds, as did the direct electromyographic investigations of Hudson (1973). More recently, several workers have suggested that fibres of intermediate type are recruited as swimming speed rises from the minimal cruising speed, before white fibres are activated and the fish attains its maximal sustained speed. In this note, we report electromyographic observations on various teleosts swimming at controlled speeds in a tunnel respirometer, which show that the activity of the myotomal fibre types during sustained swimming is different in different fishes.

Material and Methods

We studied herring, carp, and trout. Juvenile Pacific herring, *Clupea harengus pallasi* Valenciennes, 15-17.5 cm FL (fork length) were caught by seining in the Georgia Straits, B.C., and held in circulating seawater at the Department of Zoology, University of British Columbia, until swum in a tunnel respirometer (Brett 1964). Herring are delicate fish and did not settle quietly in the respirometer at flow lengths below 2-3 body lengths per second (BL/s). Instead, they darted upstream and fell back again in an irregular manner, so that it was necessary to force them to swim at such speeds from their first entry to the apparatus, without the acclimation period usual when working with other fishes.

Varnished copper wire (40 standard wire gauge) electrodes bared at the tips were placed in the postanal myotomes. The fish were anaesthetized with MS-222[1] (Sandoz) and the electrodes sutured to the dorsal surface before being led downward and backward to enter the myotomes. After recovery for 30 min or so in a bucket of seawater, the fish were introduced to the respirometer and muscle potentials recorded on a Gould Brush 220 pen recorder via Tektronix 122 preamplifiers. It proved difficult to record from electrodes whose tips lay amongst the white muscle fibres, but activity from

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

these fibres was picked up by electrodes whose tips lay in the thin lateral red muscle strip. Relative proportions of red and white muscle fibres were determined by dissection, and their innervation patterns were examined in Formalin-fixed material. Cryostat sections stained for lipid and for succinic dehydrogenase by routine methods were used to distinguish different fibre types.

Similar studies were carried out on carp, *Cyprinus carpio* Linnaeus, 25-30 cm FL, caught by seining in the Fraser Valley, B.C., and rainbow trout, *Salmo gairdneri* Richardson, 17-30 cm FL obtained from a commercial supplier. Before trial in the respirometer both species were held in circular tanks around which water was pumped to give a constant flow of 30-40 cm/s around the circumference where the fish normally swam. For these freshwater fish, much improved signal : noise ratios were obtained by adding small amounts of seawater to the freshwater in the respirometer; this did not affect the behavior of the fish, which were allowed to acclimate for 18-20 h in the apparatus before testing.

Results

Pacific Herring

The records of muscle activity shown in Figure 1A-C are from electrodes with their tips lying in the lateral strip of red muscle. These records show that bursts of irregular potentials around 200-300 μV peak to peak are recorded from the red fibres during slow sustained swiming, becoming more synchronous and shorter as swimming speed increases and tail beat frequency rises. At sustained

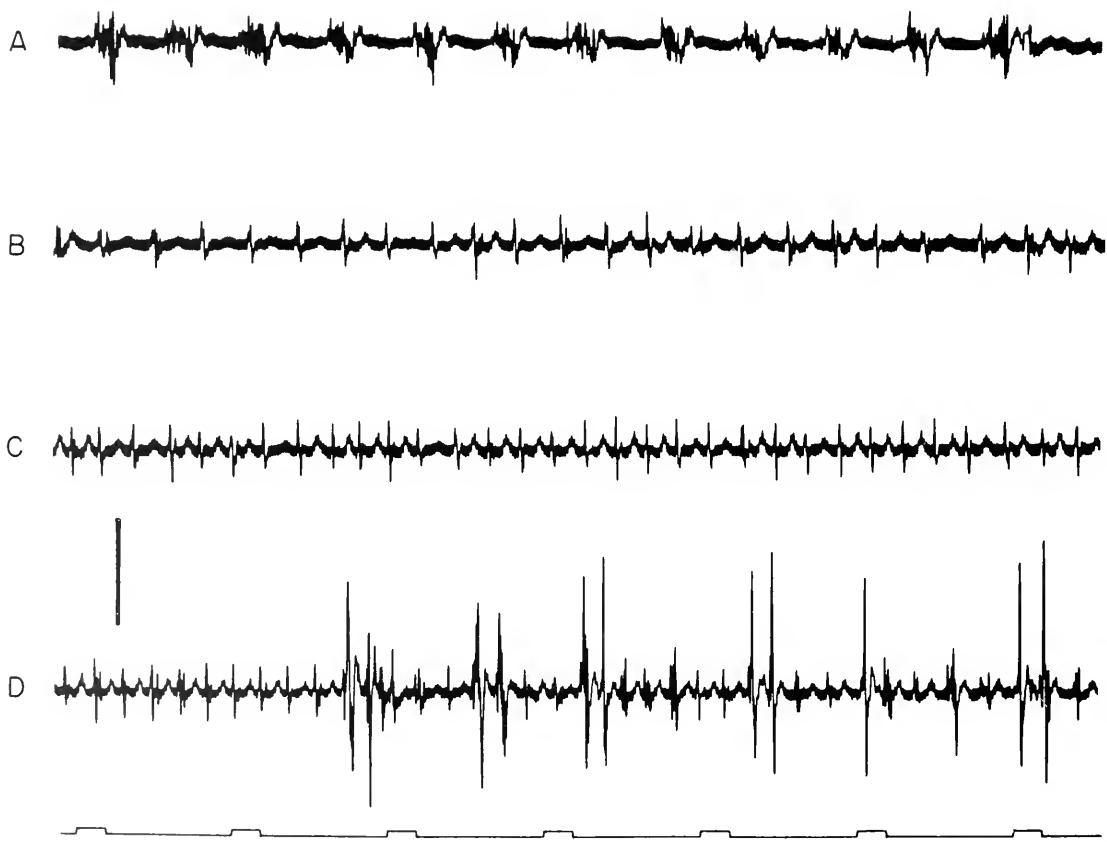

FIGURE 1.—Records from lateral red muscle of a juvenile Pacific herring (16.4 cm fork length) swimming at different speeds. A: 1.8 body lengths per second; B: 2.8 body lengths per second; C: 3.1 body lengths per second; and D: 4.3 body lengths per second. Note gradually increasing synchrony of potentials as swimming speed and tail beat frequency rise (A-C), and the appearance of large potentials in D (picked up from underlying white fibres) when the fish struggled to maintain position at high flow speed. Vertical bar: 500 μV; time marker: seconds.

swimming speeds up to 4-5 BL/s, these are the only kind of potentials recorded; no larger potentials are observed. Because herring are delicate fish, velocity/endurance experiments in respirometers or water tunnels are likely to underestimate their real capabilities, for it is probable that they slowly deteriorate during their sojourn under experimental conditions. Our limited series of measurements of sustained swimming speeds (Figure 2) showed that juvenile herring were able to maintain speeds around 4 BL/s for periods of at least 5 h, a performance about double that previously observed by Boyar (1961), but similar to that seen in large circular tanks by Hempel (in Blaxter 1969).

Boyar's study was very much more extensive than ours; some of his results are plotted in Figure 2 for comparison, where it can be seen that the form of the velocity/endurance curves we obtained is similar to those found for other fish (e.g., Hunter 1971). It seems probable that 4-5 BL/s represents a sensible upper value for continuous sustained cruising by herring of this size.

If the speed of flow in the respirometer is increased above this speed, or if the fish becomes progressively exhausted, it intersperses periods of steady swimming, as before, (during which it slowly falls back to the downstream electrified grid) with a few rapid tail beats, which drive it upstream, and the cycle is repeated. During these rapid beats (Figure 1D), large potentials around 1 mV are observed. Similar potentials are seen when the fish is struggling, and there can be no doubt that (as in dogfish, Bone 1966) the electrodes in the red fibre layer pick up these large potentials from the underlying white fibres. White fibres in herring are similar to those of dogfish in that they are focally innervated (Bone 1964) and they must therefore propagate action potentials. The white fibre system in herring was rapidly exhausted, for the fish could not swim at velocities above 5 BL/s for more than 1-2 min (as indicated in Figure 2). Thus there is good accord between our electromyographic observations and the values obtained for maximum sustained swimming velocities: in herring only red muscle fibres are employed during sustained cruising.

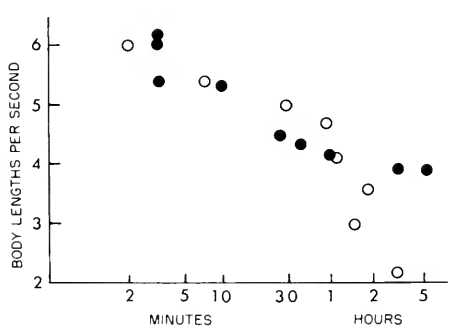

FIGURE 2.—Swimming speeds (in body lengths per second) plotted against the time that the speeds were sustainable (abscissa). Dots: present observations; open circles: data plotted for comparable fish from Boyar (1961). Note the different forms of the velocity/endurance curves given by the two sets of fish, probably the consequence of damage to Boyar's fish in his apparatus.

Histologically, the red and white fibres are different from each other. The red fibres are of more or less uniform diameter, are multiply innervated, and lipid and succinic dehydrogenase (SDH) positive. In contrast, the white zone of the myotome contains both large fibres, and much smaller fibres arrayed around them in a sort of lattice. Both types contain little lipid, are SDH negative, and there are no intermediate fibres either in the juvenile herring which we examined in the respirometer, or in adults. These histological arrangements are summarized in Figure 3A.

Carp

The carp used were much more robust and larger fish than the Pacific herring and it proved possible to make simultaneous recordings of activity within white and red portions of the myotomes. The results obtained were entirely different from those seen in the herring. At speeds between 0.5 BL/s (the lowest speed at which the fish would swim reliably) and the maximum speed used, around 4 BL/s, electrical activity was always detectable from both sets of electrodes in red and white zones of the myotomes (Figure 4). As speed increases from the lowest values, the bursts of activity from each zone became more synchronous and shorter and their amplitude increased. Occasional spikes of greater amplitude were observed from the white muscle zone (Figure 4B), these were faster events than those composing the remainder of the motor bursts. When the fish was swimming near the maximum speed sustainable in the respirometer (Figure 4C), these rapid potentials formed the larger part of the motor bursts and were always seen on both red and white recordings, though smaller from the former. Presumably, they represent spikelike activity from the white zone of the myotome, picked up (as in herring) by electrodes in the red zone. Since the red and white electrodes did not lie in the same

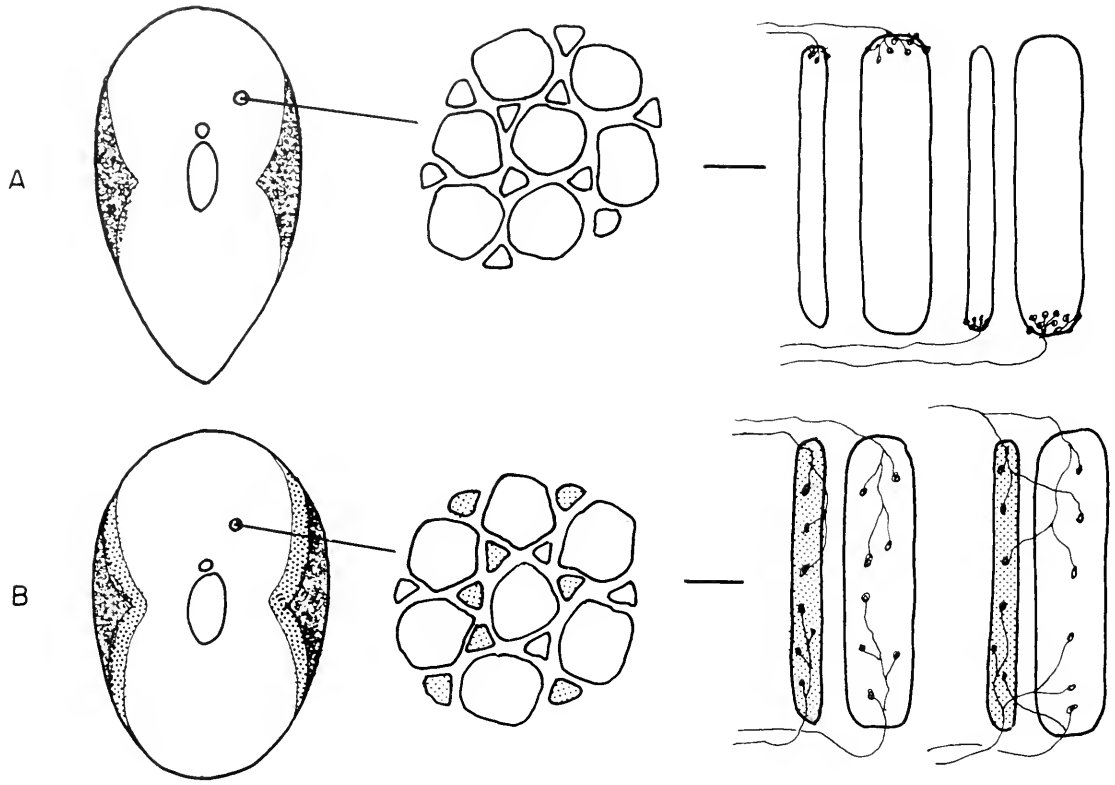

FIGURE 3.—Diagram summarizing the organization of white muscle fibres in the myotome of Pacific herring (A), compared with those of rainbow trout and carp (B). It is not known whether a single axon may supply both large and small white fibres in herring (though both are focally innervated), nor is it known which of the two alternative innervation patterns for rainbow trout and carp are actually present. An overlap of innervation between small and large fibres seems most likely. Note the presence of intermediate fibres between red and white zones of the myotome in carp and rainbow trout; they are absent in herring. (B partly after Patterson et al. 1975 and Johnston et al. 1977.)

myotome (though on the same side of the fish and fairly close to each other), the appearance of occasional spikelike potentials in the white zone was not always reflected directly in the record from the red. At lower swimming speeds, when the electrodes in the white zone did not pick up spikelike potentials at every tail beat, higher recording speed (Figure 4D) showed the variety of response from the white zone of the same myotome at successive tail beats.

Spikelike potentials were present (although usually <0.5 mV in amplitude) and were often reflected at lesser amplitude by the electrodes in the red portion of the myotome, but there were also much smaller irregular potentials from the white region of the myotome, resembling the smaller irregular potential bursts from the multiply innervated red fibres. In carp, both red and white muscle fibres are multiply innervated and there are intermediate fibres lying between red and white fibre zones (Figure 3B). The electrodes in the white portion of the myotome were placed close to the spinal column so that they did not lie near the intermediate zone recently described by Johnston et al. (1977).

Our results clearly indicated that the white fibres were active even at low swimming speeds, and that the activity at these speeds did not resemble the spikelike muscle potentials observed when the fish are swimming faster.

Rainbow Trout

Rainbow trout were examined last of the three fish studied and, to our surprise, gave results comparable with those from the herring, although in salmonids the white fibres are multiply innervated, as they are in carp. At speeds below 2 BL/s, no activity was detectable from the white (mosaic)

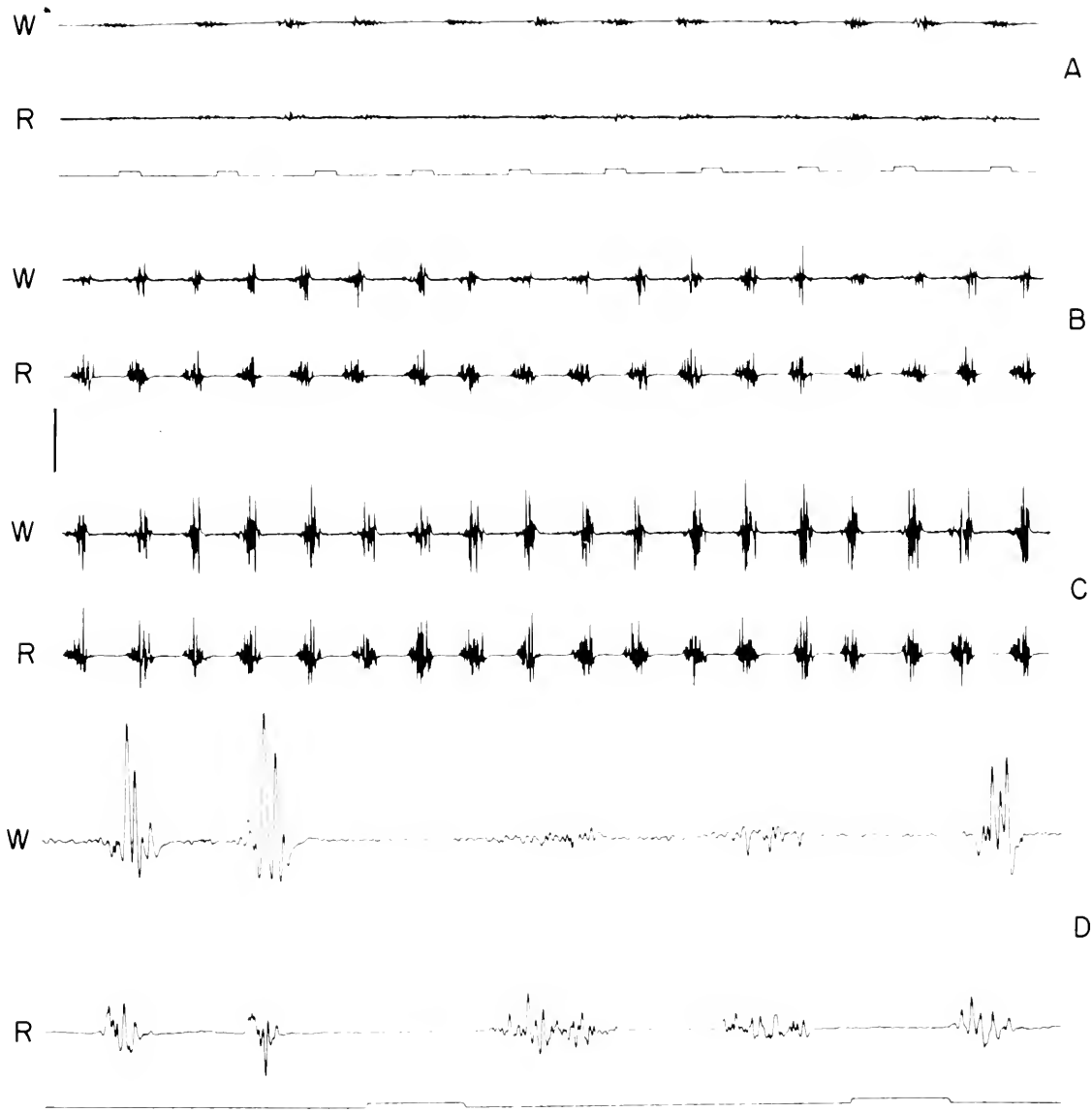

FIGURE 4.—Records of activity from red (R) and white (W) regions of a carp myotome at different swimming speeds. A: 0.75 body length per second; B: 0.9 body length per second; C: 1.26 body lengths per second: and D: 2.0 body lengths per second. Note that the white fibres are active even at low swimming speed and that there is spikelike activity at each tail beat in C. The lowest record (D) taken at higher chart speed shows the appearance of irregular bursts containing spikelike potentials. Note pick-up of these events by the overlying red fibre electrode. Vertical bar: 500 μV; time marker: seconds.

zone of the myotome: 1-200 μV potentials of the usual kind were obtained from the lateral red musculature (Figure 5A). When startled, a few rapid tail beats drove the fish forward and, under these conditions, larger spikelike potentials around 0.5 mV peak to peak were recorded from the white zone of the myotome corresponding to the rapid tail beats. As can be seen from Figure 5B, these events were picked up at lower amplitude by the electrodes whose tips lay in the lateral red muscle layer. After a few rapid tail beats, the fish coasted forward before dropping back and resuming regular swimming: the normal rhythm of the red fibre system was inhibited for a few cycles.

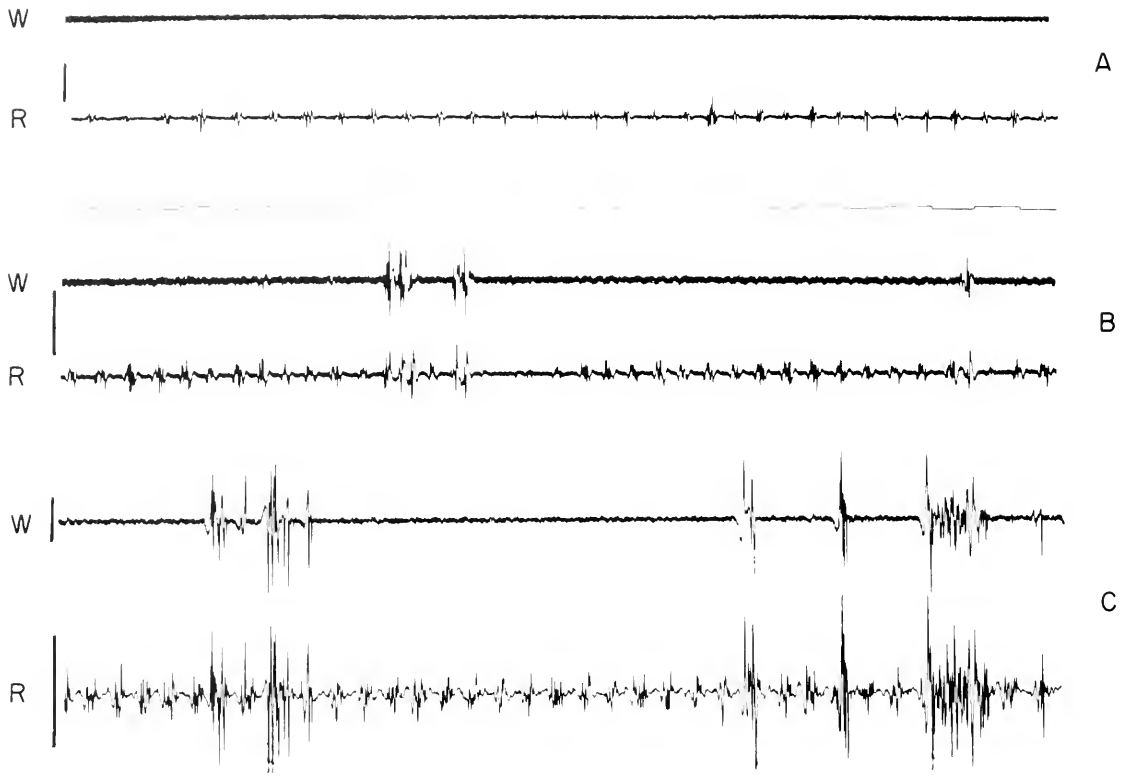

FIGURE 5.—Records of activity from red (R) and white (W) regions of the myotome of different rainbow trout swimming at various speeds. A: 1.8 body lengths per second; B: 4.6 body lengths per second; C: 2.2 body lengths per second. Note that during regular sustained swimming involving red muscle activity, no activity is detected from the white zone of the myotome. Occasional spikelike activity from the white zone of the myotome is seen in B and C (also picked up by the electrode lying in the overlying red zone of the myotome), sometimes inhibits the red muscle bursts (B) and sometimes does not (C). Vertical bars: 1 mV; time marker: seconds.

A single rapid tail beat (to the right of the record) interrupted the red muscle for a single cycle. At higher sustained speeds, above 2 BL/s (as in Figure 5C) this inhibition of red activity following single rapid movement no longer took place. Rather, the behavior was similar to that of the herring in that the fish fell gradually back despite the regular activity of the red system, until driven forward again by a few rapid beats; to drop back again and repeat the cycle until the white system was exhausted. Under these conditions, the fish did not "coast" following rapid tail movements.

No electrical activity was observed from the white zone of the myotome (the so-called mosaic zone) apart from the spikelike potentials shown in Figure 5B and C, although particular pains were taken to ensure that the electrodes were recording satisfactorily. All the fish recorded from gave this same result. We conclude from our observations that this part of the motor system is not active at speeds below 2-2.5 BL/s. Figure 3B summarizes the structure of the system.

Discussion

Our observations have shown once again that the lateral red musculature is used by fish for sustained slow cruising, and that rapid movements of the tail are brought about by the activity of the white motor system, during which spikelike potentials can be recorded from the white zone of the myotome. At intermediate speeds, there are manifest differences between different fishes.

The simplest situation is shown by the Pacific herring, where sustained activity depends only on the activity of the red motor system of the myotome: the white fibres play no part in any activity except rapid movements of short duration. It is true that such movements can "top up," as it were, the sustained activity of the red motor sys-

tem, but this process cannot be long continued: in the respirometer flow velocities which overload the red system and involve occasional activity from the white system soon exhaust the fish. Presumably this artificial situation, where the fish are forced to swim at such speeds, is not found in nature.

The taxonomic position of clupeids is not yet agreed upon (see Greenwood et al. 1966), but in the organization of their myotomal motor system they show the primitive pattern of focal innervation of the white fibres (Bone 1970) found also in elasmobranches, Agnatha, and dipnoi, but in few other teleosts.

We may surmise that in all fish where the white motor system is innervated in this way, sustained swimming will be the responsibility of the red system alone, as it is in herring and dogfish. It is important to notice that this is not to say that gradation may not take place separately within either system. For example, there are five fibre types in the dogfish myotome (three slow and two fast) distinguishable by histochemical and ultrastructural criteria, and it is entirely reasonable to suppose that the two fast fibre types are recruited for movements of different rapidity as Kryvi and Totland (1977) have suggested. At present, our preliminary ultrastructural and histochemical investigations of young and adult herring myotomal fibres have only shown one type of red fibre and two types of white fibre. The two white fibre types may operate at different stages during rapid swimming, but there is no direct evidence for this assumption, and it may be more reasonable to interpret the smaller white fibres as growth stages in the development of the larger (see Bone in press).

In carp, the situation during sustained swimming at all speeds is entirely different. There is inevitably some ambiguity in the interpretation of electromyographic records since the position of the electrode tip may not be certainly known, and the records obtained may be from nearby small electrical events or from distant larger ones, but it certainly does not seem probable that the small events recorded from the carp white muscle at slow sustained swimming speeds can have been picked up from the distant red muscle system. To judge from our records taken deep within the white muscle, as far as possible from the lateral red strip, some fibres within the white zone are active even at the slowest sustained speeds, and this activity increases as the fish increases its swimming speed. This kind of electrical activity at the slower sustained speeds is very similar to that of the red motor system, and presumably represents the activity of fibres which are not propagating muscle action potentials. Such records could not, naturally, be obtained from the white system of fish where the white fibres are focally innervated, and in fact are not seen in herring or dogfish. At higher sustained speeds, or when the carp is disturbed, much larger rapid potentials are observed from the electrode within the white zone. Plainly, two alternative explanations are possible for the variety of electrical response from a single recording site within the white muscle. Either the electrode tip lies close to fibres of two different types, one of which is capable of propagating muscle spikes and the other is not. In this situation, the potentials observed simply reflect the fact that the former system is only activated at higher speeds, the latter operating during slow swimming and so resembling the red motor system. In other words, in the carp myotome, the arrangement is essentially a mosaic one, in which red fibres are intermingled with the usual fast fibres of the white zone. Or, alternatively, the white zone contains only a single muscle fibre type, which is capable of local contractions not involving muscle action potentials, but can also be stimulated to twitch rapidly and, in this state, propagates muscle action potentials. As pointed out earlier (Bone 1975) this would be an ingenious way of ensuring for a single muscle fibre that it always operated at the flattened upper part of the power curve, contracting at very different rates whilst swimming slowly and rapidly.

Our electromyographic records do not allow us to distinguish between these two alternatives but there is no evidence from the histochemical studies by Patterson et al. (1975), or the recent excellent paper by Johnston (1977), that there are "red" fibres in the white zone of the carp myotome. These authors have demonstrated clearly, however, that there is a zone of intermediate fibres between the lateral red and deep white fibres of the carp myotome. They have also shown that these three fibre types are active at different swimming speeds. At 1 BL/s only red fibres were found to be active; at 1.3-1.5 BL/s both red and pink fibres were active, whereas at 2.0 BL/s and above, electrical activity appeared from the white zone of the myotome. These results clearly indicated the sort of recruitment of intermediate fibres at intermediate sustained swimming speeds

which was implied by their accompanying biochemical studies. Interestingly enough, Johnston et al. (1977) observed the same kind of electrical activity from the white zone of the myotome that we observed at low speeds, and it seems therefore extremely probable that such activity (around 75 μV in their records at 2.0 BL/s) is indeed generated by muscle fibres in the white zone. They did not observe spikelike activity from the white zone, presumably because their fish were not swimming sufficiently fast, i.e., they investigated only the lower sustained swimming speed range.

It is then still an open question whether individual fibres in the white zone can sometimes operate producing only local potentials, at other times generating muscle action potentials; or whether there are two different fibre types in the white zone, as yet not distinguishable histochemically. We incline to the former opinion, but to settle the matter evidence from intracellular studies will be essential.

In rainbow trout, our results were again different. We obtained no evidence for activity of the mosaic zone of the myotome during sustained activity even at 4.5 BL/s (the maximum speed at which we could swim the smaller fish). Considering Hudson's (1973) electromyographic evidence from the same species, where he observed activity from the mosaic zone at speeds above 3.0BL/s, this seemed at first rather surprising.

However, the fish Hudson used came from a stock of notoriously poor swimming performance (see Webb 1971), and it is therefore quite possible that we never attained the critical speed at which the mosaic muscle became active in our fish. The main muscle mass in rainbow trout consists of a mosaic of small reddish fibres scattered amongst larger pale fibres (Johnston et al. (1975) have studied them histochemically), and it is thus unclear whether the low-level electrical activity which Hudson (1973) recorded from this region (similar to that which we found in carp white muscle) comes from the same fibres as those generating muscle action potentials during burst swimming. In other words, the two kinds of electrical responses from the rainbow trout mosaic muscle may result from the activity of two different kinds of muscle fibres.

Fish are so diverse, and their patterns of life so varied, that it is hardly surprising that there should be differences on their locomotor musculature. We perhaps ought rather to be surprised at the general uniformity of design of the locomotor system imposed by the aquatic medium. It seems probable, from the distribution of patterns of innervation amongst different fish groups, and indeed amongst the teleosts alone, that focally innervated, twitch fibres operating by anaerobic glycolysis for short bursts of swimming represent the primitive arrangement of the aquatic fast motor system (see Bone 1970).

This fast-motor system contrasts markedly with the universally found multiply innervated nontwitch red fibre system for sustained movement that operates aerobically. However, histological and biochemical investigations of the white myotomal zones of some specialized teleosts such as tuna (Guppy et al. in press) or carp (Johnston et al. 1977) have shown a definite aerobic capacity in the white fibre system, and the original simple dichotomy between anaerobic white fibres and aerobic red fibres rather naively suggested from elasmobranch studies (Bone 1966) is plainly not a good description of the operation of the myotome in all teleosts.

On the whole, it seems reasonable to assume that in most teleosts where the white portion of the myotome is multiply innervated, there will be aerobic intermediate fibres for use during fast sustained cruising, and that at the maximum cruising speed at least some fibres in the white zone of the myotome will also be active aerobically. This seems to be the situation in rainbow trout, and it probably also obtains in most scombrids.

The situation in carp is less clear. The work of Smit et al. (1971) has shown that goldfish (close to carp) are able to sustain high speeds in a respirometer apparently using the white muscle system anaerobically. In line with this, Driedzic and Hochachka (1975) were unable to detect other energy sources than anaerobic glycolysis in carp white muscle, and Johnston et al. (1977) only found low values of aerobic enzymes in this system. We have provided clear evidence that the white motor system is operating over a wide speed range, from the lowest speed at which the fish will swim in the respirometer, and it seems bizarre that a relatively inefficient anaerobic metabolism should drive sustained activity. At low sustained swimming speeds carp might keep in overall aerobic balance by transferring lactate from the white zone to other regions of the body, where lactate could be completely metabolized (Bone 1975). Driedzic and Hochachka found only low lactate levels in the white zone after severe

hypoxic stress, and suggested that this could be explained by lactate transfer out of the system. It is very hard to believe that such a process could account for the extremely interesting results of Smit and his colleagues (Driedzic and Hochachka entitled their paper "The unanswered question of high anaerobic capabilities of carp white muscle"), and we agree with Johnston et al. (1977) in their conclusion that carp would appear to be an ideal species for studying the relationship between muscle design and locomotor function.

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SUMMER FOOD OF THE PACIFIC COD, *GADUS MACROCEPHALUS*, NEAR KODIAK ISLAND, ALASKA[1,2,3]

The Pacific cod, *Gadus macrocephalus* Tilesius, was the target of the earliest United States commercial fishery in the North Pacific (Buck[4]). Its fleet, organized in spring 1865 (Bean 1887), began to fish along the Alaska Peninsula and the Aleutian Islands and eventually expanded into the Bering Sea (Cobb 1916). Dwindling stocks and poor market prices ultimately resulted in the collapse of this fishery shortly after World War II (Ketchen 1961).

Growing pressures in recent years on domestic fishing stocks, in addition to increased worldwide protein demand, improved technological skills and readily available investment capital, have resulted in renewed interest in Pacific cod in the United States (Jones 1977). A bottomfish survey off the coast of Kodiak Island and throughout Shelikof Strait by the National Marine Fisheries Service in 1973 showed the Pacific cod to be one of the most abundant fishes inhabiting the area and the standing stock was conservatively estimated to be about 36,363 t (Hughes and Parks 1975). A small experimental trawl fishery for the Pacific cod and other bottom fishes has been proposed for the Kodiak region by Jones (1977).

Preliminary examination of *G. macrocephalus* stomach contents by Alaska Department of Fish and Game (ADF&G) biologist Guy C. Powell and the author during ADF&G crab investigations off Kodiak Island indicated a high frequency of occurrence of the commercially important snow crab, *Chionoecetes bairdi*. In view of the probable predation pressure on existing snow crab populations by *G. macrocephalus* and in view of the potential commercial importance of the Pacific cod, the summer food habits of this fish in the Kodiak area were examined by me. Ancillary goals included a comparison of food data from pot- and trawl-captured cod.

Methods

Specimens were taken near Kodiak Island, Alaska, (Figure 1) in conjunction with the crab-assessment studies of ADF&G and the surveys of the International Pacific Halibut Commission. Fishing gear consisted of commercial king crab pots, measuring 203 × 203 × 76 cm (inside) and weighing 340 kg; baited with chopped, frozen herring. Webbing was #72 tarred nylon thread with mesh stretched to 7.6 cm. The gear used on the halibut-survey vessels in July 1975 and July 1976 was a standard 400-mesh Eastern otter trawl (Greenwood 1958). Sampling by pots was from 26 June to 3 August 1973, 28 June to 31 July 1974, and 30 June to 27 July 1975. Stations usually consisted of 4-12 pots in a straight line, equally spaced every 0.46 km. Gear was pulled every 18-24 h except when weather conditions prolonged fishing time.

A haphazard sample of 3,933 of Pacific cod was taken from 10,857 cod caught in pots (the number sampled was contingent on the shipboard time available for analysis of stomach contents). Food items were identified to the lowest taxon practical aboard ship, and unidentifiable contents were preserved for later laboratory examination. Analysis of stomach contents was carried out using the frequency of occurrence method in which the prey organisms are expressed as the percent of stomachs containing various food items from the total number of stomachs analyzed. Cod were arbitrarily divided into 33-52 cm, 53-72 cm, and 73-92 cm size (total length) groups for analysis.

The frequency of occurrence method was also used for food data from trawl-caught Pacific cod. The stomachs of 344 cod were examined from 24 trawl stations, which were located in the same general area as the pot stations (Figure 1).

Results and Discussion

As determined from the pot data, the summer diet of *G. macrocephalus* was fishes, crabs, shrimps, and amphipods, in decreasing order of occurrence (Table 1). The most frequently occurring fish was walleye pollock, *Theragra chalcogramma*. Flatfishes (Pleuronectidae) and Pacific sand lance, *Ammodytes hexapterus*, were also frequent. Suyehiro (1942:233-236), Moiseev (1953, 1960), and Mito (1974) also reported that Pacific cod feed on these fishes.

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[3]Based on a thesis submitted in partial fulfillment of the requirements for the M.S. degree, University of Alaska.

[4]Buck, E. H. 1973. Alaska and the law of the sea. National patterns and trends of fishery development on the North Pacific. Alaska Sea Grant Rep. No. 73-4, 65 p.

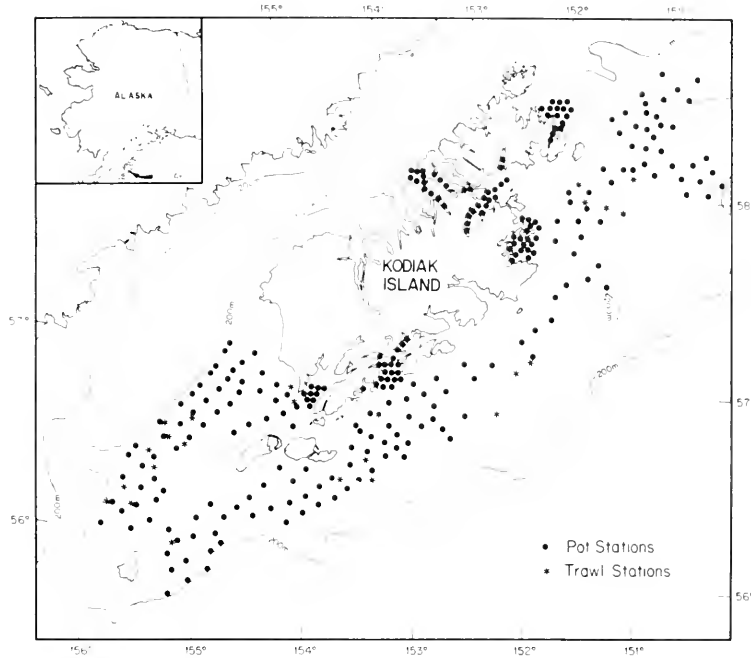

FIGURE 1.—Stations near Kodiak Island, Alaska, where Pacific cod were collected by pots and trawls during summers of 1973-75.

Crab occurrences were dominated by juvenile *C. bairdi*. Snow crabs were the single most frequently occurring food species found in Pacific cod stomachs and occurred in nearly 40% of the cod (Table 2). The average number of snow crabs occurring in cod feeding on snow crabs was 3.3 and they ranged from 1.8 to 70 mm carapace width[5] (Hilsinger et al.[6]); 78% were between 7 and 23 mm. Up to 32 crabs were found in a single cod stomach.

Chionoecetes bairdi had become important in the Alaskan and world markets with landings for Kodiak increasing from 50.3 t in 1967 to 12,400 t in 1976 (North Pacific Fishery Management Council[7]). Since juvenile snow crabs are a major item in the diet of the Pacific cod, reduction of cod stocks by the anticipated new bottomfish fishery should improve the chances for survival of young crabs. Enhanced recruitment of snow crabs to fishable stocks might result from such improved survival.

Pandalid and crangonid shrimps were important in the diet of the Pacific cod in the Kodiak area, a region where both groups are abundant in species and numbers (Ronholt 1963; Barr 1970; Feder and Jewett[8]).

Anonyx nugax may be the principal amphipod. Amphipods which were occasionally preserved from the stomach contents as well as from the perforated bait cans in the crab pots were later identified as *A. nugax*. Because of attraction to the bait, the occurrence of amphipods in stomachs of the pot-caught cod was probably artificially high.

Occurrence of food organisms in trawl-caught cod, in decreasing order was also fishes, crabs, shrimps, and amphipods (Table 3). The most common fishes were *A. hexapterus*, *T. chalcogramma*, and flatfishes. The most frequently consumed crab was *C. bairdi*. Shrimps were primarily Crangonidae.

Wilcoxon's paired-sample test indicated no significant difference ($\alpha = 0.05$) among food groups from cod caught by the two methods, or between sexes (Table 4). No sex differences were found in

[5]Females mature at about 72 mm carapace width (Hilsinger et al. see footnote 6) and males at about 110 mm carapace width (Brown and Powell 1972).

[6]Hilsinger, J. R., W. E. Donaldson, and R. T. Cooney. 1975. The Alaska snow crab, *Chionoecetes bairdi*, size and growth. Unpubl. manuscr., 38 p. Univ. Alaska Sea Grant Rep. No. 75-12 (Inst. Mar. Sci. Rep. No. 75-6).

[7]Fishery Management Plan and environmental impact statement for the tanner crab off Alaska. Sept. 23, 1977. Unpubl. manuscr., 346 p., prepared by the North Pac. Fish. Manage. Counc.

[8]Feder, H. M., and S. C. Jewett. 1977. The distribution, abundance, and diversity of the epifauna of two bays (Alitak and Ugak) of Kodiak Island, Alaska. Inst. Mar. Sci. [Univ. Alaska] Rep. R77-3, 74 p.

TABLE 1.—Frequency and percent frequency of occurrence of summer food items in stomachs of *Gadus macrocephalus* collected during 1973-75 by pots near Kodiak Island, Alaska. N = number of stomachs examined. Subtotals in parentheses.

FOOD ITEMS	1973 N=689 Freq.	1973 % Freq.	1974 N=1183 Freq.	1974 % Freq.	1975 N=2061 Freq.	1975 % Freq.	TOTAL 1973-75 N=3933 Freq.	TOTAL 1973-75 % Freq.
Coelenterata								
Hydrozoa (hydroids)	2	0.3	-	-	1	0.1	3	0.08
Scyphozoa (jellyfishes)	-	-	-	-	1	0.1	1	0.03
Anthozoa (anemones)	5	0.7 (1.0)	3	0.3	1	0.1 (0.3)	9	0.2 (0.31)
Annelida								
Polychaeta (segmented worms)	-	-	53	4.5	74	3.6	127	3.2
Aphrodita sp.	15	2.1	10	0.9 (5.4)	24	1.2 (4.8)	49	1.2 (4.4)
Mollusca								
Polyplacophora (chitons)	-	-	1	0.1	-	-	1	0.03
Pelecypoda (clams, mussels, cockles)								
Astarte polaris	-	-	1	0.1	1	0.1	2	0.05
Chlamys sp.	-	-	-	-	1	0.1	1	0.03
Clinocardium sp.	1	0.1	-	-	4	0.2	5	0.1
Cyclocardia crassidens	1	0.1	1	0.1	1	0.1	3	0.08
Cyclocardia crebricostata	1	-	1	0.1	-	-	1	0.03
Cyclocardia sp.	-	-	-	-	2	0.1	2	0.05
Glycymeris subobsoleta	1	0.1	-	-	-	-	1	0.03
Hiatella arctica	1	0.1	-	-	-	-	1	0.03
Limopsis akutanica	-	-	1	0.1	-	-	1	0.03
Limopsis vaginatus	-	-	2	0.2	-	-	2	0.05
Macoma brota	-	-	-	-	1	0.1	1	0.03
Macoma calcarea	-	-	-	-	1	0.1	1	0.03
Macoma expansa	1	0.1	-	-	-	-	1	0.03
Macoma moesta	-	-	1	0.1	1	0.1	2	0.05
Macoma sp.	1	0.1	1	0.1	1	0.1	3	0.08
Modiolus sp.	-	-	-	-	2	0.1	2	0.05
Musculus discors	-	-	-	-	1	0.1	1	0.03
Musculus olivaceus	1	0.1	1	0.1	1	0.1	3	0.08
Nucula tenuis	1	0.1	-	-	4	0.2	5	0.1
Nuculana fossa	30	4.3	43	3.6	36	1.8	109	2.7
Panomya ampla	1	0.1	-	-	-	-	1	0.03
Patinopecten caurinus	-	-	7	0.6	5	0.2	12	0.3
Pododesmus macroschisma	-	-	1	0.1	1	0.1	2	0.05
Psephidia lordi	1	0.1	-	-	-	-	1	0.03
Punctarella galeata	-	-	1	0.1	-	-	1	0.03
Serripes groenlandicus	-	-	3	0.3	3	0.1	6	0.1
Siliqua sloati	-	-	-	-	1	0.1	1	0.03
Tellina nuculoides	-	-	-	-	1	0.1	1	0.03
Velutina velutina	1	0.1	-	-	-	-	1	0.03
Yoldia beringiana	2	0.3	-	-	5	0.2	7	0.2
Yoldia myalis	-	-	2	0.2	-	-	2	0.05
Yoldia thraciaeformis	-	-	1	0.1	-	-	1	0.03
Yoldia sp.	7	1.0	4	0.3	-	-	11	0.3
Unidentified Pelecypods	26	3.8	27	2.3	53	2.6	106	2.7
Gastropoda (snails)								
Admete couthouyi	-	-	-	-	1	0.1	1	0.03
Aforia circinata	-	-	-	-	1	0.1	1	0.03
Amphissa columbiana	1	0.1	-	-	1	0.1	2	0.05
Beringius kennicotti	-	-	-	-	1	0.1	1	0.03
Boreotrophon pacifica	-	-	1	0.1	1	0.1	2	0.05
Buccinum sp.	1	0.1	-	-	-	-	1	0.01
Colus halli	-	-	-	-	2	0.1	2	0.05
Cylichna alba	1	0.1	1	0.1	-	-	2	0.05
Fusitriton oregonensis	1	0.1	-	-	2	0.1	3	0.08
Margarites baxter	-	-	1	0.1	-	-	1	0.03
Margarites obscura	-	-	1	0.1	2	0.1	3	0.08
Margarites pupillus	-	-	-	-	1	0.1	1	0.03
Mitrella gouldi	-	-	-	-	1	0.1	1	0.03
Natica aleutica	1	0.1	2	0.2	-	-	3	0.08
Natica clausa	-	-	1	0.1	-	-	1	0.03
Natica sp.	-	-	-	-	5	0.2	5	0.1
Neptunea sp.	1	0.1	-	-	1	0.1	2	0.05
Polinices nanus	-	-	-	-	1	0.1	1	0.03
Polinices pallida	2	0.3	2	0.2	3	0.2	7	0.2
Solariella variosa	-	-	1	0.1	-	-	1	0.03
Tachyrhynchus sp.	-	-	1	0.1	-	-	1	0.03
Trichotropis cancellata	1	0.1	1	0.1	3	0.2	5	0.01
Turridae	-	-	-	-	1	0.1	1	0.03
Unidentified gastropods	1	0.1 (11.6)	26	2.2 (11.9)	34	1.7 (10.3)	61	1.5 (10.2)
Cephalopoda								
Octopi	53	7.6	108	9.1	164	8.0	326	8.3
Squid	-	-	1	0.1 (9.2)	-	-	-	-
Arthropoda								
Crustacea								

TABLE 1.—Continued.

FOOD ITEMS	1973 N=689 Freq.	1973 % Freq.		1974 N=1183 Freq.	1974 % Freq.		1975 N=2061 Freq.	1975 % Freq.		TOTAL 1973-75 N=3933 Freq.	TOTAL 1973-75 % Freq.	
Malacostraca												
Euphausiacea (krill) and Mysidacea (mysids)	20	2.9		34	2.9		181	8.8		235	6.0	
Isopoda (pill bugs)	3	0.4		4	0.3		10	0.5		17	0.4	
Amphipoda (sand fleas)	192	27.8		195	16.5		407	19.8		794	20.2	
Ampelisca macrocephala	-	-		-	-		52	2.5	(22.3)	52	1.3	(21.5)
Decapoda												
Pandalidae (shrimps)	67	9.7		118	10.0		-	-		185	4.7	
Pandalus borealis	-	-		-	-		166	8.1		166	4.2	
Pandalopsis dispar	-	-		4	0.3		19	0.9		23	0.6	
Pandalus goniurus	-	-		-	-		4	0.2		4	0.1	
Pandalus hypsinotus	-	-		-	-		7	0.3		7	0.2	
Pandalus montagui tridens	-	-		-	-		8	0.4		8	0.2	
Pandalus platyceros	-	-		1	0.1		3	0.2		4	0.1	
Crangonidae (shrimps)	77	11.1		95	8.0		286	13.9		458	11.6	
Argis rossa	-	-		-	-		3	0.2		3	0.08	
Sclerocrangon boreas	-	-		-	-		5	0.2		5	0.1	
Hippolytidae												
Spirontocaris sp.	-	-		-	-		5	0.2		5	0.1	
Unidentified shrimps	131	19.0	(39.8)	82	6.9	(25.3)	171	8.3	(32.9)	384	9.8	(31.8)
Paguridae (hermit crabs)	24	3.4		21	1.8		55	2.7		100	2.5	
Elassochirus cavimanus	-	-		-	-		2	0.1		2	0.05	
Elassochirus tenuimanus	-	-		1	0.1		3	0.2		4	0.1	
Lithodidae (crabs)												
Paralithodes camtschatica	2	0.3		9	0.8		31	1.5		42	1.1	
Placetron wosnessenskii	-	-		1	0.1		2	0.1		3	0.08	
Rhinolithodes wosnessenskii	-	-		-	-		1	0.1		1	0.03	
Galatheidae (crabs)												
Munida quadrispina	-	-		-	-		1	0.1		1	0.03	
Cancridae (crabs)	-	-		1	0.1		13	0.6		14	0.4	
Cancer sp.	4	0.5		-	-		-	-		4	0.1	
Telmessus cheiragonus	1	0.1		-	-		2	0.1		3	0.08	
Pinnotheridae (pea crabs)												
Pinnixa sp.	5	0.7		36	3.0		23	1.1		64	1.6	
Majidae (spider crabs)												
Chionoecetes bairdi	281	40.7		428	36.2		735	35.6		1444	36.7	
Hyas lyratus	13	1.8		44	3.7		42	2.0		99	2.5	
Oregonia gracilis	-	-		3	0.3		6	0.3		9	0.2	
Unidentified crabs	12	1.7	(49.2)	3	0.3	(46.4)	4	0.2	(44.7)	19	0.5	(46.0)
Echinodermata												
Asteroidea (sea stars)	1	0.1		2	0.2		1	0.1		4	0.1	
Ctenodiscus crispatus	-	-		-	-		1	0.1		1	0.03	
Echinoidea (sea urchins)	1	0.1		-	-		1	0.1		2	0.05	
Holothuroidea (sea cucumbers)	2	0.3		5	0.4		10	0.5		17	0.4	
Ophiuroidea (brittle stars)	-	-		3	0.3		3	0.2		6	0.1	
Ophiura sarsi	-	-	(0.4)	-	-	(0.9)	2	0.1	(1.1)	2	0.05	(0.73)
Vertebrata												
Osteichthyes												
Clupeidae (herrings)												
Clupea harengus pallasi	6	0.8		1	0.1		2	0.1		9	0.2	
Osmeridae (smelts)	3	0.4		2	0.2		4	0.2		9	0.2	
Mallotus villosus	-	-		-	-		1	0.1		1	0.03	
Gadidae (codfishes)												
Theragra chalcogramma	12	1.7		32	2.7		109	5.3		153	3.9	
Gadus macrocephalus	7	1.0		13	0.9		3	0.2		23	0.6	
Zoarcidae (eelpouts)	29	4.2		9	0.8		7	0.3		45	1.1	
Lycodes brevipes	-	-		-	-		3	0.2		3	0.08	
Scorpaenidae (rockfishes)	1	0.1		1	0.1		-	-		2	0.05	
Hexigrammidae (greenlings)												
Pleurogrammus monopterigius	-	-		-	-		2	0.1		2	0.05	
Cottidae (bullheads)	8	1.1		27	2.3		6	0.3		41	1.0	
Dasycottus setiger	-	-		-	-		2	0.1		2	0.05	
Hemilepidotus jordani	-	-		-	-		1	0.1		1	0.03	
Gymnocanthus sp.	-	-		-	-		6	0.3		6	0.1	
Agonidae (poachers)	-	-		3	0.3		17	0.8		20	0.5	
Bathymasteridae (ronquils)												
Bathymaster signatus	-	-		1	0.1		2	0.1		3	0.05	
Trichodontidae (sandfishes)												
Trichodon trichodon	-	-		4	0.3		2	0.1		6	0.1	
Cyclopteridae (lumpsuckers)	1	0.1		1	0.1		5	0.2		7	0.2	
Pleuronectidae (flatfishes)	22	3.2		21	1.8		40	1.9		83	2.1	
Atheresthes stomias	-	-		-	-		2	0.1		2	0.05	
Hippoglossoides elassodon	-	-		-	-		12	0.6		12	0.3	
Hippoglossus stenolepis	-	-		-	-		2	0.1		2	0.05	
Ammodytidae (sand lances)												
Ammodytes hexapterus	20	2.9		20	1.7		9	0.4		49	1.2	
Stichaeidae (pricklebacks)	14	2.0		-	-		10	0.5		24	0.6	
Crypacanthodidae (wrymouths)												
Lyconectes aleutensis	9	1.3		4	0.3		4	0.2		17	0.4	
Unidentified fishes	256	37.1	(55.9)	476	40.2	(51.9)	655	31.8	(44.1)	1387	35.3	(48.2)
Stomachs empty	8	1.6		59	5.0		184	8.9		251	6.4	

TABLE 2.—The importance of the snow crab, *Chionoecetes bairdi*, in the summer diet of Pacific cod. Analysis based on specimens from pots. Crab incidence is given for total number of cod examined; incidence as a percent of feeding cod given in parentheses.

Sampling date	Cod examined (no.)	Feeding cod (%)	Incidence of crabs		Crabs (no.)	Average crab occurrence in cod feeding on crabs
			Number	Percent		
26 June-3 August 1973	689	98 8	281	40 7 (41.3)	1,022	3 6
28 June-31 July 1974	1,183	95.0	427	36 2 (38 0)	1,033	2 4
30 June-27 July 1975	2,061	91.0	734	35 6 (39.1)	2,682	3 6
Total	3,933	93 6	1,442	36.7 (39 2)	4,737	3 3

TABLE 3.—Frequency and percent frequency of occurrence of food items in stomachs of *Gadus macrocephalus* collected July 1975 and 1976 by otter trawl near Kodiak Island, Alaska. N = number of stomachs examined. Subtotals in parentheses.

Food items	July 1975 N = 150		July 1976 N = 194		Total 1975-1976 N = 344	
	Freq.	% Freq.	Freq.	% Freq.	Freq.	% Freq.
Annelida						
Polychaeta	2	1.3	3	1.5	5	1.4
Mollusca						
Pelecypoda and Gastropoda	17	11.3	10	5.1	27	7.8
Cephalopoda	3	2.0	8	4.1	11	3.2
Arthropoda						
Crustacea						
Euphausiacea and Mysidacea	13	8.6	10	5.1	23	6.7
Isopoda	-	-	3	1.5	3	0.9
Amphipoda	14	9.3	15	7.7	29	8.4
Decapoda						
Pandalidae	16	10.7	24	12.4	40	11.6
Crangonidae	37	24.7	37	19.1	74	21.5
Unidentified shrimps	18	12.0 (47.4)	24	12.4 (43.9)	42	12.2 (45.3)
Majidae						
Chionoecetes bairdi	55	36.7	82	42.3	137	39.8
Unidentified crabs	13	8.7 (45.4)	23	11.9 (54.2)	36	10.5 (50.3)
Echinodermata	1	0.6	-	-	1	0.3
Vertebrata						
Osteichthyes						
Gadidae						
Theragra chalcogramma	6	4.0	7	3.6	13	3.8
Pleuronectidae	5	3.3	4	2.1	9	2.6
Ammodytidae						
Ammodytes hexapterus	20	13.3	13	6.7	33	9.6
Unidentified fishes	66	44.0 (64.6)	70	36.1 (48.5)	136	39.5 (55.5)
Stomachs empty	7	4.7	13	6.7	20	5.8

TABLE 4.—Comparison of percent frequency of occurrence of summer food groups in male and female *Gadus macrocephalus* caught by pots and trawls in the Kodiak Island area.

Food groups	Percent frequency of occurrence in Pot-caught cod		Trawl-caught cod	
	Males	Females	Males	Females
Fishes	21 8	24 2	26.3	24 8
Crabs	22.0	19.3	24 2	20.9
Shrimps	15 1	14 2	15.4	24 7
Amphipods	10 0	14 3	4 1	4 3
Gastropods and pelecypods	5.0	4 7	3 3	4 5
Cephalopods	3 6	4 7	2 3	0.9
Euphausiids and mysids	2.1	4 0	4 0	2 7
Polychaetous annelids	1 4	3 1	0 3	1 1
Echinoderms	0 4	0.4	0 1	0 2
Isopods	0 2	0.2	0 5	0 4
Empty stomachs	4 4	2.0	2.8	3 0
Stomachs examined (no.)	2,106	1,827	188	156

other studies on Gadiformes (e.g., Homans and Vladykov 1954; Wigley 1956; Powles 1958; Wigley and Theroux 1965).

A significant difference (χ^2, $\alpha = 0.05$) was found for occurrence of food groups between years for each size group (Figure 2). The only similarity was among 33-52 cm fish between 1973 and 1975 and among 73-92 cm fish between 1974 and 1975. Some trends in frequency of food groups by cod size were apparent (Figure 2). Fishes and cephalopods increased in frequency with increasing cod size over all years while amphipods and polychaete worms decreased. Daan (1973) investigated the relative size of food items (crustaceans and fishes) used by the Atlantic cod, *G. morhua*, and found

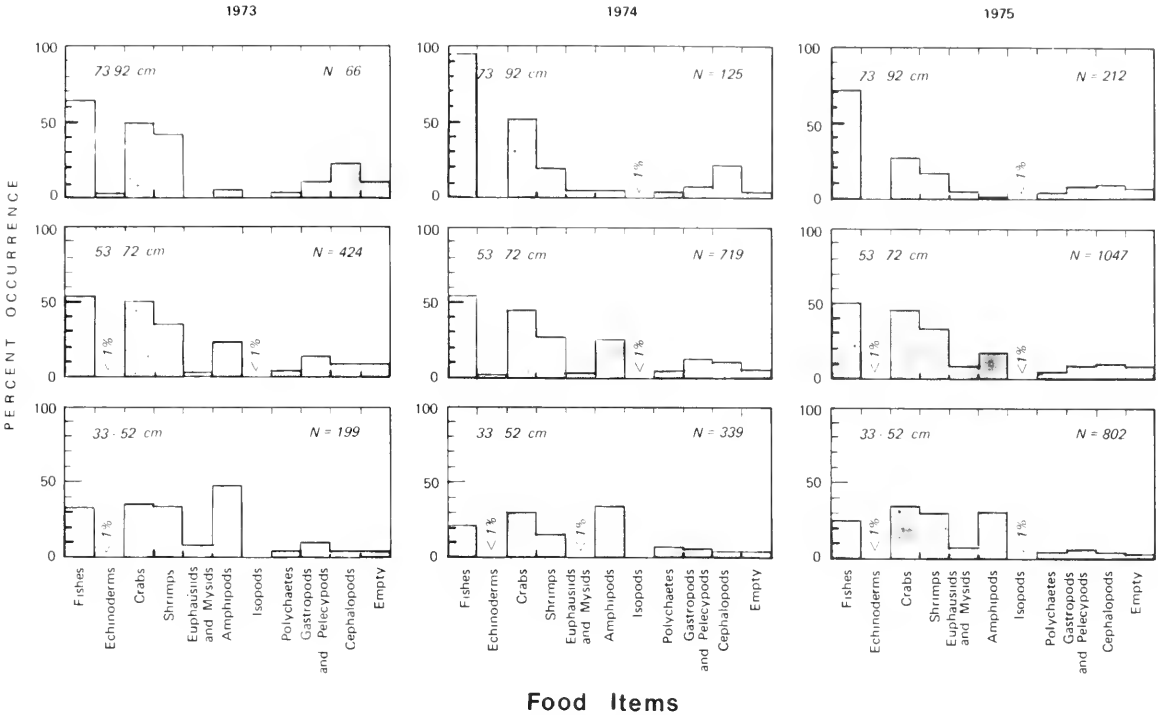

FIGURE 2.—Percent frequency of occurrence of summer food items within three size groups of pot-caught Pacific cod by year of collection—1973-75—near Kodiak Island, Alaska.

that smaller crustaceans were more commonly found in small cod while a gradual shift to a mixed diet of larger prey (primarily fishes) was noted for the larger fish. Arntz (1974) examined juvenile *G. morhua*, and found the most important food to be small crustaceans, mainly cumaceans (35.6% by weight of the total food consumed); fishes accounted for only 15.3% by weight of the total food consumed. This trend of large cod being more piscivorous than small cod has also been demonstrated by Powles (1958) and Rae (1967).

Acknowledgments

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A COMPUTER SOFTWARE SYSTEM FOR OPTIMIZING SURVEY CRUISE TRACKS[1]

Since 1972, the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, has been conducting resource assessment surveys for groundfish in the northern Gulf of Mexico. Random sampling stations were selected and cruise tracks plotted by hand requiring several mandays of effort without assurance than an optimum cruise track had been chosen. Consequently, a computer routine was developed at the NMFS National Fisheries Engineering Laboratory, Bay Saint Louis, Miss., to satisfy two requirements: Generate a set of randomly selected sampling stations from a preestablished station grid and minimize the distance the vessel must travel to sample each station once. This paper presents the resultant routine, a comparison of results with actual cruises, and a discussion of other possible applications of the program.

Background

The problem of determining the optimum cruise track to sample a given set of stations can be restated as, "determining the shortest route from one point to another which allows a vessel to visit every station once." This problem is similar to one in the field of operations research generally referred to as "the traveling salesman problem." The original formulation of the problem was to minimize the time required by a traveling salesman to visit a number of cities and return home (Bellmore and Nemhauser 1968). Several algorithms have been developed which solve the problem exactly; however, computer storage and running time increase exponentially with the number of points to be visited. Because the groundfish surveys normally deal with station numbers in excess of 100, an heuristic method of solving the problem was selected. Lin and Kernighan (1973) at the Bell Telephone Laboratories (BTL) developed an approximate procedure for solving traveling salesman problems with large number of visitation points which appeared applicable to cruise track optimization.[2] The National Fisheries Engineering Laboratory obtained

[1]Contribution No. 78-19F from the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, NSTL Station, MS 39529. MARMAP Contribution No. 154.

[2]To develop a feeling for the complexity of these problems, it should be noted that for a given number of stations, n, there are

a FORTRAN program from BTL and converted it to operate on a Univac[3] 1108 system at the National Aeronautics and Space Administration Computer Complex, Slidell, La.

Modifications to the BTL algorithm were made to satisfy requirements of the groundfish survey program. Most internal modifications were fairly general so that the program could be used for other areas and purposes. Specifics of grid locations and random selection requirements were stored on magnetic tape in a separate master file. The program, as presently configured, can handle up to 150 stations; however, 300 stations could be handled using extended core storage.

Algorithm Description

Assume a number of stations (n) have been selected, either randomly or specifically. There are a total of $n(n-1)/2$ links between the n stations. The object is to find an n-subset of these links such that (a) each station is sampled exactly one time, and (b) the total distance traveled is a minimum. A sequence of links satisfying (a) is called a tour; if it also satisfies (b), it is the optimum tour.

The optimization algorithm begins by computing all $n(n-1)/2$ distances and storing them in a matrix. A completely random tour is generated to use as a starting point. An attempt is then made to find two sets of links $X = x_1, x_2 \ldots x_k$ *and* $Y = y_1, y_2 \ldots y_k$ such that if the links in X are replaced with the links in Y, the result gives a tour of a shorter distance. This is done by identifying x_1 and y_1 as the "most-out-of-place" pair, setting them aside, then proceeding with x_2 and y_2, x_3 and y_3, and so on.

A criterion is then used to determine how many pairs of links are to be exchanged. This criterion can be explained as follows: Let the length of x_i and y_i be dx_i and dy_i, and $g_i = dx_i - dy_i$. This determines the gain (shorter distance) by exchanging x_i with y_i. After examining a sequence of proposed exchanges $x_1, x_2 \ldots x_k$ and $y_1, y_2 \ldots y_k$ with their corresponding gains $g_1, g_2 \ldots g_k$, the actual value of k that defines the number of sets to exchange is the one for which $g_1 + g_2 + \ldots + g_k$ is always zero or negative. This indicates the solution is a local optimum based on the fact that if a sequence of numbers has a positive sum, there is a cyclic permutation of these numbers such that every partial sum is positive. Hence, the algorithm looks for sequences of g_i's whose partial sum is always positive, reducing the number of sequences that need to be examined. This means that the value of k, which gives the number of links to be exchanged, is determined when $G^* = \sum_{j=1}^{k} g_j \leq 0$, i.e., when the partial sum of the gains fails to remain positive. These links are then exchanged and the process of selecting new links to be exchanged begins again at $i = 1$. When all possibilities have been tried, the tour length is recorded. The program generates a new random initial tour and the entire process begins again. Eleven distinct solutions are produced in this manner, and the tour with the shortest length is considered the optimum solution. Program operation can best be understood by a simple example.

Assume that n stations are selected and a random tour generated (Figure 1a5. The black dots represent the stations and the circle represents the random tour. Any station S_1 is selected and S_2 is designated as an adjacent station in the tour. The link connecting the two stations is designated

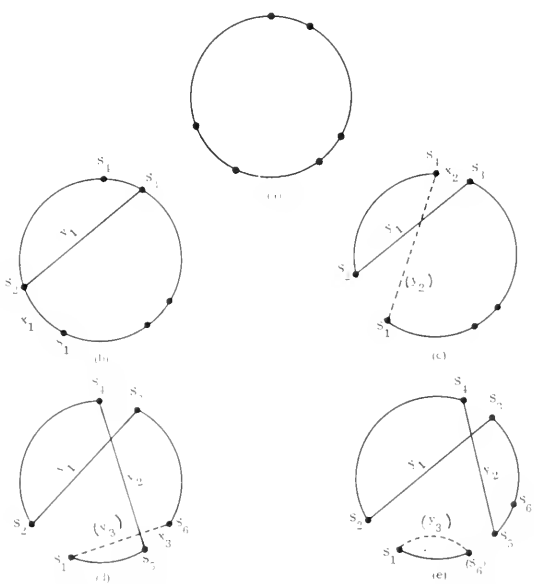

FIGURE 1.—Example of the algorithm operation (modified from Lin and Kernighan 1973).

$(n-1)$ factorial possible cruise tracks that satisfy the criterion of sampling all stations once and returning to starting position (e.g., if $n = 101$, the number of possible solutions is 9.3326×10^{157}).

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

as x_1 as shown schematically in Figure 1b. The station closest to S_2 is designated as S_3 and y_1 is the link joining S_2 and S_3. The link y_1 is not permitted to be either of the links already connected to S_2. The gain criterion is then calculated as $g_1 = dx_1 - dy_1$. If this is negative, S_2 is designated as the other neighbor of S_1 in the tour. If g_1 is positive, S_4 is designated as one of the tour neighbors of S_3 as shown in Figure 1c. If y_2 were chosen to join S_4 with S_1, the result would be a tour. The gain criterion is then calculated as $g_2 = dx_2 - dy_2$. If $g_1 + g_2 > 0$, the original tour could be improved by exchanging x_1 and x_2 with y_1 and y_2, respectively. This potential improvement, which results from closing up the tour immediately ($G^* = g_1 + g_2$), is then stored. Now S_5 is chosen as the nearest neighbor of S_4, and y_2 is designated as the link connecting the two stations. Station S_5 is not permitted to be either of the stations already connected to S_4. Figure 1d shows there is only one choice for station S_6 and the link x_3 such that if S_6 is connected to S_1, a tour remains. If S_6 were chosen as the other neighbor of S_5 in the original tour, closing up S_6 to S_1 would result in a tour of two disconnected pieces (Figure 1e). The gain associated with closing up immediately (connecting S_6 with S_1) is then compared with that obtained by joining S_4 to S_1 (G^*). The link connecting S_6 to S_1 is designated as y_3. The gain criterion is then calculated as $g_3 = dx_3 - dy_3$. If $g_1 + g_2 + g_3 \leq G^*$ (G^* is the best improvement thus far), there is no improvement, so the number of links (k) to be profitably exchanged is defined as $k = 2$. If $g_1 + g_2 + g_3 > G^*$, however, a new station S_7 and link x_4 are selected and the process is continued.

A limited backtracking feature of the program is included for the case when $G^* = 0$ (i.e., no improvement can be made). The link y_2 was chosen (Figure 1d) to join S_5 to S_4 as the closest station to S_4. When no improvement is made at some stage ($G^* = 0$), new links y_2 are considered in order of increasing length to a maximum of five choices. If still no improvement is found, the five y_1 links are examined in order of increasing length. When G^* cannot be improved, and the value k determined, a new initial station S_1 is selected and the process repeated. The procedure ends when all n stations have been examined. A new random tour is generated, and each station is examined as an S_1 again in the same manner. This limited backtracking significantly increases program effectiveness.

The computational procedure has other features that improve the calculations and reduce running time; such as limited foresight to the next links to be broken, allowance for nonsequential link exchanges, and elimination from computation of those links previously recorded in good tours. For a more complete description of the algorithm, see Lin and Kernighan (1973).

Results

Station Description

Separate station grids lere used for areas east and west of the Mississippi River Delta. A station consisted of a rectangle, lat. 2′30″ by long. 2′30″, within which three trawl tows were made. Stations were identified and located at the center point of the rectangle.

The station grid for the West Delta area consisted of an area extending from long. 89°30′W to 91°30′W (Figure 2). The station grid for the East Delta area consisted of a primary and secondary zone extending between long. 88°00′W and 89°30′W and long. 79°30′W and 88°00′W (Figure 3). Each area was limited by the 9.2-m (5-fm) and 92-m (50-fm) depth contours. Stations were excluded from random selection in both areas because of navigation and trawling hazards, and areas of known low groundfish densities.

Random Selection

Station number, latitude, and longitude were stored in a master grid file for each area. Input to station selection for the West Delta region was the number of stations to be sampled. This region had 780 stations. For the East Delta area, the number of stations must be specified separately for the primary and the secondary zones—there were 555 stations in the primary zone and 139 in the secondary region. Station selection was performed by a random number generator which selected stations based on the number required for each area.

Cruise Track Optimization

Requirements for an optimized cruise track were different for the areas east and west of the delta. A round-trip track was desired for the West Delta area, while a one-way calculation was desired for the East Delta area. The latter consisted of the shortest route from a designated starting point near Pascagoula. Miss., through each selected station and ending at a point near the mouth of the Mississippi River.

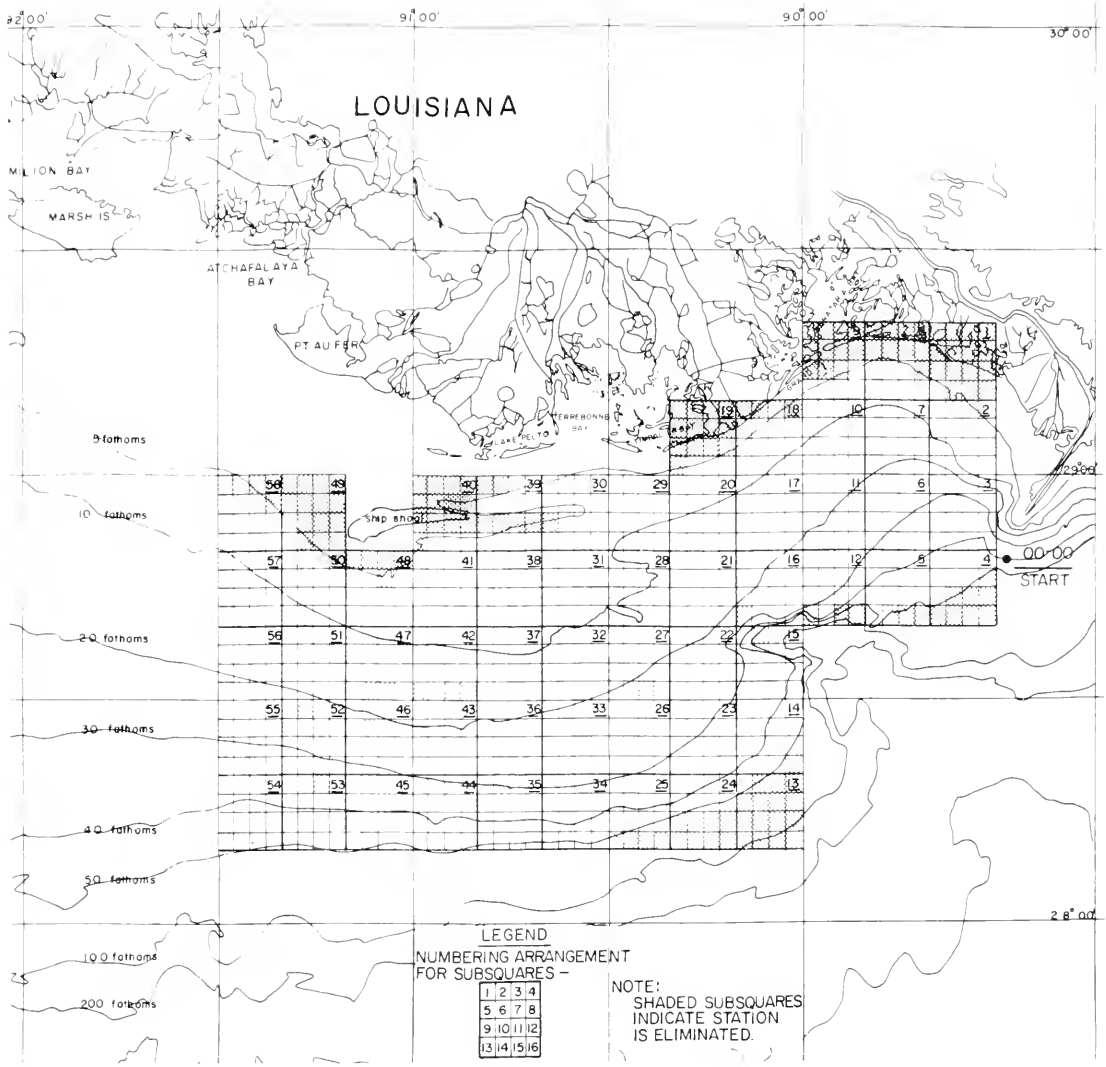

FIGURE 2.—Master station grid for groundfish survey sampling in northern Gulf of Mexico - West Delta area. Dot labeled 00-00 is start and end point for round-trip cruise track optimization.

Since the grid used in the calculations was square, a coefficient was included to account for differences in absolute distance for one unit of longitude vs. one unit of latitude. The coefficient used for optimizing groundfish survey tracks is 52.10/59.85, which is the ratio of the distance in nautical miles for 1° of longitude to that for 1° of latitude at lat. 30°N. All longitudinal Cartesian coordinate distances were multiplied by this coefficient before calculations began.

For the West Delta area, the cruise track was optimized from a point located just east of the primary survey area (Pascagoula station number 00-00) through all randomly selected stations, returning to the starting point. The optimization program computed 11 solutions and the best route in terms of the shortest distance was selected. Output consisted of a listing of stations in proper sampling order, and a plot of the stations and optimum cruise track with every fifth station labeled.

The starting point of the cruise track was south of Pascagoula for the East Delta area. Optimization was done for a cruise track that visited all

randomly selected primary and secondary stations and terminated at a point near the Mississippi River Delta designated 99-99 (Figure 3). Outputs were the same as for the West Delta except for treatment of the stations randomly selected which appear in blocks 45, 46, 47, and 48. These were not included in the optimized cruise track, but were listed at the end of the optimized cruise track listing. The stations in these blocks were added to the end of the optimized cruise track and plotted as individual points labeled with their Pascagoula number.

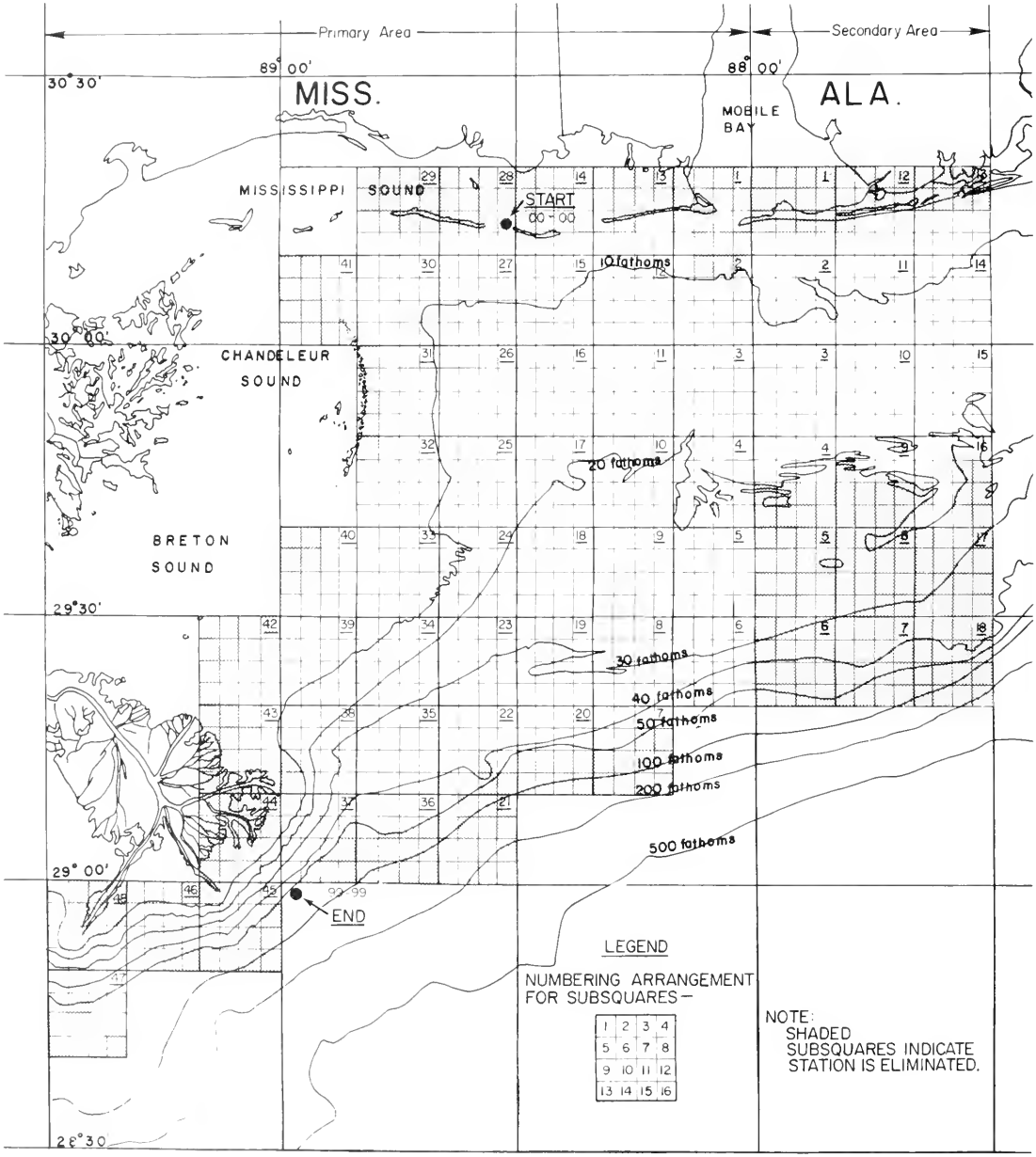

FIGURE 3.—Master station grid for groundfish survey sampling in northern Gulf of Mexico - East Delta area. Dot labeled 00-00 is starting point and dot labeled 99-99 is end point for one-way cruise track optimization. Primary and secondary areas are indicated by arrows at top of figure.

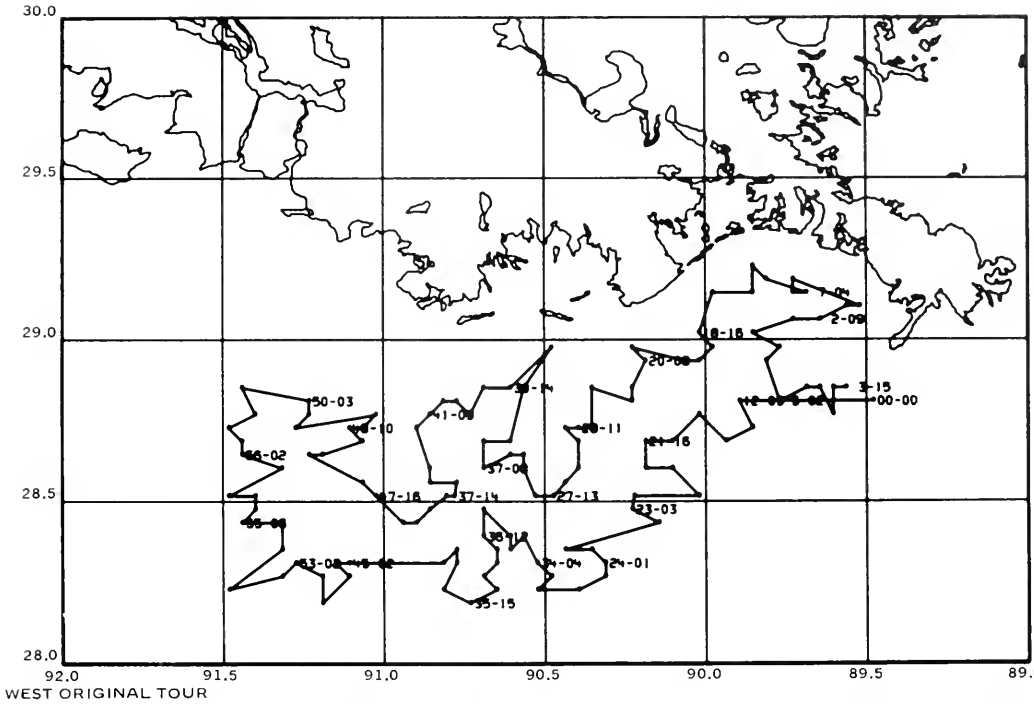

FIGURE 4.—Actual cruise track followed for West Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled.

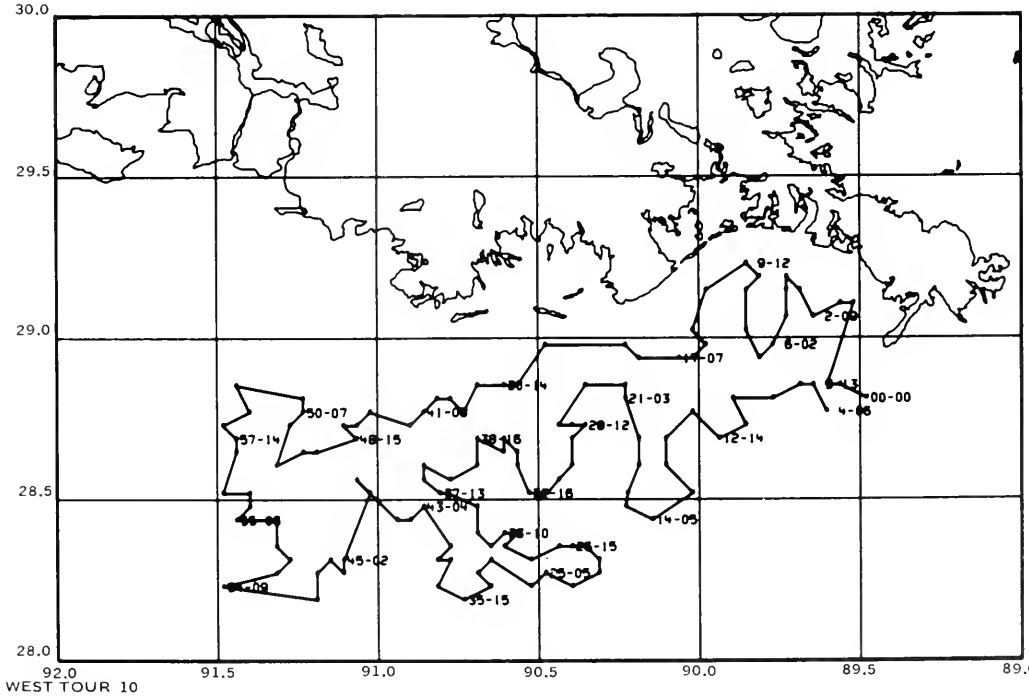

FIGURE 5.—Optimized cruise track for West Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled.

Test Case and Sample Products

The optimization program was tested to compare computational results with a cruise track actually followed during a survey—FRV *Oregon II* cruise 55, 5-29 November 1974.

West Delta

The 126 stations sampled during cruise 55 for the West Delta area were entered in the order they were sampled (Figure 4), and the total distance (in grid units) was calculated to be 254. Each grid unit was equivalent to approximately 4.6 km; thus, the total distance was about 1,176 km.

Eleven computations were performed on these stations by the optimization program, and a minimum length of 233 grid units (approximately 1,078 km) occurred three times. It can be said with confidence the optimum tour (Figure 5) represented an 8.3% improvement over the actual cruise track. Distances were calculated from the center of each subsquare; therefore, the actual dis-

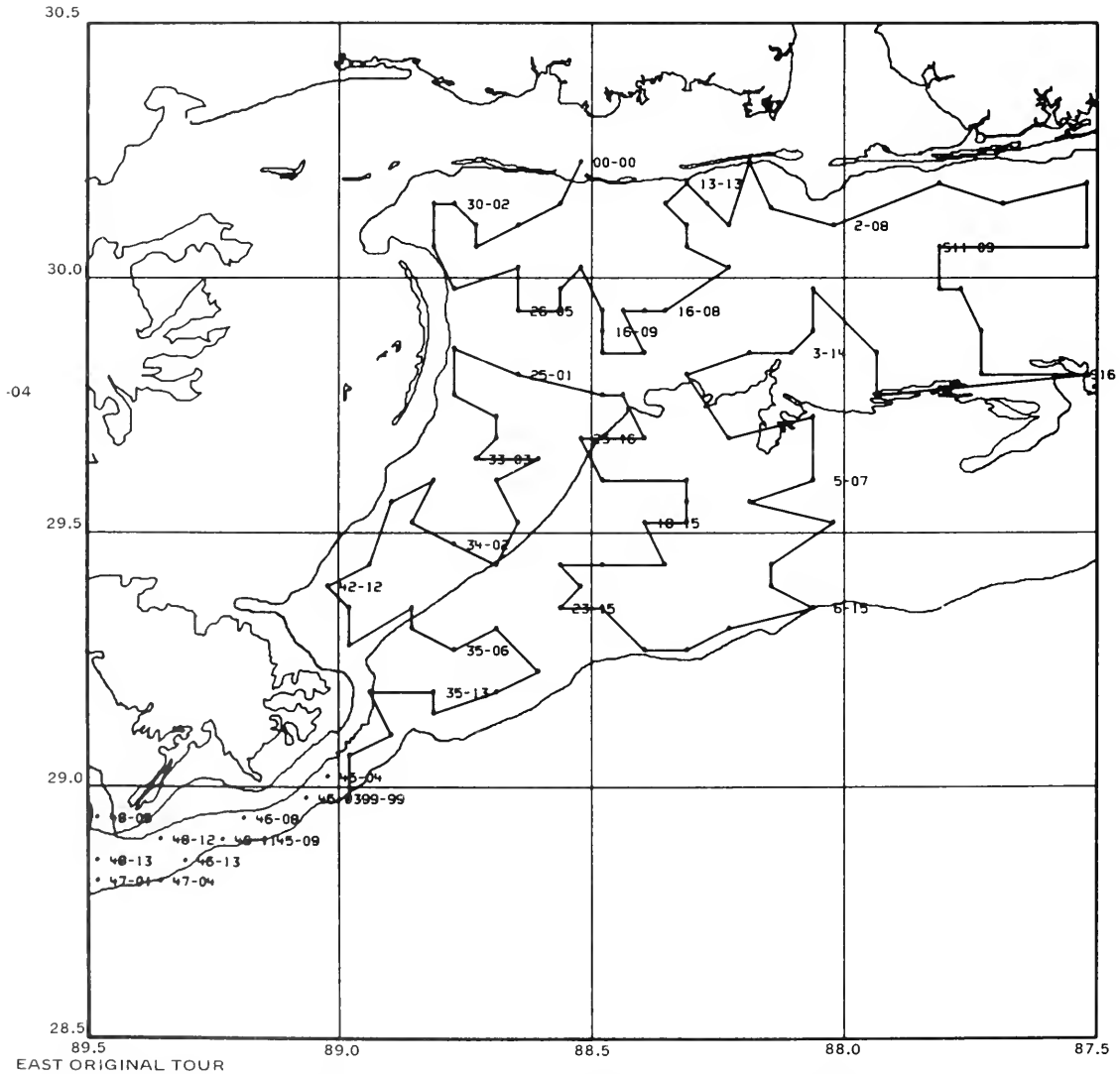

FIGURE 6.—Actual cruise track followed for East Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled. Station numbers listed at lower left are those not included in optimization calculations.

tance would be decreased by the vessel cutting corners of the subsquares. Calculations for the 126 stations on the Univac 1108 system used about 60K of core storage and required 2 min of Central Processing Unit (CPU) time.

East Delta

Cruise 55 was used to test the program for the East Delta area also. Of 116 stations sampled, 105 were included in the computation of an optimum one-way cruise track. The other 11 stations were located in blocks 45, 46, 47, and 48. They were, however, added to the end of the optimized listout, plotted, and labeled on the cruise track plot. The actual cruise track distance for the 105 stations was 229 grid units (approximately 1,061 km) (Figure 6). The optimized one-way path was calculated to be 216 grid units (1,000 km), an improvement of 5.8% (Figure 7). Calculations for the 105 stations used 60K of core storage and required 66 s of CPU time.

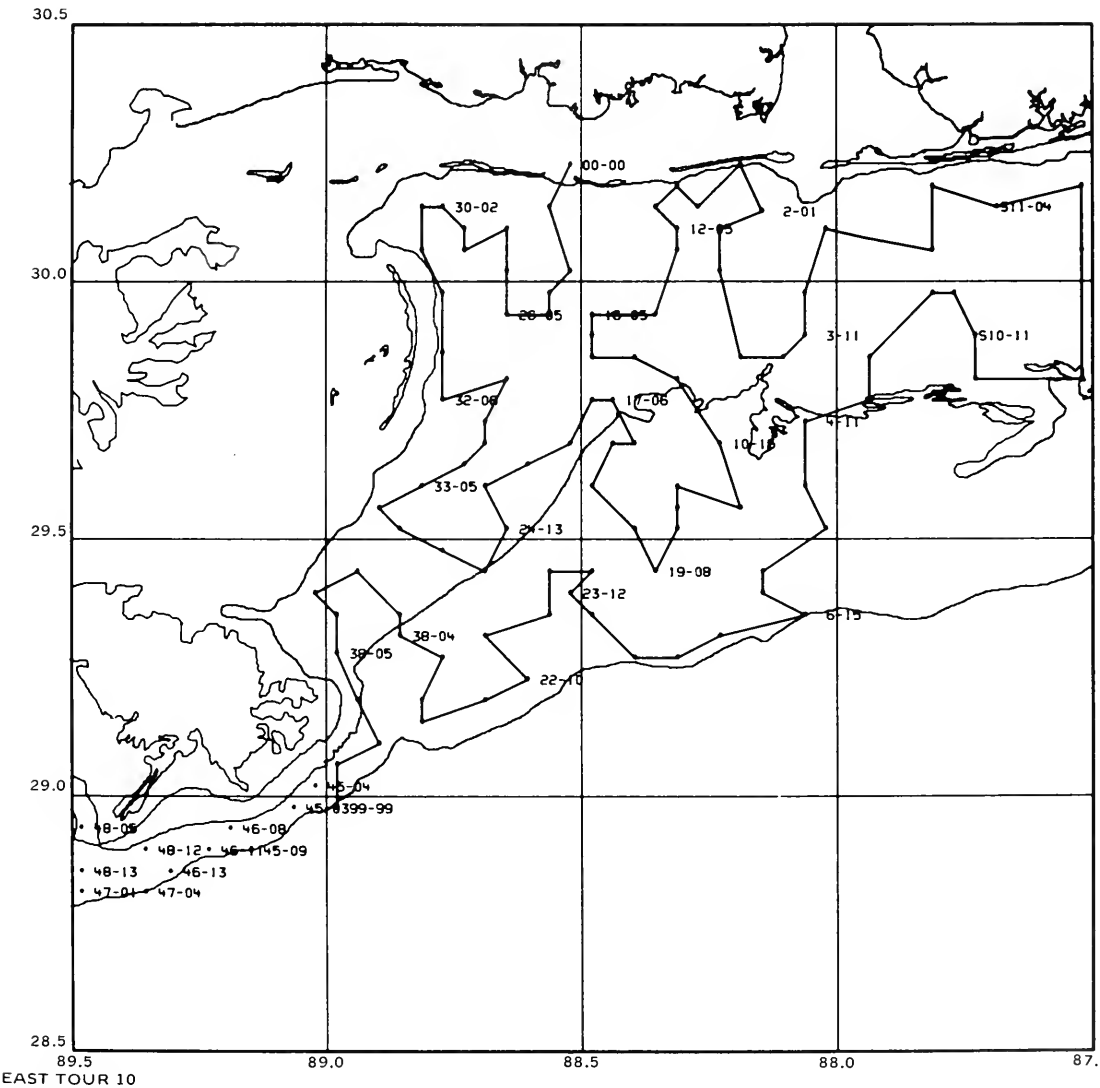

FIGURE 7.—Optimized cruise track for East Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled. Station numbers listed at lower left are those not included in optimization calculations.

Discussion

The basic optimization program has the capability and inherent versatility to be utilized for a wide range of applications. The round-trip capability can be modified to a one-way path calculation as was done for the East Delta portion of the groundfish survey by manipulating the distance matrix. Cartesian integrity of the start-stop points is kept intact but the distance between the two stations is set equal to zero in the distance matrix. The program then calculates the optimum tour as if the start-stop points were very close together when, in fact, they are not.

There is no requirement that distance be the optimization parameter. Factors such as cost, time, or suitable weighted combinations of other variables could be used to compute a cruise track considered optimum for specific user requirements. Also, there is no requirement that the problem be symmetric or Cartesian in nature. For example, the distance (cost, time, etc.) in going from station A to station B need not be equal to that from station B to station A. Applications of these characteristics and other distance matrix manipulations include:

1) The "cost" in going from station to station in the presence of strong currents, such as the Gulf Stream, could be adjusted. "Downstream" directions from station to station would be given preferential status for computing the optimum cruise track.
2) In some situations, it may be desirable to group selected stations to be sampled preferentially as a subset or subsets of the total station pattern. This might occur if certain sampling areas had a higher priority than others because of biological and/or environmental considerations.
3) Actual curvilinear distances between stations could be entered into the distance matrix when sampling in areas near the coast. This would be done for station pairs connected by a straight line that passes across land.
4) If the number of stations exceeds the present 150 maximum allowable (300 with extended core storage), and it is possible to divide them into subgroups, the problem is limited only by CPU restrictions.

Many variations of the optimum cruise track theme could be solved with this program and the requirements are usually unique to a particular problem or investigation.[4] The examples demonstrate the types of problems that could be solved. Simple problems, such as those solved for the groundfish survey, can be improved about 7% over manually produced cruise tracks.

Improvements obtained using the optimized cruise track for the cited application are not dramatic, but would be significant over a long time period and/or extensive cruising distance. The program eliminates selecting stations from random number tables and hand plotting the cruise track, which may require several man-days

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[4]Inquiries regarding possible uses and applications of this system should be directed to the Director, Southeast Fisheries Center National Fisheries Engineering Laboratory, National Space Technology Laboratories, NSTL Station, MS 39529.

Notices

NOAA Technical Reports NMFS published during the first 6 mo of 1978.

Circulars

409. Marine flora and fauna of the northeastern United States. Copepoda: cyclopoids parasitic on fishes. By Ju-Shey Ho. February 1978, iii + 12 p., 17 fig.

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412. Synopsis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus). By Charles S. Manooch III and William W. Hassler. May 1978, iii + 19 p., 12 fig., 7 tables. Also FAO Fisheries Synopsis No. 116. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00418-0.

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Special Scientific Report—Fisheries

719. Seasonal description of winds and surface and bottom salinities and temperatures in the northern Gulf of Mexico, October 1972 to January 1976. By Perry A. Thompson, Jr. and Thomas D. Leming. February 1978, iv + 44 p., 43 fig., 2 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00414-7.

720. Sea surface temperature distributions obtained off San Diego, California, using an airborne infrared radiometer. By James L. Squire, Jr. March 1978, iii + 30 p., 15 fig., 1 table, 90 app. fig. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00415-5.

721. National Marine Fisheries Service survey of trace elements in the fishery resource. By R. A. Hall, E. G. Zook, and G. M. Meaburn. March 1978, iii + 313 p., 5 tables, 3 app. fig., 1 app. table.

722. Gulf menhaden, *Brevoortia patronus*, purse seine fishery: catch, fishing activity, and age and size composition, 1964-73. By William R. Nicholson. March 1978, iii + 8 p., 1 fig., 12 tables.

723. Ichthyoplankton composition and plankton volumes from inland coastal waters of southeastern Alaska, April-November 1972. By Chester R. Mattson and Bruce L. Wing. April 1978, iii + 11 p., 1 fig., 4 tables, 1 app. table.

724. Estimated average daily instantaneous numbers of recreational and commercial fishermen and boaters in the St. Andrew Bay system, Florida, and adjacent coastal waters, 1973. By Doyle F. Sutherland. May 1978, iv + 23 p., 31 fig., 11 tables.

725. Seasonal bottom-water temperature trends in the Gulf of Maine and on Georges Bank, 1963-75. By Clarence W. Davis. May 1978, iv + 17 p., 22 fig., 5 tables.

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Data on fisheries subjects accessioned through NMFS by NODC during the first 6 mo of 1978.

Drift bottle, northwestern Gulf of Mexico, February 1962 to December 1963. Fifty data sheets in manuscript form. By R. F. Temple and John R. Martin, Gulf Fisheries Center, NMFS. Ref: NAPIS 78-0035.

This material is available from the National Oceanographic Data Center (D7514), National Oceanic and Atmospheric Administration, Washington, DC 20235.

ERRATA

Fishery Bulletin, Vol. 76, No. 2

Fletcher, R. Ian., "Time-dependent solutions and efficient parameters for stock-production models," p. 377-388.

1) Page 377, right column, line 4, correct line to read:
growth rate k and B_∞, Graham's formula for latent

2) Page 378, left column, Equation (2), correct equation to read:

$$\dot{P}(B) = c_1 B + c_2 B^n, \qquad (2)$$

3) Page 378, left column, line 14, correct line to read:
antecedents of this analysis appear there.

4) Page 378, right column, line 7, correct line to read:
by average effort $\bar{f}$ on the assumption that $F =$

5) Page 379, left column, the equation that immediately follows Equation (1a), correct equation to read:

$$k = \frac{4m}{B_\infty} \left[\equiv 4 \frac{\dot{P}_{\max}}{B_{\max}} \right].$$

6) Page 381, right column, line 4, correct line to read:
Equation (6), $\dot{B} = 0, F = F_1$ and $B = B_1$. If we now

7) Page 381, right column, line 28, correct line to read:
$F = 2m/B_\infty$; stock size $B(t) \rightarrow p$ (p being

8) Page 383, right column, Equation (15), correct equation to read:

$$\dot{B} = \gamma m \left[\frac{B}{B_\infty} \right] - \gamma m \left[\frac{B}{B_\infty} \right]^n - FB. \quad (15)$$

9) Page 383, Figure 5, caption under right figure, line 3, correct line to read:
$\dot{P}_{\max}$ in Equation (12)].

10) Page 385, left column, line 14, correct line to read:
then $B(t) \rightarrow p$ and $\dot{Y} \rightarrow m$, irrespective of initial con-

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.

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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.

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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.

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Contents–continued

Notices

GPO 796-049

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Vol. 76, No. 4

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

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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. 1104. 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.

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Fishery Bulletin

CONTENTS

Vol. 76, No. 4

Notes

(Continued on next page)

Seattle, Washington

1979

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POLLUTION-ASSOCIATED DISEASES AND ABNORMALITIES OF FISH AND SHELLFISH: A REVIEW

CARL J. SINDERMANN[1]

ABSTRACT

The relationship of disease and environmental stress is becoming increasingly well established with time. Human activities—particularly those that result in chemical additions to the coastal/estuarine environment—have increased the potential stresses on fish and shellfish inhabiting those areas. Circumstantial evidence for associations of pollutants with certain fish and shellfish diseases and abnormalities is accumulating.

This paper attempts to review and evaluate existing information about associations of diseases and marine environmental degradation. Emphasis has been placed on: diseases caused by contaminant stress and related facultative pathogens; stress-provoked latent infections; environmentally induced abnormalities; genetic abnormalities associated with mutagenic and other properties of contaminants; experimentally induced lesions; contaminant effects on resistance and immune responses; and pollutant-parasite interactions.

There are several diseases, particularly fin erosion and ulcers in fish and shell disease in crustaceans, for which a relationship with pollution seems evident, and there are a number of other diseases or abnormalities (such as certain neoplasms and skeletal anomalies) for which a relationship with pollution is indicated. Furthermore, there is some evidence that certain latent viral infections may be provoked into patency by environmental stress.

Disease is a constant concomitant of life for any species, normally removing individuals from the population continuously. Marine animals are, of course, subject to a wide spectrum of diseases of infectious or noninfectious etiology ("disease" can be defined in the broad sense as "any departure from normal structure or function of an animal" or as "the end result of interaction between a noxious stimulus and a biological system").

Disfunction and death due to the activity of infectious agents constitute the narrower, but often predominant concept of disease. *Infectious diseases*—caused by viruses, bacteria, fungi, protozoa, and other pathogenic organisms—are usually prime suspects in searches for causes of mortalities, often to the exclusion of other possible causes. *Noninfectious diseases* include such phenomena as environmentally induced skeletal anomalies, genetic abnormalities, physiological malfunctions caused by chemical environmental factors, metabolic disorders resulting from nutritional deficiencies, many forms of neoplasia, and a host of others (Sparks 1972). In many instances, it is probably the combination of an infectious agent and environmental stress that eventually causes mortality.

The distinction between "infection" and "disease" must be kept in mind. Most organisms are constantly hosts to potentially pathogenic microorganisms, but disease results from imbalance of the interactive system which includes virulence of the pathogen, resistance of the host, and effects of environmental stresses.

Infectious disease usually exists in an enzootic form, weakening or disabling individuals and rendering them more susceptible to predators or other environmental stresses. Occasionally, though, epizootics and mortalities comparable to the great plagues of the Middle Ages may sweep through animal populations. In marine species we have seen such massive epizootics result in the great herring mortalities of the mid-1950's in the Gulf of Saint Lawrence (Sindermann 1958), and the extensive oyster mortalities of the 1960's in the Middle Atlantic states (Sindermann 1968). These epizootics are triggered by a complex interplay of pathogen, environment, and host population. Considering only the environmental aspects of such outbreaks, any departure from normal conditions produces a degree of stress on the population, and may contribute to an increase in prevalence of a pathogen, or of facultative invad-

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FISHERY BULLETIN: VOL. 76, NO. 4, 1979.

ers. Some of these environmental factors are drastic changes in temperature, lack of adequate food, or overcrowding. Resistance of the host animal to the disease is, of course, intimately related to these stresses (Snieszko 1974).

Environmental stresses have been implicated in a number of fish and shellfish diseases, but are difficult to quantify. Even a definition of stress can be elusive. Selye (1950, 1952) defined stress as the sum of all the physiological responses by which an animal tries to maintain or reestablish a normal metabolism in the face of a physical or chemical force. Brett (1958) defined it as "A state produced by any environmental or other factor which extends the adaptive responses of an animal beyond the normal range, or which disturbs the normal functioning to such an extent that, in either case, the chances of survival are significantly reduced." Another definition which identifies stress as the product and not the cause of homeostatic change is that of Esch et al. (1975): "Stress is the effect of any force which tends to extend any homeostatic or stabilizing process beyond its normal limit, at any level of biological organization."

Human activity has introduced or has increased environmental stresses for fish in estuarine and coastal waters. We have, for instance, added pesticides and other synthetic chemicals which can, even in low concentrations, drastically affect the physiology of fish and shellfish, and with which the species may have had no previous evolutionary experience. We have added heavy organic loads, in the form of sewage sludge and effluents, which can produce anaerobic or low-oxygen environments and which are often accompanied by other contaminants such as heavy metals, that can interfere with enzymes of the fish and the food organisms they consume.

During the past decade, several diseases and abnormalities of fish and shellfish have been described that seem associated with pollutant stresses. These can be categorized and discussed as:

1. Diseases caused by contaminant stress and related pathogens;
2. Stress-provoked latent infections;
3. Environmentally induced abnormalities;
4. Genetic abnormalities associated with mutagenic and other properties of contaminants;
5. Experimentally induced lesions;
6. Contaminant effects on resistance and immune response; and
7. Pollutant-parasite interactions.

In the first and second categories a synergistic activity of chemical contaminants (or other form of pollutant stress) and an infectious agent seems to be a plausible explanation for at least some of the observed effects. In categories three and four, it is sometimes difficult to determine conclusively whether environmental contaminants act directly on target tissues or biochemical pathways, or if the genetic material is first affected, with subsequent changes in structure and/or function.

During the past several years there have been signs of increasing interest in relationships between marine fish and shellfish diseases and environmental pollution. Several conferences have been held recently, including the 1974 Symposium on Tumors in Aquatic Animals, held in Cork, Ireland; the 1975 Symposium on Sublethal Effects of Pollution on Aquatic Organisms, held as part of the 13th Pacific Science Congress in Vancouver, B.C.; and the 1976 Conference on Aquatic Pollutants and Biological Effects with Emphasis on Neoplasia, held in New York. The amount of relevant literature available for consideration within the title "pollution-associated diseases and abnormalities of fish and shellfish" is somewhat overwhelming. Even the list of books containing pertinent material is impressive (Dawe and Harshbarger 1969; Snieszko 1970; Ruivo 1972; Vernberg and Vernberg 1974; Koeman and Strik 1975; Ribelin and Migaki 1975; Dawe et al. 1976; Lockwood 1976; Kraybill et al. 1977; Vernberg et al. 1977). Additionally, significant recent reviews have appeared, for example, Rosenthal and Alderdice (1976) and McIntyre[2].

This paper attempts to summarize the present state of knowledge about possible associations of fish and shellfish diseases (infectious and noninfectious) with estuarine and coastal pollution. Much of the evidence for such associations is still circumstantial and is presented as such. The original literature on this subject, as for any pollution-related subject, is voluminous. The references cited here constitute only a small but, I hope, a representative fraction of the published information available. It should also be pointed out here that this paper does not consider

[2]McIntyre, A. D. (Convenor). 1976. ICES working group on pollution baseline and monitoring studies in the Oslo Commission and ICNAF areas. Report of the subgroup on the feasibility of effects monitoring. Int. Counc. Explor. Sea, Doc. CM1976/E:44, 36 p.

physiological and behavioral disorders, which might be included in a broad definition of disease.

Finally, in these introductory comments, it should be noted that to make any firm association of a disease with environmental pollution there are several basic requirements: 1) knowledge of the history of occurrence of the disease in a particular species in the geographic area of concern; 2) knowledge of the history of occurrence and levels of particular pollutants in that area; 3) a review of the biology, life history, and occurrence of the disease in other areas, in other species, and under different environmental conditions; 4) an intensive baseline survey of the current disease and pollution situation, with attention to statistical reliability of sampling; 5) laboratory and field experimentation with the principal objective of reproducing the disease by exposure to known levels of contaminants; and 6) resurveys of the disease and pollution levels over several years, looking for changes or trends. As will become apparent in this paper, these requirements have been fully satisfied for few if any of the diseases discussed.

DISEASES CAUSED BY CONTAMINANT STRESS AND RELATED FACULTATIVE PATHOGENS

Fin Erosion

Probably the best known but least understood disease of fish from polluted waters is a nonspecific condition known as "fin rot" or "fin erosion" (Figures 1, 2), a syndrome which seems rather clearly associated with degraded estuarine or coastal environments. Fin rot has been reported from the New York Bight (Mahoney et al. 1973; Ziskowski and Murchelano 1975; Murchelano 1975), California (Young 1964; Southern California Coastal Water Research Project[3]; Mearns and Sherwood 1974), Puget Sound (Wellings et al. 1976), Biscayne Bay and Escambia Bay in Florida (Couch 1974a; Sindermann et al. 1978), the Gulf of Mexico (Overstreet and Howse 1977), the Irish Sea (Perkins et al. 1972), and the Japanese coast (Nakai et al. 1973).

Fin rot seems to occur in at least two types: one in bottom fish, where damage to fins seems site-specific and related to direct contact with contaminated sediments, and another in pelagic nearshore species, characterized by more generalized erosion, but with predominant involvement of the caudal fin.

Recent quantitative surveys along the Middle Atlantic coast have disclosed high prevalence (up to 38%) of fin rot in samples of trawled marine fishes from the New York Bight. Thus far, 22 affected species have been found. While bacteria of the genera *Vibrio*, *Aeromonas*, and *Pseudomonas* were frequently isolated from abnormal fish, a definite bacterial etiology has not been established. Fin rot disease was significantly more abundant in the New York Bight Apex, the area of greatest environmental damage, than in any comparable coastal area from Block Island, R.I., to Cape Hatteras, N.C. (Murchelano and Ziskowski 1976). An association between high fin rot prevalence and high coliform counts in sediments is emerging (Mahoney et al. 1973), as is an association between high fin rot prevalences and high heavy metal levels in sediments (Carmody et al. 1973). The disease signs can be produced experimentally by exposure of fish to polluted sediments. Fin erosion has also been observed in striped bass, *Morone saxatilis*, overwintering in heated effluents of power plants in the Middle Atlantic States.

The histopathology of fin erosion in winter flounder, *Pseudopleuronectes americanus*, from the New York Bight was examined by Murchelano (1975). Significant descriptive findings were epidermal hyperplasia accompanied by dermal fibrosis, hyperemia, and hemorrhage. Bacterial infections were not found, nor was pronounced inflammatory response. However, reference was made to acute fin lesions seen in summer flounder, *Paralichthys dentatus*, in which bacteria were readily demonstrable. The absence of pronounced inflammatory response in either species of flounder led Murchelano to suggest that the necrotic process is not primarily microbial and that activities of a chemical irritant may be involved.

Another histopathological and bacteriological study of fin rot in winter flounder from Narragansett Bay, R.I., by Levin et al. (1972) described acute ulcerative lesions as well as fin erosion, thought to be produced by *Vibrio anguillarum*. Acute inflammatory response was observed, and ulcerations were reproduced in fish exposed experimentally to *V. anguillarum* isolates. It is possible that several poorly defined disease entities or

[3]Southern California Coastal Water Research Project. 1973. The ecology of the Southern California Bight: Implications for water quality management. Ref. No. SCCWRP TR 104, El Segundo, Calif.

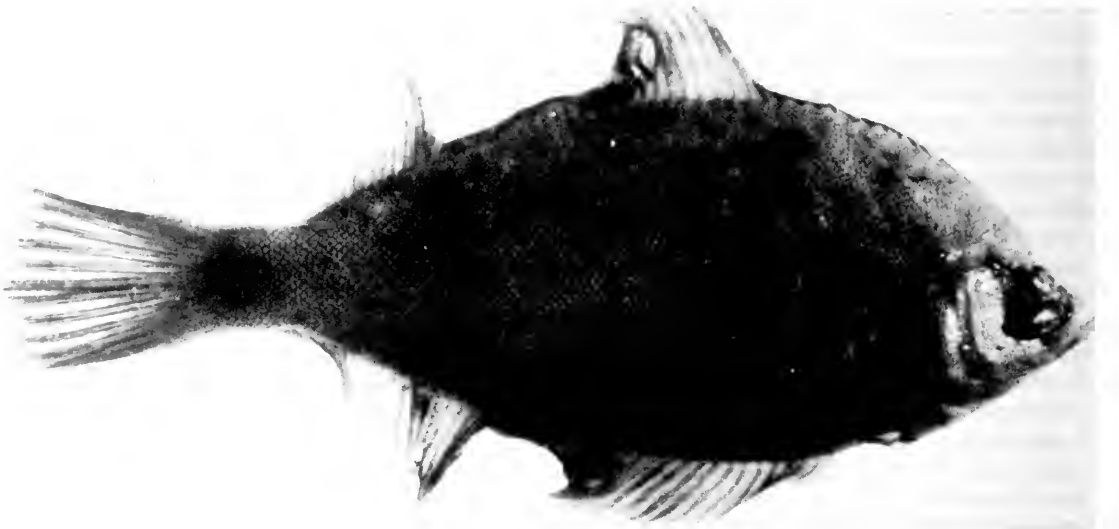

FIGURE 1.—Site-specific fin erosion concentrated in the midportion of fins in winter flounder (anterior dorsal fin is folded over in this picture). Note melanism in areas of erosion. (Photograph courtesy of J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, Highlands, N.J.)

generalized disease signs (one of which is fin erosion) may be responsible for the disparate nature of histopathological findings in this report, as compared with those of Murchelano (1975).

Fin rot, with associated mortalities, was reported by Couch and Nimmo (1974b) in Atlantic croaker, *Micropogon undulatus*, and spot, *Leiostomus xanthurus*, from Escambia Bay, Fla. The disease syndrome and mortalities were observed for several years during periods of high temperature and low dissolved oxygen. Escambia Bay has been polluted by the PCB (polychlorinated biphenyl), Aroclor[4] 1254, for a number of years (Duke et al. 1970).

Information from southern California (Southern California Coastal Water Research Project, see footnote 3) also indicates an association of fin rot with degraded habitats; relevant statements are: "The incidence of fin erosion was high in areas with high concentrations of waste water constituents in the sediments . . . ." "Although there is a definite association between fin erosion and waste water discharges, the causal factors are unknown." "Nearly half of the 72 species caught off the Palos Verdes Peninsula were affected with this syndrome" (eroded fins). It is interesting that a histopathological study of fin erosion in Dover sole, *Microstomus pacificus*, from the California coast (Mearns and Sherwood 1974; Klontz and Bendele[5]) produced findings similar to those of Murchelano (1975)—hyperplasia, fibrosis, absence of inflammation, and absence of microbial infection.

Some species either seem more resistant to fin erosion or are exposed differentially to toxic substances in water or sediments. A recent study by Wellings et al. (1976) in a heavily polluted arm of Puget Sound (the Duwamish River) in which over 6,000 fish of 29 species were examined, disclosed fin erosion only in starry flounder, *Platichthys stellatus*, and English sole, *Parophrys vetulus*. Average incidences were 8 and 0.5% respectively. Histopathological findings were similar to those for east coast and California flatfishes—epidermal hyperplasia, fibrosis, resorption of fin rays, aggregation of melanophores, mucus cell changes, and absence of bacterial invasion. The authors described briefly what may be highly relevant observations of liver pathology in starry flounder from the area where fin erosion was common. Histopathology included increased fat deposition in hepatic cells, fibrosis, and vascular distension.

Recent Japanese publications have mentioned fin erosion in fish from polluted bays. Nakai et al.

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

[5]Klontz, G. W., and R. A. Bendele. 1973. Histopathological analysis of fin erosion in southern California marine fishes. Southern Calif. Coastal Water Res. Proj., El Segundo, Calif., Rep. TM203, 8 p.

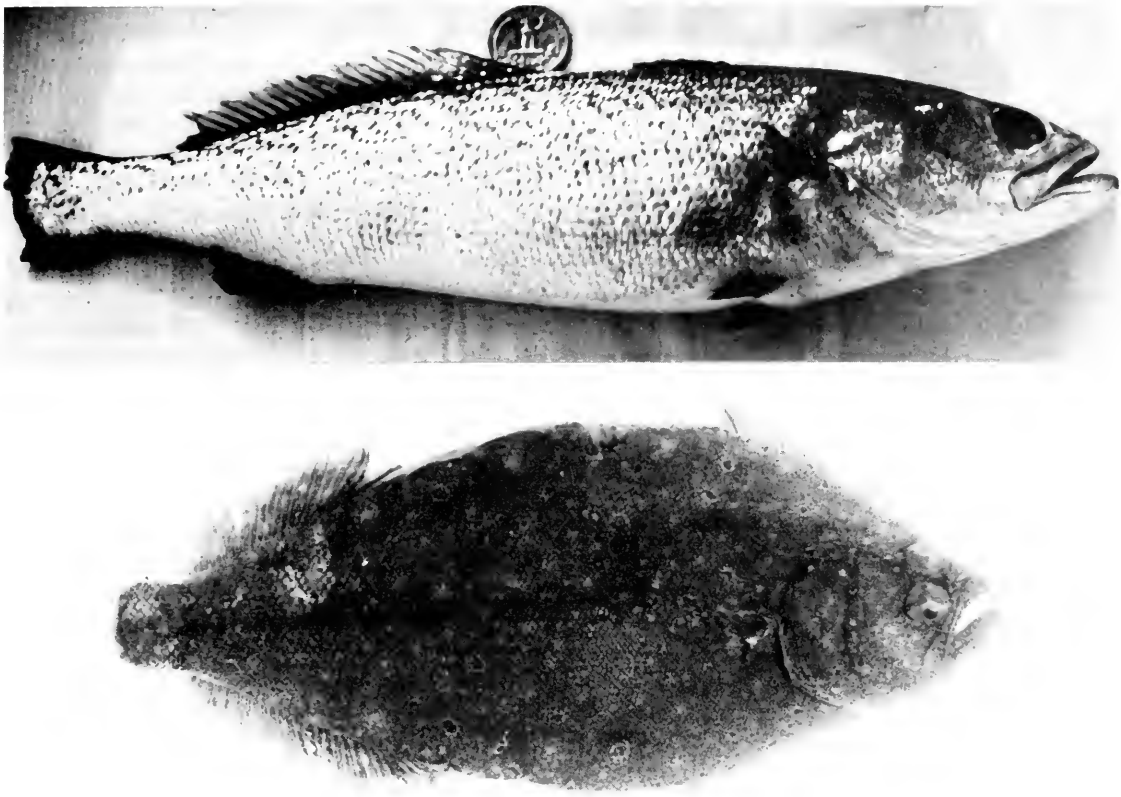

FIGURE 2.—Generalized fin erosion in weakfish, *Cynoscion regalis*, (above) and in summer flounder (below). Note that in the weakfish the anal, caudal, and pelvic fins are eroded, while the dorsal fins are not usually damaged. In contrast the summer flounder shows erosion of wide areas of the fin fringes.

(1973) found that as many as 60% of all stargazer, *Uranoscopus japonicus*, sampled from Suruga Bay had evidence of disintegration of caudal and pectoral fins. Six other species also had abnormal fins.

An increase in occurrence of fin erosion and other epidermal lesions (ulcers and lymphocystis) in flatfish from the Irish Sea since 1970 was reported by Perkins et al. (1972). Fin damage, unknown before 1970, was observed in plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, taking the form of erosion or total loss of caudal and lateral fins. Ulcers were described that "did not have the typical appearance of bacterial ulcers . . . ." The authors pointed to ocean dumping of toxic wastes, particularly of PCB's, as a possible factor contributing to observed prevalences of epidermal lesions, but no clear relationship was demonstrated. Another study conducted in the Irish Sea in 1972 (Shelton and Wilson 1973) did not identify fin erosion in plaice or dab, but did find a low incidence of "healed fin damage (probably caused by previous capture and rejection or by passage through the cod-end mesh)."

The possible role of environmental chemical contamination in the etiology of fin erosion emerges more clearly as additional studies are reported. Fish from the New York Bight, reported in studies by Mahoney et al. (1973), Murchelano (1975), and Ziskowski and Murchelano (1975), exist in a highly contaminated area, with chemicals such as heavy metals and petroleum residues in sediments far above background levels. In California, McDermott and Sherwood[6] fount DDT to be significantly higher in fish with fin erosion, and PCB levels slightly higher in such fish than in normal individuals. Both contaminants were significantly higher in Palos Verdes fish than in fish

[6]McDermott, D. J., and J. Sherwood. 1975. Annual report. Dep. Fish. Mar. Fish. Program, Coastal Water Res. Proj., El Segundo, Calif., p. 37.

from a distant control area (Dana Point). Wellings et al. (1976) found abnormally high concentrations of PCB's in English sole and starry flounders from the Duwamish River in Washington.

Several authors have postulated that fin erosion in flatfish may be initiated by direct contact of tissues with contaminated sediments. Mearns and Sherwood (1974) and Sherwood and Mearns (1977), for example, suggested that toxic substances (sulfides, heavy metals, chlorinated hydrocarbons, etc.) could remove or modify the protective mucus coat and expose epithelial tissues to the chemicals. Sherwood and Bendele[7] reported that Dover sole from the California coast with severe fin erosion produced much less mucus than normal fish.

It seems quite likely that the "fin erosion" syndrome in fish includes chemical stress, possibly acting on mucus and/or epithelium; stress resulting from marginal dissolved oxygen concentrations, possibly enhanced by a sulfide-rich environment; and secondary bacterial invasion in at least some instances. Some recent experimental information tends to support this hypothesis.

A series of experiments at the Gulf Breeze (Fla.) Environmental Research Laboratory of the U.S. Environmental Protection Agency, using the spot, resulted in experimental production of fin rot disease following exposure to 3-5 μg/l of Aroclor 1254 (Couch 1974a). Mortalities of up to 80% were reported.

Minchew and Yarbrough (1977) exposed *Mugil cephalus* in brackish water ponds (12‰) to 4-5 ppm crude oil and found that fin erosion developed in most of the exposed fish within 6-8 days. Lesions were often hemorrhagic, and a tentative *Vibrio* sp. was isolated consistently from surfaces of diseased fish, but was rarely found systemically. Fin regeneration characterized most experimental fish 2 mo after exposure. This experiment should be repeated and extended.

Experimental induction of fin erosion has followed exposure to several other contaminant chemicals. Chronic exposure of fingerling rainbow trout, *Salmo gairdneri*, to lead caused a variety of grossly visible abnormalities, including fin erosion (Davies and Everhart[8]); and chronic exposure of minnows (*Phoxinus phoxinus*) to zinc and cadmium resulted in similar abnormalities (Bengtsson 1974, 1975).

A recent report by Overstreet and Howse (1977) pointed to fin erosion and other abnormalities as indicators of gradually increasing pollution stress on the Mississippi gulf coast. Among other disease conditions noted by Overstreet and Howse was "red sore," characterized by hemorrhagic lesions beneath scales, occasional hyperplasia, and accompanying ciliate (*Epistylis* sp.) infestation of the body surfaces. The authors indicated that red sores now occur in many of the fish in some freshwater and low salinity areas of the gulf coast of Mississippi, a striking similarity to recent observations in Biscayne Bay, Fla., where many fish of many species now exhibit hemorrhagic lesions beneath the scales, a condition which was unknown a decade ago (Sindermann 1976). Red sores and associated mortalities have also been described by Rogers (1970, 1972) and Esch et al. (1976) from centrarchid fishes in freshwater reservoirs of the southeastern United States. The disease condition in freshwater seems clearly related to *Epistylis* infestation, probably abetted by secondary bacterial infections, particularly by *Aeromonas,* although there is still some question about which organism is the primary invader.

It seems likely that generalized disease signs, such as fin rot and red sores (and probably other epidermal lesions such as ulcerations, papillomas, and lymphocystis), may be characteristic of fishes resident in degraded habitats, where environmental stresses of toxic chemicals, low dissolved oxygen, and high microbial populations exist. The extent and nature of these external manifestations are probably variable with resistance of the particular species and the extent and nature of environmental degradation.

Ulcers

Next to fin erosion, probably the commonest abnormality reported from fish taken in polluted waters can be identified as "ulceration of bacterial etiology," even though precise bacterial etiology has not been demonstrated in every case. Where bacterial isolations have been made from ulcerated tissue, *Vibrio anguillarum* has been by far the most predominant organism, with pseudomonads and aeromonads in lesser abundance.

[7]Sherwood, M. J., and R. A. Bendele. 1975. Mucous production in Dover sole. Annu. rep., Coastal Water Res. Proj., El Segundo, Calif., p. 51.

[8]Davies, P. H., and J. H. Everhart. 1973. Effects of chemical variations in aquatic environments. III. Lead toxicity to rainbow trout and testing application factor concept. EPA-R3-73-011C, 80 p.

The report on ulcerations and fin rot in winter flounders from Narragansett Bay, by Levin et al. (1972) has been mentioned in the previous section. The acute ulcerative lesions were thought to be caused by *V. anguillarum* infections, and the ulcerative phase was reproduced in fish exposed experimentally to cultured *V. anguillarum* isolates.

A more recent report by Robohm and Brown (1977) described systemic bacterial infections and ulcerative lesions of the tail and dorsal muscles in summer flounder from Connecticut waters. A highly pathogenic *Vibrio* sp. was isolated, and experimental infections were produced by subcutaneous inoculation and by seeding holding tanks with bacteria at levels of 360/ml. Ulcers at the inoculation site and subcutaneous hemorrhages along the bases of fins characterized experimental infections (Figure 3). These observations resemble those of Levin et al. (1972) in winter flounder.

Ulcerations, probably of bacterial etiology, have been reported in fish of several species from the Irish Sea. Perkins et al. (1972) and Shelton and Wilson (1973) reported ulcers from European flounders (*Platichthys flesus*), dab, and plaice. Prevalences were low (1-4%) in most instances.

An "ulcer syndrome" in cod, *Gadus morhua*, from Danish coastal waters has been studied for several years and seems associated with localized areas of severe pollution (Jensen and Larsen 1976, 1977; Larsen and Jensen 1977a, b). *Vibrio anguillarum* and an *Aeromonas* species have been implicated (Sørensen 1977).

Ulcerations or external lesions on fish may, of course, have a number of causes other than bacterial infection. They may be due to net damage or other surface abrasions, or to predator attacks. Some protozoa (Myxosporida and Microsporida) can infect muscle or skin tissue and multiply to produce gross cysts. These infections mature to produce many characteristic microscopic spores, and in the process the overlying epidermis may be sloughed, producing ulcers with usually smooth borders (Figure 4). However, it seems to be a

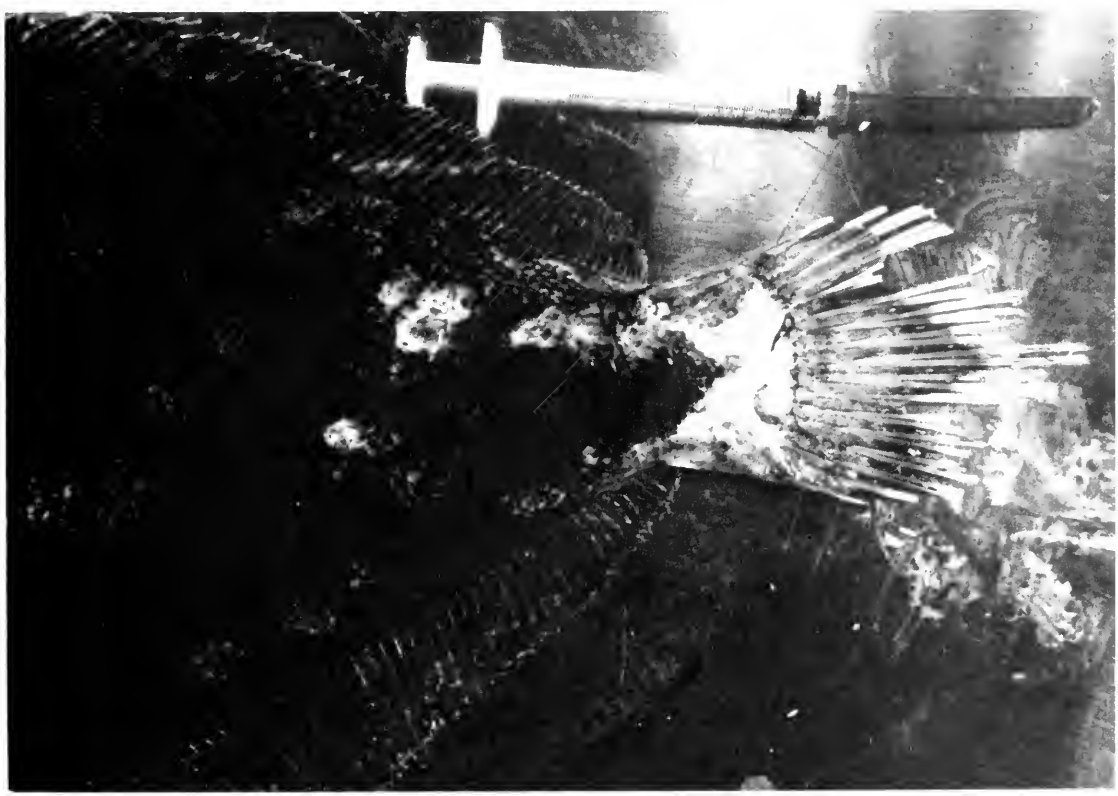

FIGURE 3.—Ulcers and fin erosion in summer flounder produced by experimental inoculation of *Vibrio* sp. (Photograph courtesy of R. Robohm, Northeast Fisheries Center Milford Laboratory, NMFS, NOAA, Milford, Conn.)

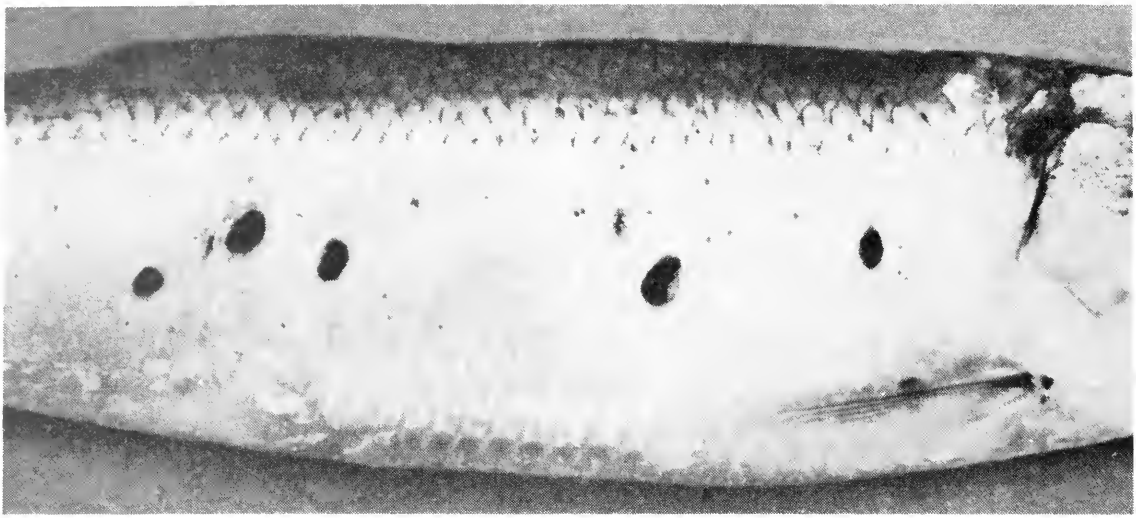

FIGURE 4.—Ulcer with smooth margins in Atlantic herring, resulting from infection by the myxosporidan protozoan, *Kudoa clupeidae*.

reasonable generalization that many of the infections that produce grossly visible ulcerations in fish are bacterial, and are often due to pathogens of the genera *Vibrio*, *Pseudomonas*, or *Aeromonas* (Lamolet et al. 1976). Ulceration often begins with scale loss or formation of small papules, followed by sloughing of the skin, exposing the underlying muscles, which may also be destroyed. Bacterial ulcers may have rough or raised irregular margins, and will often be hemorrhagic. Ulcers may or may not be associated with fin erosion.

Shell Disease of Crustacea

Also associated with badly degraded estuarine and coastal waters is a disease condition in Crustacea commonly referred to as "shell disease" or "exoskeletal disease" or "shell erosion." This can be considered in some ways as the invertebrate counterpart of fin erosion.

Homarus americanus and rock crabs (*Cancer irroratus*) from grossly polluted areas of the New York Bight were found to be abnormal, with appendage and gill erosion a most common sign, by Young and Pearce (1975). Skeletal erosion occurred principally on the tips of the walking legs, ventral sides of chelipeds, exoskeletal spines, gill lamellae, and around areas of exoskeletal articulation where contaminated sediments could accumulate. Gills of crabs and lobsters sampled at the dump sites were usually clogged with detritus, possessed a dark brown coating, contained localized thickenings, and displayed areas of erosion and necrosis. Similar disease signs were produced experimentally in animals held for 6 wk in aquaria containing sediments from sewage sludge or dredge spoil disposal sites. Initial discrete areas of erosion became confluent, covering large areas of the exoskeleton, and often parts of appendages were lost. The chitinous covering of the gill filaments was also eroded, and often the underlying tissues became necrotic.

Dead and moribund crabs and lobsters have been reported on several occasions by divers in the New York Bight Apex, and dissolved oxygen concentrations near the bottom during the summer often approach zero (Pearce 1972; Young 1973). Low oxygen stress, when combined with gill fouling, erosion, and necrosis, could readily lead to mortality.

In a related study, Gopalan and Young (1975) examined "shell disease" in the caridean shrimp, *Crangon septemspinosa*, an estuarine and coastal food chain organism common on the east coast of North America and important in the diets of bluefish, weakfish, flounders, sea bass, and other economic species. Examinations of samples of *Crangon* from the New York Bight disclosed high prevalences (up to 15%) of eroded appendages and blackened erosions of the exoskeleton. The disease condition was only rarely observed at other collecting sites (Beaufort, N.C., and Woods Hole, Mass.). Histological examination of diseased specimens produced findings similar to those of

Young and Pearce (1975) with crabs and lobsters. All layers of the exoskeleton were eroded; affected portions were brittle and easily fragmented; cracking and pitting of calcified layers occurred; and underlying tissues were often necrotic. Laboratory experiments using seawater from the highly polluted inner New York Bight resulted in appearance of the disease in 50% of individuals. Erosion was progressive, crippled individuals were cannibalized, and eroded segments of appendages did not regenerate after ecdysis. No disease signs developed in control animals held in artificial seawater.

A German study of the effects of industrial wastes on the brown shrimp, *Crangon crangon* (Schlotfeldt 1972), disclosed high prevalence of so-called "black spot disease," with signs very similar to those seen in *C. septemspinosa* from the New York Bight. Juvenile and adult shrimps from the Föhr Estuary had black areas of erosion on the carapace and appendages, with necrosis of underlying tissues, and, frequently, missing terminal segments of appendages. The disease condition varied in prevalence seasonally, with a peak of 8.9% in summer. Lesions persisted and worsened after ecdysis, and experimental exposure to detergent accelerated the course of the disease.

Shell disease of Crustacea has been observed in many species and under many conditions, both natural and artificial (Rosen 1970; Sindermann 1970). Actual shell erosion seems to involve activity of chitinoclastic bacteria, with subsequent secondary infection of underlying tissue by facultative pathogens. Initial preparation of the exoskeletal substrate by mechanical, chemical, or microbial action probably is significant; thus high bacterial populations and the presence of contaminant chemicals in polluted environments, as well as extensive detrital and epibiotic fouling of gills, could combine to make shell disease a common phenomenon and a significant mortality factor in crustaceans inhabiting degraded environments.

There is much room for study in this cloudy territory at the boundary between infectious and noninfectious disese processes, as exemplified by fin and shell erosion. This is the area where environmental stress and facultative microorganisms exert their impacts; where high bacterial populations in eutrophic waters interact with exposed, or injured, or chemically modified surface membranes; where epibiotic fouling organisms can assume pathogenic roles; and where nonspecific lesions such as fin rot and skeletal erosions can occur in epizootic proportions.

Lymphocystis

While fin erosion, ulcers, and shell disease seem to have reasonable associations with degraded environments, it is difficult to find additional good examples in the category of "Diseases caused by facultative pathogens." Probably the most likely candidate (in an obviously poor field) would be lymphocystis, a virus disease which causes extreme hypertrophy of fibroblast cells in a large number of freshwater and marine fishes, and which has been postulated to be associated with environmental stresses. Perkins et al. (1972) found in a 1971 survey that three diseases—lymphocystis, epidermal ulcers, and fin erosion—were abundant in plaice and dab from the Northeast Irish Sea. Lymphocystis infection levels in individual trawl catches ranged from 0 to 25% in plaice and from 0 to 17% in dab. The authors pointed out that the Irish Sea has been used recently for dumping of toxic wastes, particularly PCB's, but their concluding statement is "... there is insufficient evidence to be certain whether the increased incidence of the diseases noted in 1971 is the result of an outbreak of epidemics of purely biological origin or if the dumping of toxic wastes is responsible."

Another survey of lymphocystis in the Irish Sea, this one in 1972, was reported by Shelton and Wilson (1973). They found lymphocystis to be the most abundant of observable pathological conditions, with highest prevalence (14.6%) in flounder, *Platichthys flesus*, and lesser prevalences in other flatfish (1.9% in plaice and 1.1% in dab). Unlike Perkins et al. (1972), Shelton and Wilson considered recent pollution of the Northeast Irish Sea to be the least likely explanation for high levels of lymphocystis—pointing out that the disease has been known from that area for 70 yr, having been described early in the century by Woodcock (1904) and Johnstone (1905) from flounders taken in the Irish Sea. Van Banning (1971) studied lymphocystis in North Sea plaice (Figure 5) and also concluded that pollution was not a likely cause of high prevalences.

A recent lymphocystis epizootic with over 50% prevalence was reported from flatfish in the North Sea by Mann (1970) and earlier epizootics have occurred in Europe (Weissenberg 1965). Templeman (1965) reported an epizootic in American

FIGURE 5.—Lymphocystis in European plaice, *Pleuronectes platessa*. (Photograph courtesy of P. Van Banning, Rijkinstituut voor Visserijonderzoek, IJmuiden, Netherlands.)

plaice, *Hippoglossoides platessoides*, from the Grand Banks of Newfoundland. He suggested several possible explanations for the outbreak, including the possibility that the disease is enzootic in the population and may increase in intensity periodically. Earlier, Awerinzew (1911) found annual lymphocystis prevalences of 11% in *P. flesus* from the Murmansk coast, and Nordenberg (1962) found infections as high as 12% in the same species from the Öresund, with some indication of higher prevalence in the warmer months of the year. None of these outbreaks seems to have any apparent association with environmental contamination.

Lymphocystis has been reported recently in Baltic herring (*Clupea harengus* var. *membras*) by Aneer and Ljungberg (1976). Of the 2,629 individuals examined, 14 had gross signs of the disease. The authors pointed out that a number of infections were slight and might easily have been overlooked. It is quite likely that this is the case with other species also.

The presence of lymphocystis cells in the viscera of herring was noted by Aneer and Ljungberg, and there are several other reports of systemic lymphocystis infections, particularly that of Dukes and Lawler (1975) in which lymphocystis cells were found in and behind the eyes and in the kidney, spleen, liver, heart, ovaries, and mesenteries of silver perch, *Bardiella chrysura*, from the Mississippi coast.

Lymphocystis has also been recognized in 4.3% of yellowfin sole, *Limanda aspera*, sampled in the Bering Sea by Alpers et al. (1977a) and in 68% of winter flounder sampled in 1975 from Casco Bay in the Gulf of Maine (Murchelano and Bridges 1976).

Despite inconclusive attempts to relate lymphocystis epizootics in flatfish to specific environmental factors, including pollutants, there are recent observations of the disease in fishes of the Gulf of Mexico that reopen the issue. Christmas and Howse (1970) found lymphocystis in Atlantic croaker and sand seatrout, *Cynoscion arenarius*, from the Mississippi coast of the Gulf of Mexico and observed that "The pollution load was much greater in estuarine systems where lymphocystis was encountered." However, only 12 infected fish were found in a 10-mo trawling survey with monthly collections at 35 stations, which is not overwhelming evidence for a relationship of the disease to pollution. In a later study, Edwards and Overstreet (1976) reported marked increases in lymphocystis incidences in Atlantic croakers from the Mississippi coast, with as high as 50% infected fish in some trawl collections. Increased prevalences of another strain of lymphocystis were also observed in silver perch. In a later paper Over-

street and Howse (1977) stated that (with reference to the silver perch strain) "prevalence appears to relate to rainfall, suggesting that toxicants, salinity, or enriched water could play a major role in infections."

Lymphocystis in striped bass, *Morone saxatilis*, on the U.S. east coast seems to have some tenuous association with heated effluents. Recent unpublished observations by staff members of the Sandy Hook Laboratory (J. S. Young, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732. Pers. commun., September 1975), pointed to high prevalence of lymphocystis disease (Figure 6) in limited samples of striped bass overwintering in the heated effluent of a Long Island generating station (Northport, N.Y.). This disease is considered rare in striped bass (Anonymous 1951; Krantz 1970), and its unusual abundance in a localized population may well be related to the abnormally high winter temperature regime in which the population exists, or to abnormal crowding, with consequent increase in stress and ease of transfer of the pathogen. The high temperature may promote survival or transfer of the pathogen, or lower resistance of the host, or provoke latent infections into patency, resulting in grossly recognizable stages of infection. Lymphocystis is considered to be highly infectious; initial lesions often develop where injuries to the fish have occurred; and lymphocystis virus reaches peak infectivity when water temperatures are high (Midlige and Malsberger 1968). Some or all of these factors may be important in fostering the high prevalences observed in striped bass. An important concern about fish diseases such as lymphocystis in populations overwintering in heated effluents is that a focus of infection will be provided for incoming spring migrants.

STRESS-PROVOKED LATENT INFECTIONS

A number of microbial diseases of fish have been shown to be provoked into patency by environmental stress (Wedemeyer 1970; Snieszko 1974). This seems to be true for kidney disease and furunculosis of salmonids, which often exist in carrier or latent states that can develop into active infections if fish are stressed. It is also probably true for anaerobic bacterial (*Eubacterium* sp.) infections of mullet and 10 other species of fish from Biscayne Bay (Udey et al. 1977). A report of vibriosis in eels held in freshwater (Rødsaether et al. 1977) suggested that latent infections with *Vibrio anguillarum* produced disease and mortalities when eels were exposed experimentally to 30-60 μg/l copper for 50 days in freshwater. Similarly an epizootic of *Aeromonas liquefaciens* (= *A. hydrophila*) in Atlantic salmon, *Salmo salar*, and the sucker, *Catostomus commersoni*, in the Miramichi River, Canada, seemed to be related to combined stresses of copper and zinc pollution and high water temperatures (Pippy and Hare 1969).

FIGURE 6.—Lymphocystis disease in striped bass from heated effluent of a power plant.

Snieszko (1962) stated, concerning *A. liquefaciens* that "... fish may have latent infections that flare up when the fish are exposed to stress."

There are recent published accounts of two viral diseases of marine invertebrates which also indicate that latent infections may be provoked into patency by environmental stress. One, a *Baculovirus* infection of pink shrimp, *Penaeus duorarum*, was first recognized in stressed laboratory populations (Couch 1974b, 1976). The other, a herpes-like viral infection of oysters, was discovered in a population held in a heated power plant effluent in Maine (Farley et al. 1972).

An association of shrimp virus disease and low-level chronic exposure to pollutant chemicals is being explored at the Gulf Breeze Environmental Research Laboratory of the U.S. Environmental Protection Agency (Couch 1974a, 1978). In this work a virus disease of pink shrimp caused by *B. penaei* reached patent levels and caused mortalities of 50-80% in shrimp exposed to the PCB Aroclor 1254 and to the organochlorine insecticide Mirex (Couch and Nimmo 1974a, b; Couch 1974a, b, 1976). Other experiments in which the shrimp were crowded, but not exposed to chemicals, resulted in similar enhancement of virus infections, indicating that environmental stress may be an important determinant of patent infections. The virus infection has been found subsequently in brown and white shrimp (Overstreet and Howse 1977; Couch 1978).

Couch and Courtney (1977) have recently proposed an elaborate and unique conceptual scheme to utilize the shrimp virus for interactive bioassays for chronic sublethal effects of contaminants. The authors point out that there are a number of possible interactions of host, pathogen, and chemical stressors—change in resistance of shrimp to the virus, enhancement of widespread latent infections in the shrimp population, change in virulence of the virus, and losses of diseased shrimps by cannibalism. Criteria developed by Couch and Courtney for interaction include increased viral prevalence in stressed populations (as indicated by numbers of inclusion bodies), increased infection intensity in stressed individuals, increased mortality in stressed populations, and greater cytopathic effects in infected and stressed individuals. The shrimp virus infection has great potential for elucidating effects of pollutants on host-pathogen relationships.

An association of high environmental temperatures with high disease prevalence (or disease enhancement) in molluscan shellfish sampled from thermal effluents has been made recently. Farley et al. (1972) described a lethal herpes-type virus disease of oysters held in heated discharge water in Maine. The disease, which apparently existed at a low enzootic level in oysters growing at normal low environmental temperatures (12°-18°C summer temperatures), seemed to proliferate in oysters maintained at elevated temperatures (28°-30°C) and to produce mortalities in those populations. Intranuclear inclusion bodies, containing viral particles, characterized advanced infections. Mortalities of oysters held at higher temperatures were correlated with greater prevalence of the viral inclusions. Elevated water temperatures were considered by the authors to favor spread of the infection or to activate latent infections, or both.

This evidence for a possible role of environmental stress in activating latent viral infections could hardly be termed overwhelming, since it is possible that new infections produce the effects discussed. However, the two viral diseases may provide an insight into the total effect of pollutant and other environmental factors on disease prevalence and disease-caused mortalities. The carrier state is often difficult to diagnose, but it may play a much larger role in the epizootiology of marine disease than can be demonstrated at present.

ENVIRONMENTALLY INDUCED ABNORMALITIES

Neoplasms (Tumors)

The terms "neoplasia" and "neoplasms," particularly as they concern lower animals, are difficult to define precisely. The Oxford Dictionary definition of neoplasm is "a new formation in some part of the body; a tumor." More elaborate definitions exist. Warren and Meissner (1971) defined a neoplasm as "a disturbance of growth characterized primarily by an unceasing, abnormal, and excessive proliferation of cells." Prehn (1971) defined neoplasia as "that form of hyperplasia which is caused, at least in part, by an intrinsically heritable abnormality in the involved cells." Although neoplasia has been studied most extensively in humans and laboratory mammals, the existence of tumors in fish and shellfish has been recognized for almost a century (the first oyster tumor, for example, was reported by Ryder in

1887, and Bonnet mentioned thyroid hyperplasia in fish due to iodine deficiency in 1883).

Circumstantial evidence associating environmental contamination with neoplasms (tumors) in fish has accumulated from a number of studies:

1. Lucké and Schlumberger (1941) described 166 catfish (*Ameiurus nebulosus*) with epitheliomas of lips and mouth, taken from the Delaware and Schuylkill Rivers near Philadelphia. The rivers were grossly polluted. Tumors of this type may result from mechanical, infectious, or chemical irritation. Catfish from other areas did not have a high prevalence of tumors. The authors did not exclude the possibility that the lesions were induced by chemical carcinogens in the water. The lesions developed into epidermoid carcinomas, some of which were invasive.
2. Russell and Kotin (1957) found 10 of 353 white croakers, *Genyonemus lineatus*, from Santa Monica Bay, Calif., with papillomas of lips and mouth. Fish were taken 2 m from an ocean outfall. No tumors were found in 1,116 croakers from unspecified nonpolluted waters 70 km away.
3. Cauliflower disease (epidermal papilloma) has been increasing in prevalence in eels (*Anguilla anguilla*) from the Baltic since 1957. The pattern of spread and high prevalence indicates an infectious process (viral arrays have been seen) or progressive accumulation of industrial contaminants such as fuel oil and smelter wastes (known to contain carcinogenic hydrocarbons such as benzopyrene and heavy metals such as arsenic).
4. Cooper and Keller (1969) reported that 12% of nearly 16,000 English sole from San Francisco Bay had epidermal papillomas, with as many as 33 tumors per fish. Incidence of tumorous fish in the northern part of the Bay was twice that in the southern part. The greatest concentration of industrial waste discharge, especially petrochemicals, existed in the northern part of the Bay. A later survey (Kelly 1971) failed to confirm the areal difference in tumor abundance.
5. Young (1964) found many small (10-15 cm) Dover sole from Santa Monica Bay with tumors. Fish above 15 cm did not have tumors. According to Young, numerous white croakers from Santa Monica and Los Angeles-Long Beach were found with papillomas of the lips, and papillomas were observed on tongue soles, cusk eels, and Pacific sanddabs. Such tumors were not seen by Young on fish from unpolluted areas, but Dover sole with epidermal papillomas have since been collected off Baja California as far south as Cedros Island (Sherwood and Mearns 1976). The prevalence of lip tumors in white croakers from Santa Monica and the Palos Verdes shelf has been <1% since 1970 (Mearns and Sherwood 1977).
6. Carlisle (1969) found "growths" frequent on white croakers and Dover sole from Santa Monica.
7. Sindermann (1976) found wartlike tumors histologically resembling fibromas in *Mugil cephalus* from Biscayne Bay in 1969-70 (Figure 7). Other fibrous tumors have been reported since then by Lightner (1974) and Edwards and Overstreet (1976) in mullet from the Gulf of Mexico.

From the foregoing, it is apparent that much attention has been given, and continues to be given, to the common occurrence of epidermal papillomas in a number of Pacific flatfishes (Wellings et al. 1964, 1965; Wellings 1969a, b). The tumors of English sole from the Pacific coast, for example, have been studied for almost half a century (Pacis 1932; McArn et al. 1968; Good 1940; Angell et al. 1975). Stich et al. (1976) in their review of fish tumors and sublethal effects of pollutants, found highest prevalences to occur in young-of-the-year fish. Maximum prevalences reported in the literature were 58% in English sole (Stich and Acton 1976); 55% in starry flounder (McArn and Wellings 1971); 15% in flathead sole, *Hippoglossoides elassodon* (Miller and Wellings 1971); and over 40% in sand sole, *Psettichthys melanostictus* (Nigrelli et al. 1965). A relationship of high frequencies of such papillomas with coastal pollution is still uncertain. Stich et al. (1976) stated "There seems to be a higher skin tumor frequency among English sole inhabiting areas of urban contamination (Vancouver) than among fish populations in regions remote from human activities . . . ."

In an extension of this study, Stich et al. (1977) reported prevalences of skin neoplasms in 1-yr-old English sole of from 20 to 70% in samples taken near eight cities on the Pacific coast, while prevalences did not exceed 0.1% in several samples taken on the British Columbia coast more distant from cities. However, Oishi et al. (1976) examin-

FIGURE 7.—Wartlike fibrous tumors in *Mugil cephalus* from Biscayne Bay, Fla.

ing prevalences of similar epidermal papillomas in flatfish from relatively unpolluted waters of northern Japan felt that a possible association existed between high tumor occurrence (up to 20% in certain samples) and parasitization of the flesh by a nematode, *Philometra mariae*, but then they suggested that the involvement of naturally occurring chemical contaminants as well as man-made pollutants must be considered in the etiology of flatfish neoplasms.

Wellings et al. (1977) found 1.0% of rock sole, *Lepidopsetta bilineata*, sampled in the still-unpolluted Bering Sea, with epidermal papillomas. Infections were widely distributed geographically, mostly in older individuals. The age distribution of infection was quite different from that in Puget Sound flatfishes, where predominantly younger fish are involved.

The etiology of skin tumors in English sole from the Pacific coast of North America was reviewed in a recent paper by Angel et al. (1975), with the conclusion that the cause is unknown, and may be multifactorial. Three stages of tumorigenesis were described in young-of-the-year English sole, beginning with angioepithelial nodules and progressing to epidermal papillomas and angioepithelial polyps. No conclusive role of an environmental carcinogen has been demonstrated; there seem to be subpopulation differences in disease prevalences; and electron microscopy has disclosed the presence of viruslike particles in cells of papillomatous fish (Wellings and Chuinard 1964), but attempts to isolate a viral agent have been unsuccessful.

To further complicate the story, an unknown cell type, called an "X cell," has been found in all three tumor stages in English sole. The cells may be parasitic, as was suggested by Brooks et al. (1969), and Alpers et al. (1977b), or they may be transformed host cells, analogous to lymphocystis cells, as was suggested by Angell et al. (1975). Angell et al. concluded by stating that "given the pervasiveness of certain pollutants, experimental evidence and further field studies will be necessary to clarify the relationship between tumorous flatfishes and pollution."

Another observation on the possible relationship of flatfish tumors and pollutants has been supplied by Mearns and Sherwood (1974). The distribution and abundance of skin tumors and fin

erosion were studied simultaneously in Dover sole from the California coast. Fin erosion was more common in specimens collected near major sewer outfalls, whereas tumorous fish were distributed more evenly throughout southern California coastal waters. The authors concluded that "The spatial and temporal distribution of tumor-bearing Dover sole suggest that initiation of the disease was not related to [municipal] wastewater discharges [in southern California]."

A recent report of neoplasms in the Atlantic hagfish, *Myxine glutinosa*, by Falkmer et al. (1977) suggested a possible relationship of PCB contamination and tumor prevalence. During a 5-yr (1972-76) study in Gullmar Fjord, Sweden, neoplasm prevalences, particularly hepatomas, decreased from 5.8 to 0.6%. PCB levels in livers of hagfish were appreciable (5 ppm), but the use of PCB was prohibited in 1971. Liver PCB levels in hagfish caught inside the fjord were five times higher than in those caught outside. However, the association of PCB contamination with liver tumors must be considered to be tenuous. Earlier reports of neoplasms in hagfish (Fänge et al. 1975; Falkmer et al. 1976) described remarkably high frequencies in Gullmar Fjord, but only low concentrations (0.5-1.0 ppm) of PCB in livers, and low environmental levels of PCB and other contaminants.

The role of environmental chemical factors in induction of neoplasms in shellfish is even less clear than for fish, but there is some limited information. Yevich and associates (Barry and Yevich 1975; Yevich and Barszcz 1976, 1977) have for a number of years examined the occurrence of neoplastic growths in the soft-shell clam, *Mya arenaria*, in relation to petroleum contamination. Gonadal and hematopoietic neoplasms were observed in animals collected from two chronically contaminated sites on the Maine cost, with prevalences up to 29% in certain samples. Yevich and Barszcz (1976) stated that "no tumors similar to those described [from the petroleum contaminated area] have been encountered in animals collected from any other area." They described the scope of their study as "several thousand animals from all coastal areas of the United States." Additional samples of clams from a number of other coastal locations are needed, as is a more precise description and confirmation of the neoplastic condition.

It is interesting that a counterpart study of soft-shell clams from Rhode Island and Massachusetts (Brown et al. 1976) reported occurrences of neoplasia, apparently of hematopoietic origin, in up to 26%, with the highest frequency in samples from a 1975 oil spill area near Bourne, Mass. A later report (Brown et al. 1977) included additional samples from other geographic areas. Neoplasms of gonadal origin, similar to those reported by Yevich and associates, were found in clams from an oil-contaminated site at Searsport, Maine. The highest prevalence of neoplasms of hematopoietic origin was 64%, in a small sample from Bourne. The authors pointed out, however, that clams from some oil-contaminated sites had no neoplasms, and stated that "These results suggest that the type and degree of hydrocarbon pollution are possibly related to the frequency of neoplasms and other lesions in *Mya*, but they are by no means the only causative factors."

Other types of cellular abnormalities have been reported from soft-shell clams. In earlier studies by Yevich and associates (Barry et al. 1971) atypical epidermal hyperplasia in gills and kidney was reported in up to 40% of clams sampled near Providence, R.I. Lesions occurred more frequently in large individuals, and seasonal changes were not observed. Lower prevalences were found in limited samples from Maine, Maryland, and California. Unlike the oil spill studies, no association with environmental factors was made by the authors.

Yevich and associates (Yevich and Barry 1969; Barry and Yevich 1972) have also described gonadal neoplasms in quahogs, *Mercenaria mercenaria*, from Narragansett Bay. Samples collected in 1968, 1969, and 1970 had tumor frequencies of 0.2, 2.3, and 2.7% respectively.

Epizootic neoplasms with a possible environmental etiology were reported from several molluscan species of Yaquina Bay, Oreg. (Farley 1969b; Farley and Sparks 1970; Mix et al. 1977). Blue mussels, *Mytilus edulis*, native oysters, *Ostrea lurida*, and two species of *Macoma* were affected, and winter mortalities were associated with the disease. Neoplasms have not been found in bivalve molluscs sampled elsewhere on the Oregon coast (Mix et al. 1977).

In another study (Christensen et al. 1974) similar epizootic neoplasms (up to 10% prevalence) were found in a localized population of the clam *Macoma balthica* from a tributary of Chesapeake Bay. The neoplasms were invasive and systemic, with initial foci in the gill epithelia. Holding experiments indicated that the disease was usually

fatal. The authors suggested, but did not demonstrate, an environmental contaminant etiology, possibly associated with bottom detritus. Other bivalve molluscs in Chesapeake Bay contain neoplasms. American oysters, *Crassostrea virginica*, were found with hematopoietic neoplasms (Farley 1969a; Couch 1969, Frierman 1976), and individual oysters have been reported to contain other types of neoplasms (Pauley 1969; Couch 1970).

Much of the evidence associating certain neoplasms of fish and shellfish with pollutants should be considered as circumstantial but provocative (Rentchnick 1976). Many of the neoplasms have been reported from bottom-feeding fish and detritus or filter-feeding bivalves, as was pointed out by Harshbarger.[9] Chemical carcinogens such as certain heavy metals and hydrocarbons can be concentrated in surficial layers of bottom sediments and can thus be readily available to animals inhabiting that zone. It should be noted, though, that a number of recent studies of neoplasms in fish and shellfish have found no obvious relationship between neoplasms and specific environmental factors.

Skeletal Anomalies

Skeletal anomalies, particularly those of the spinal column, are commonly observed in fish and are the subject of an extensive literature (see Hickey 1972, for a recent summary and Dawson 1964, 1966, 1971, and Dawson and Heal 1976 for a complete bibliography).

Such anomalies may be genetic, resulting from mutations or recombinations; epigenetic, acquired during embryonic development; or postembryonic, acquired during larval development, at metamorphosis, or during juvenile development (Hickey 1972). Spinal flexures and compressions, as well as vertebral fusions, have been observed in many teleost species, as have head and fin abnormalities. Evidence exists for a hereditary basis for some skeletal anomalies (Gordon 1954; Rosenthal and Rosenthal 1950), but other evidence points to effects of environmental factors such as temperature, salinity, dissolved oxygen, radiation, dietary deficiencies, and toxic chemicals. For example, increased percentages of abnormal embryos and larvae of Atlantic herring, *Clupea harengus*, resulted from experimental exposures to sulfuric acid waste water (Kinne and Rosenthal 1967) and to the algicides 2,4- and 2,5 dinitrophenol (Rosenthal and Stelzer 1970).

Recently, increased prevalences of skeletal deformities and anomalies, considered to be pollution-associated, have been recognized in a few fish species from southern California, the British Isles, and Japan. In studies carried out in California, skeletal deformities occurred with greater frequency in samples from areas with significant pollutant stress (Valentine and Bridges 1969; Valentine et al. 1973). Exposure of fry to very low concentrations of DDT (<1 ppb) produced anomalies in fin rays (Valentine and Soulé 1973).

Probably the most convincing observational evidence for environmental influences on induction of skeletal abnormalities in marine fish is that presented by Valentine (1975). Examining samples of barred sand bass, *Paralabrax nebulifer*, Valentine found significantly higher prevalences of anomalies, particularly gill raker deformities, in fish from the southern California coast (Los Angeles and San Diego) than from the Baja California coast. The anomalies increased in frequency and severity with increasing size of the fish and an association with disturbed calcium metabolism was suggested. The author pointed to the high chlorinated hydrocarbon and heavy metal levels which characterize the California coastal area (Schmidt et al. 1971; Galloway 1972), but emphasized that a causal relationship with increased prevalence of anomalies had not been established. However, Valentine's suggestion of a possible causal relationship between high environmental levels of chlorinated hydrocarbons and heavy metals, both of which are known to interfere with calcium metabolism, and skeletal anomalies in fish seems reasonable, in view of experimental evidence from a wide range of vertebrates (Ferm and Carpenter 1967; Lehner and Egbert 1969; Peakall and Lincer 1970; Pichirallo 1971; McCaull 1971; Galloway 1972).

Valentine (1975) referred briefly to additional observations on two other Pacific coastal species—California grunion, *Leuresthes tenuis*, and barred surfperch, *Amphistichus argenteus*—in which gill raker anomalies increased in frequency with age, and were "virtually restricted to [samples from] fishes from Southern California." This finding in three species reduces the likelihood that frequency differences could be attributable to

[9]Harshbarger, J. C. 1974. Activities report (of the) registry of tumors in lower animals 1965-1973. Smithson. Inst., Wash., D.C., 141 p.

inherited subpopulation differences in one of the three species studied.

While the deformed gill rakers were the most prevalent anomalies observed in southern California barred sand bass by Valentine, other abnormalities (pugheadedness, cranial asymmetries, deformed vertebrae, and fin anomalies) occurred and were associated directly in frequency and severity with gill raker deformity.

An analysis of vertebral deformities in herring taken in waters around the British Isles (van de Kamp[10]) indicated a slight but significant increase in prevalences from 1960 to 1975. The predominant abnormality was a cluster of two or three incomplete vertebrae located near the pelvic fins or anus. The highest percentages of abnormalities were found, according to the author, in areas "which probably had the highest degree of pollution." It was in these areas where prevalences also showed slight increases during the study period, supporting the author's hypothesis that vertebral deformities in herring can be related to "unusual substances" in the environment. However, van de Kamp concluded by stating that more experimental work on the causal relationship between pollution and deformities will be required.

Several reports from Japan refer to high and increasing occurrences of skeletal anomalies in fish. Komada (1974) and Ueki and Sugiyama (1976) observed increasing numbers of malformed sweetfish or ayu, *Plecoglossus altivelis*, in rivers and culture farms. Skeletal abnormalities in mullet and eight other species from the Inland Sea of Japan were reported by Matsusato (1973).

Deformed fin rays (Figure 8) and associated skeletal abnormalities have been observed repeatedly in winter flounders from the highly polluted waters of the New York Bight (Ziskowski et al. in press), and a summarization of observations on skeletal anomalies and related developmental defects has been published recently (Sindermann et al. 1978).

There is some evidence from studies of a few other fish species for an involvement of various kinds of environmental stress in the occurrence of skeletal anomalies. Gabriel (1944) noted anomalies in vertebrae of *Fundulus heteroclitus* due to temperature changes, and Mottley (1937) found anomalies in vertebral numbers of trout due to temperature (and possible oxygen). Hubbs (1959) found high prevalences of vertebral abnormalities in mosquitofish, *Gambusia affinis*, from Texas warm springs and concluded that the high temperature was responsible.

There is also an appreciable literature concerned with induction of skeletal injuries in fish by exposure to contaminants. Vertebral damage following experimental exposure to aquatic contaminants has been reported for a number of freshwater fishes (Bengtsson 1975). Long-term (10 wk) exposure of minnows (*Phoxinus phoxinus*) to sublethal concentrations of zinc and cadmium resulted in hemorrhaging, spinal curvatures, and vertebral fractures, particulary in the caudal region, in up to 70% of individuals. Spinal curvatures and muscle atrophy were produced in rainbow trout by chronic exposure to lead. It is interesting that caudal fin erosion was also observed in these experiments. In earlier studies, summarized by Bengtsson, exposure to sublethal concentrations of the chlorinated hydrocarbon Toxaphene as well as to Malathion, parathion, and certain other organophosphorus pesticides produced vertebral damage or spinal flexures in several fish species. Vertebral damage was considered to have a neuromuscular origin, or, in the case of long-term exposure, to be a consequence of demineralization.

John Couch and associates at the Gulf Breeze Environmental Research Laboratory of the U.S. Environmental Protection Agency are developing experimental evidence for induction of skeletal abnormalities by exposure to environmental contaminants. Couch et al. (1977) reported severe scoliosis and associated pathology in the sheepshead minnow, *Cyprinodon variegatus*, exposed to the organochloride pesticide Kepone. The authors concluded that scoliosis was a secondary effect of Kepone toxicity, with the nervous system or calcium metabolism as the primary target.

Couch and associates (J. A. Couch, Research Pathologist, Environmental Research Laboratory, U.S. Environmental Protection Agency, Gulf Breeze, FL 32561. Pers. commun., June 1977) have also found that trifluralin (Treflan) induced extensive osseous hyperplasia in vertebrae of sheepshead minnows when life history stages from zygote to 28-day juveniles were exposed to 25-50 ppb trifluralin. Centra of vertebrae, thickened by active osteoblasts and fibroblasts, increased in size up to 10-30 times their normal dimensions—a striking sublethal effect.

[10]van de Kamp, G. 1977. Vertebral deformities in herring around the British Isles and their usefulness for a pollution monitoring programme. Int. Counc. Explor. Sea, Fish. Improv. Comm., Doc. CM1977/E:5, 9 p.

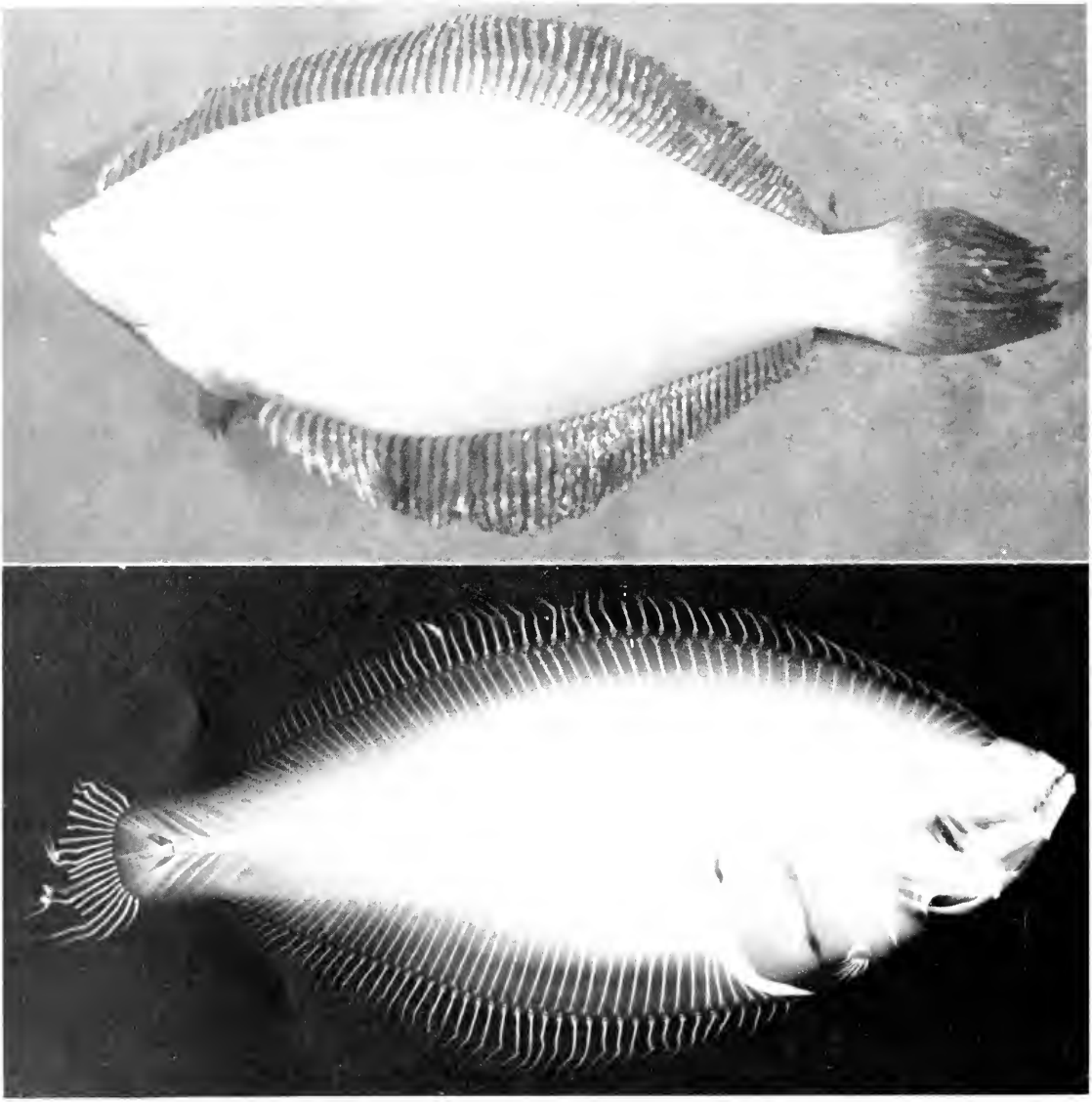

FIGURE 8.—Deformed fin rays in winter flounder from New York Bight. External appearance (above) and radiograph (below). (From Sindermann et al. 1978.)

GENETIC ABNORMALITIES

The mutagenic properties of a number of chemical contaminants including heavy metals, pesticides, and petroleum-derived polycyclic hydrocarbons have been demonstrated in experimental studies with terrestrial animals (Huberman 1975; Longwell[11]). Fish eggs can be vulnerable to contaminant effects from the body burden of the parent female and from exposure to contaminants in surface water and/or sediments (depending on where in the water column spawning and development occur). Sperm cells are sensitive to contaminants, and eggs are especially sensitive during meiosis and early cleavage stages. Furthermore, chemical mutagens can reduce the rate

[11]Longwell, A. C. 1975. Mutagenicity of marine pollutants as it could be affecting inshore and offshore marine fisheries. Middle Atl. Coastal Fish. Cent., Natl. Mar. Fish. Serv., Inf. Rep. 79, 72 p.

of cell division and can damage the mitotic spindle apparatus. Pelagic eggs may be most severely damaged, since the surface film of the ocean has been found to contain high concentrations of contaminants such as petroleum components, halogenated hydrocarbons, and heavy metals (MacIntyre 1974).

Some experimental evidence is available. Fish larvae incubated in cadmium-polluted water accumulated the metal (Westernhagen et al. 1974; Rosenthal and Sperling 1974), and eggs incubated in as little as 1 ppm cadmium produced low percentages of viable larvae (Westernhagen et al. 1975; Westernhagen and Dethlefsen 1975).

Some relevant experimental research on radionuclide-induced mutagenesis (Romashov and Belyayeva 1966; Ivanov 1967; AEC-TR-7299[12]) has disclosed that many fish embryos with severe chromosomal damage died during the transition from blastula to gastrula. Abnormal postgastrula embryos contained higher numbers of chromosomal aberrations than normal embryos, and the abnormal embryos had high mortality just before hatching. However, even the normal-appearing embryos with radiation exposure (and consequent genetic disturbances) had low viability and high mortality at hatching and subsequent to hatching.

Recently, Longwell (1976a, b) reported high prevalences of chromosomal anomalies in Atlantic mackerel, *Scomber scombrus*, eggs and embryos in certain samples taken from the New York Bight. All degrees of chromosomal damage were found, including failure to align at the metaphase plate, incomplete spindle formation, translocation bridges, chromosomal "stickiness," losses of portions of chromosomes and "pulverization." Eggs with at least one chromosome or mitotic abnormality varied from 13 to 79%. Higher percentages seemed associated generally with degrees of environmental degradation. In addition to chromosomal anomalies, one station (the one with highest prevalence of anomalies) was also characterized by significant (26%) egg mortality.

The techniques developed by Longwell (1976b) permitted examination of historical collections of eggs and embryos for chromosomal damage. A limited collection taken in 1966 from the same geographic area disclosed a lower incidence of cytogenetic abnormalities than that found in the 1974 collection.

Samples examined to date from normal and degraded waters are still insufficient, as Longwell (1976b) pointed out, to make definitive statements about the relationship of pollutants and extent of damage to genetic material, but the data presented so far indicates that such a relationship may exist. Because of the implications of these findings in survival and abundance of economic marine species, it is particularly important that this kind of research be pursued vigorously. It may well be that a new and significant mortality factor for estuarine and coastal populations—increased genetic damage—may have been introduced with increasing chemical pollution.

It is likely that marine organisms will respond to mutagens in species-specific ways and with differing sensitivities. Some indication of this can be found in a recent paper by Vandermeulen and Lee[13] in which cultures of the alga *Chlamydomonas reinhardtii* were exposed to crude and refined oils (Kuwait crude, Saran Gach crude, diesel 25, and bunker C). No enhanced mutation rates (as detected by streptomycin resistance) were found after 3 wk of exposure (40-50 generations), a surprising finding, since the alga is susceptible to certain other known mutagens and since the test oils contain various polycyclic aromatics which are known mutagens. No cytological examinations were reported. The authors pointed out that concentrations of mutagenic components in the test oils may be low compared with concentrations used in cell and tissue culture to elicit enhanced mutation rates, and that extrapolation of laboratory results to the marine environment should be done very conservatively.

An indirect test for the presence of mutagens in the marine environment has been reported recently by Parry et al. (1976). *Mytilus edulis* were sampled from polluted and unpolluted waters of the United Kingdom, and extracts of their tissues were tested for ability to induce genetic changes in bacterial and yeast cultures. Significant increases in mutation rates for specific gene loci characterized cultures exposed to extracts of mussels from polluted waters, but not those from clean waters—providing evidence for the presence of mutagens that had been concentrated in the tis-

[12]AEC-TR-7299. Marine radioecology. 1972. (Distributed by NTIS, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22151.)

[13]Vandermeulen, J. H., and R. W. Lee. 1977. Absence of mutagenicity due to crude and refined oils in the alga *Chlamydomonas reinhardtii*. Int. Counc. Explor. Sea, Plankton Comm., Doc. CM1977/E:69, 5 p.

sues of mussels from polluted areas. The chemical nature of the mutagens was not identified, except that the mussels came from areas with heavy industrial pollution.

EXPERIMENTALLY INDUCED LESIONS

There is a vast and almost unmanageable amount of published information about the induction of various lesions in fish by experimental exposure to chemical contaminants (see for example Ribelin and Migaki 1975). A "lesion" may be defined generally as "any localized abnormal structural change in the body." Such a definition obviously includes too much, so the term can be reduced to encompass "those cellular and tissue changes, demonstrable histologically, that result from a disease process." Histopathology of fish and shellfish is still a developing science, and as such it still draws from human and veterinary (mammalian) pathology for its concepts and much of its terminology. Histopathology has been a basic tool in human medicine for some time, and a large amount of information is available about cellular responses to toxicants. A similar core of knowledge is being developed for fish and shellfish—relating cell and tissue changes to kinds and amounts of contaminants.

Early experimental exposures of estuarine and marine animals to contaminants usually had the purpose of determining lethal dosages, either from acute or chronic exposures. More recently, attention has been redirected to sublethal toxic effects—expressed in behavioral, physiological, or cytological responses to specific contaminants. An extensive literature exists concerning cell and tissue damage resulting from experimental exposure to contaminant chemicals. Generalizations that can be made are almost predictable: 1) increasing dosages, beyond a threshold level, produce increasingly severe tissue abnormalities; 2) particular contaminants often exert effects on specific target tissues; 3) principal target tissues seem to be gill epithelium, liver (or in the invertebrate, the hepatopancreas), and neurosensory cells; 4) specific lesions cannot usually be described as characteristic of any group or class of chemicals; and 5) effects that may be of chemical origin can be obscured by stress-provoked infections with facultative pathogens. Some information about experimental induction of fin erosion and skeletal abnormalities has been included in earlier sections of this paper, but because of the sheer volume of published information about other types of experimental lesions, it seems worthwhile to summarize some of the observations here.

Couch (1975) published a recent and excellent review of the histopathological effects of pesticides and related chemicals on the livers of fishes. The liver and fatty tissues of fish from natural waters are known to accumulate a number of chlorinated hydrocarbons (Duke and Wilson 1971), and experimental exposures of fish to pesticides result in high concentrations and greatest effects on the liver (Johnson 1968; Eisler and Edmunds 1969; Hansen et al. 1971; Eller 1971). Some of the observed liver histopathology includes:

Chlorinated hydrocarbon pesticides: Focal areas of parenchymal cell vacuolation and degeneration (Eller 1971), inflammation, and loss of glycogen and fat (Lowe 1965).

Clorinated hydrocarbon herbicides: Increase in connective tissue, massive focal necrosis (Cope et al. 1969), and loss of glycogen (Cope et al. 1970).

PCB's: Focal degenerative regions, parenchymal cell vacuolation and pleomorphism (Eller[14]), lipid accumulation in hepatic cell vacuoles, and leucocytic infiltration (Couch 1975).

Organophosphates: Edema, hyperemia, vacuolation, and necrosis of parenchymal cells (Eller, see footnote 14).

Carbamates: Hypertrophy and vacuolation of acinar cells (Couch 1975).

It should be noted that not all experimental exposures to pesticides, even for prolonged periods, necessarily caused demonstrable tissue pathology, but in many instances additional exposure experiments are needed (even though the literature as summarized by Couch (1975) seems voluminous). Couch pointed out that over 900 commercial pesticide formulations are in general use, and of these fewer than 30 have been tested for pathological effects on livers of fishes.

Pesticides can, of course, affect fish tissues other than liver. A summarization of general histopathological effects of pesticides on fish was published by Walsh and Ribelin (1975). Data from their own studies with coho salmon, *Oncorhynchus kisutch*, and lake trout, as well as from other

[14]Eller, L. L. 1970 and 1971. Annual reports. U.S. Bur. Sport Fish. Wildl., Fish Pestic. Lab., Columbia, Mo.

published work, led them to the conclusion that tissue changes observed as a result of exposure to an array of common pesticides were largely nonspecific, and therefore of limited diagnostic value. Their attempts to identify specific lesions as characteristic of any group or class of pesticides were described by them as "futile," but the amount of histopathological information presented in the paper is substantial, and their summarization of pathology produced by exposure to widely used pesticides is instructive.

DDT: Necrosis of hepatic cells; lymphocytic infiltration of intestinal lamina propria; possible degeneration of kidney tubules.
Carbaryl (Sevin): Intramuscular hemorrhages adjacent to vertebral column; atrophy of the lateral line musculature; myxomatous degeneration of fat; vacuoles within the optic tectum of the brain.
Malathion: Subcutaneous hemorrhages at the bases of pectoral fins.
Endosulfan (Thiodan): Hyperemia of intestine and brain; adrenal cortical hyperplasia.
2,4-D: Striking degree of brain hyperemia; hyperemia of intestine.
Atrazine: Marked edema of all tissues; changes in skin pigmentation.

It is interesting that Walsh and Ribelin (1975) (unlike Couch 1975) found liver changes in fish exposed to pesticides ". . . minimal and diagnostically unimportant . . . ." They also considered gill epithelial hyperplasia, gill hemorrhages, and lymphocyte reduction in the spleen to be nonspecific responses to stress and/or infection. They further pointed out that rapid autolysis of fish tissues after death rather than direct effects of pesticides might account for some reported histopathological findings. These are all points of importance in evaluating histological findings after exposure to any contaminant.

There are still other histopathological studies of the effects of pesticides on fish that disclose damage to neurosensory tissue. Epithelial necrosis was found in lateral line canals of killifish, *Fundulus heteroclitus*, that survived 96-h exposures to the chlorinated hydrocarbon methoxychlor at 25 mg/l (Gardner 1975). No damage to the mechanoreceptors was evident, but the radius of the canal lumina was reduced.

Pesticides can produce tissue pathology in invertebrates as well. Oysters exposed chronically to 3 ppb DDT, Toxaphene, and parathion exhibited variable lesions, including leucocytic infiltration or hyperplasia of the gonadal germinal epithelium, necrosis of digestive tubule epithelium, and edema (Lowe et al. 1971). In another study, chronic exposure of oysters to 5 ppb PCB produced atrophy of digestive epithelium, leucocytic infiltration, and degeneration of vesicular connective tissue (Lowe et al. 1972). Gill edema and progressive necrosis of filaments in the crustacean *Gammarus oceanicus* resulted from exposure to sublethal concentrations of PCB (Wildish 1970). Examination of pink shrimp, exposed experimentally to PCB's, disclosed a variety of nonspecific tissue changes, especially in the hepatopancreas (Couch et al. 1974). Histological changes included lysis of hepatopancreatic epithelium, nuclear pycnosis, vacuolization of secretory cells, and a variety of ultrastructural changes in absorptive cells.

The literature on experimentally induced lesions in estuarine/marine fish caused by exposure to heavy metals was reviewed recently by Gardner (1975) in a paper which also presented significant new information. His general conclusion was that sensory organ systems of some species are vulnerable to copper, mercury, and silver. Short-term exposure of the killifish to sublethal concentrations of copper resulted in degeneration of anterior lateral line and olfactory sensory tissues (Gardner and LaRoche 1973). Prolonged exposure to copper (copper chloride) resulted in hyperplasia or necrosis of sustentacular epithelium of the olfactory organs and necrosis of the epithelial lining of olfactory pits. Mercury (mercuric chloride) also produced severe degenerative changes in cells of the lateral line canals and olfactory organs of killifish, but without associated necrosis of supporting tissues. Exposure to silver produced histopathological changes very similar to copper. Cadmium (cadmium chloride), however, did not seem to affect the sensory tissues discussed above, at least in terms of causing demonstrable tissue changes. Cadmium exposure did result in transient thyroid hyperplasia and altered blood cell ratios in long-term exposures.

Experimental exposure of the cunner, *Tautogolabrus adspersus*, to cadmium caused pathological changes in kidney, intestine, hemopoietic tissue, epidermis, and gills (Newman and MacLean 1974). Necrosis of tubular epithelium of the kidney, sloughing of intestinal epithelium, hypertrophy and hyperplasia of gill epithelium, and decrease in mucus secretion were

the principal histopathologic findings. Mortality following acute exposures was attributed to renal failure. These results were similar in most respects to cadmium-induced pathology in killifish, reported earlier by Gardner and Yevich (1970).

Experimental cadmium exposures can cause gill lesions in shrimp, as reported in recent papers by Nimmo et al. (1977) and Couch (1977). Exposure of pink shrimp to 763 μg/l of cadmium for 15 days resulted in a "black gill" condition characterized by necrosis of all cell types in the distal gill filaments, with coincident appearance of black granules in the cytoplasm, and some hemocyte infiltration at the bases of the necrotic filaments. Couch suggested that the black deposits could be a metallic sulfide or even cadmium. He further pointed out that the distal filament tissue has been postulated to have detoxifying, as well as osmoregulatory and respiratory functions, so that cell death could result from cadmium filtration and accumulation as part of a detoxification process.

Zinc has been shown to be toxic for fish (see reviews by Skidmore 1964, 1970). Gill tissues can be destroyed in acute exposures, while chronic levels induce stress which may result in mortality and may also produce severe degenerative changes in the liver and kidneys (Crandall and Goodnight 1963). Synergistic activity of zinc with a wide range of environmental variables—other contaminant heavy metals, low dissolved oxygen, and temperature—has been demonstrated for a number of fish species (Doudoroff 1957; Lloyd 1960, 1961a, b). Resistance to zinc poisoning varies with individuals, with age, with degree of acclimatization, and with species (Jones 1938, 1940).

Histopathological effects of sublethal concentrations of copper on the winter flounder were described by Baker (1969). At dosages of 1,000-3,200 μg/l, the kidney hemopoietic tissue became necrotic; gill epithelium became disoriented; chloride cells increased in number and size; gill lamellar fusions occurred; and fatty metamorphosis of the liver was observed. Experimental concentrations were far above those levels expected in most marine environments (concentrations in polluted waters have been reported to reach 300μg/l by Fujiya (1960)).

An interesting study of pathology in American lobsters was made following disclosure of severe yellow phosphorus industrial contamination of Placentia Bay, Newfoundland (Aiken and Byard 1972). Experimental lobsters, exposed to phosphorus contaminated sediments in aquaria, exhibited degenerative changes in antennal glands and in all cell types in the hepatopancreas, as well as massive coagulation of hemolymph.

Experimental exposure to petroleum components and residues may also induce histopathological changes in fish. Hyperplasia of the olfactory sustentacular epithelium and degeneration of the olfactory mucosa of the Atlantic silverside, *Menidia menidia*, resulted from exposure to crude oil (Gardner 1975). Additionally, degeneration of the ventricular myocardium of the heart and pseudobranch secretory cells was seen. Soluble components of the crude oil also caused epithelial metaplasia, replacing the sensory epithelium of the olfactory organs by poorly defined cell types (Gardner 1975). Liver damage occurred in fish fed cyclopropenoid fatty acids (Malevski et al. 1974), but Brocksen and Bailey (1973) found no histopathology in chinook salmon and striped bass exposed to sublethal concentrations of benzene.

Histopathological effects of petroleum on bivalve molluscs are varied in the extreme. Effects, particularly on gill epithelium, have been observed by Barry et al. (1971), Jeffries (1972), LaRoche (1972), Clark et al. (1974), and Gardner et al. (1975). Fries and Tripp (1976) found damage to gill epithelium in hard (hard-shell) clams, *Mercenaria mercenaria*, exposed to as little as 1 ppm phenol. Vaughan[15], however, found little histopathology after chronic exposures of oysters to No. 2 fuel oil. Stainken (1975) found that exposure of soft-shell clams to No. 2 fuel oil at winter seawater temperatures (4°C) for 28 days had little histopathological effect, beyond signs of starvation (glycogen depletion and vacuolization of digestive diverticula cells), and a generalized leucocytosis, even at 100 ppm. No mortalities occurred, and exposure concentrations dropped rapidly, possibly because much of the oil was trapped in mucus as part of the mucociliary feeding mechanism, and ejected from the clam.

Experimental lesions are instructive in identifying target organs and tissues for particular contaminants, but they have numerous flaws when attempts are made to relate experimental findings to events in the natural (polluted) environment: 1) dosage levels are often beyond

[15]Vaughn, B. E. (editor). 1973. Effects of oil and chemically dispersed oil on selected marine biota - a laboratory study. Am. Pet. Inst. Publ. 4191.

maximum observed environmental levels; 2) usually single chemicals are tested, ignoring possible synergisms and antagonisms; 3) tests are often static acute rather than chronic exposures in flow-through systems; and 4) experimental animals are often under stress from the mere act of confinement.

These and other limitations of experimental studies degrade the evidence obtained to circumstantial when attempts are made to extrapolate findings to natural populations in polluted habitats. Despite this handicap, there is a large and useful literature on experimental lesions in fish and shellfish produced by chemicals which occur as contaminants in the coastal environment.

The presence of specific pollutants cannot be recognized by the occurrence of specific lesions, but a general description of pathological responses can be useful. Categories of pathological responses which should be considered in experimental studies are: 1)inflammation (acute and chronic); 2) degeneration (including edema, necrosis, and metaplasia); 3) repair and regeneration (proliferation, hyperplasia, and scar formation); 4) neoplasia (including consideration of cell origin, stage, and type—whether benign or malignant); and 5) genetic derangement (including chromosomal changes and skeletal abnormalities).

CONTAMINANT EFFECTS ON RESISTANCE AND IMMUNE RESPONSES

Suppression of immune responses by toxicants such as heavy metals and pesticides has been demonstrated repeatedly in mammals (Kolomiitseva et al. 1969; Hemphill et al. 1971; Khan and Hill 1971; Jones et al. 1971; Koller 1973; Street and Sharma 1975). Therefore, it might be expected that environmental pollutants could influence the ability of fish and shellfish to resist infection by reducing the effectiveness of external and internal defense mechanisms, and indeed there is some evidence that this is so. Changes in the principal external defenses—mucus secretion of fish and the epicuticle of Crustacea—have already been mentioned in connection with fin erosion and exoskeletal erosion. Some specific information is available about contaminant influences on internal defenses, principally through suppression of immune responses. Environmental stress from contaminants can affect internal resistance to infection in fish by causing a decrease in phagocytic activity (Wedemeyer 1970) or a decrease in antibody synthesis (Goncharov and Mikyakov 1971). Both mechanisms have been demonstrated experimentally.

One of the best pieces of supporting information about suppression of host responses was derived from a recent multidisciplinary experimental study of the effects of short-term sublethal exposures to cadmium on the teleost *Tautogolabrus adspersus* (Calabrese et al. 1974). The study included chemical analyses of tissue uptake, physiological and biochemical effects, histopathological changes, and effects on the immune system. Robohm and Nitkowski (1974), who were responsible for the immunology, found that exposure of fish to 12 ppm cadmium affected phagocyte response to foreign antigen, but not the humoral response. The rate of bacterial uptake in phagocytes of liver and spleen was increased, but the rate of bacterial destruction within the phagocytes was decreased significantly. No change was observed in the antibody response of immunized control and experimental fish as determined by hemagglutination techniques. The authors postulated that cadmium may prevent delivery of lysosomal substances to the phagocytic vacuole, or may inhibit the action of these substances on bacteria, but that cadmium does not seem to inhibit antibody synthesis by lymphocytic cells. The authors further suggested that cadmium and possibly other pollutants may affect fish populations by causing phagocytic dysfunction, reducing the resistance of fish to facultative and other pathogens.

The effect of sublethal copper exposure on the immune response of juvenile coho salmon, *Oncorhynchus kisutch*, was examined by Stevens.[16] At copper levels of 18 μg/l, agglutinin titers in fingerlings injected intraperitoneally with *Vibrio anguillarum* bacterin were significantly lower than those of controls. Copper exposure also reduced survival of coho salmon fingerlings during saltwater acclimation.

Reduction in immunological competence may well have been involved in observed outbreaks of vibrosis (*V. anguillarum*) in eels exposed to copper (Rødsaether et al. 1977) and in epizootics of *Aeromonas liquefaciens* (= *A. hydrophila*) in salmon and suckers exposed to copper and zinc pollution (Pippy and Hare 1969), although in

[16]Stevens, D. G. 1977. Survival and immune response of coho salmon exposed to copper. Environ. Prot. Agency - 600/3-77-031, 37 p.

neither instance were antibody titers determined. In the latter instance, *A. liquefaciens* is an ubiquitous water bacterium, but only causes disease and mortalities in fish with lowered resistance (Snieszko 1962).

Reduction in antibody response to injected virus was demonstrated by Perlmutter et al. (1973) in blue gourami, *Trichogaster trichopterus*, to result from overcrowding. The authors postulated that stressed fish released a pheromonelike immunosuppressive factor under crowded conditions. It is reasonable to expect that other types of environmental stresses could result in a similar response.

Among the invertebrates, indirect evidence for reduction of disease resistance caused by contaminant exposure is available and has already been discussed in previous sections on crustacean shell disease and shrimp virus disease. Direct experimental evidence however, is scarce. Fries and Tripp (1976) exposed hard (hard-shell) clams to phenol and found damage to gill and digestive tract epithelia—tissues which are considered important components of internal defense mechanisms. The authors suggested, but did not demonstrate, that phenol-treated clams may be more susceptible to microbial infections than normal ones. In other studies with invertebrates, Telford (1968, 1974) demonstrated that environmental stress affected blood glucose levels in *Homarus americanus* and crayfish, *Cambarus clarkii*.

POLLUTANT-PARASITE INTERACTIONS

Much has been said and much documentation exists about the role of environmental stress in induction, severity, and persistence of disease. Some of the best information about stress and disease in fish comes from studies concerned with aquaculture—where environmental factors such as temperature, oxygen, water quality, salinity, and diets clearly influence the course of disease and the impact of disease on cultured populations.

There is also a developing body of information, from experimental work as well as from field observations and surveys, about the possible relationship of parasitism and pollution. The relationship is not simple, and in essence involves a double-edged phenomenon, in which pollutant stress may result in an increase (or in some instances decrease) in the prevalence of certain parasites, or in which parasitization may decrease host resistance to toxic pollutants. Subsidiary issues quickly emerge however, such as the effects of pollutants on intermediate or alternate hosts in parasite life cycles, possible effects of pollutants on free-living life cycle stages of parasites, and effects of pollutants on host defenses against parasite invasion.

Thus far in this review, the role of microbial infectious agents, principally viruses and bacteria, has been emphasized, but there is some limited evidence that environmental pollution may change the relationships among animal parasites and their fish hosts (Esch et al. 1975).

Looking first at the influence of parasites on host susceptibility to contaminants, several recent papers (principally from studies in freshwater) offer significant insights. Boyce and Yamada (1977) found in laboratory experiments that sockeye salmon, *Oncorhynchus nerka*, smolts with preexisting parasitization by the intestinal pseudophyllidean cestode *Eubothrium salvelini* were more susceptible to zinc poisoning than unparasitized siblings. Similarly, Pascoe and Cram (1977) found that survival times of the threespine stickleback, *Gasterosteus aculeatus*, exposed to various concentrations of cadmium, were much shortened if the fish were parasitized by the larval cestode *Schistocephalus solidus*. Perevozchenko and Davydov (1974) found that juvenile carp parasitized by the intestinal cestode *Bothriocephalus gowkongensis* were more susceptible to DDT poisoning than were nonparasitized individuals. These results are not surprising, since fish already weakened by parasites would undoubtedly be less able to tolerate other environmental stresses. The nature and degree of parasitization of fish clearly must be considered in bioassays and in studies of effects of contaminants on fish and shellfish species.

Looking next at the reverse viewpoint, the influence of contaminants on parasite prevalence, definitive information is less readily available for marine species, but some information is available for freshwater species. Thermal loading was associated with changes in the distribution and abundance of two larval trematodes in mosquitofish (Aho et al. 1976). Similarly, thermal loading from a nuclear power plant was directly correlated with incidence of the ciliate *Epistylis* sp. and the bacterium *Aeromonas liquifaciens* (= *A. hydrophila*) in six species of centrarchids in South Carolina (Esch et al. 1976). Effects of ther-

mal effluents on parasitism of largemouth bass, *Micropterus salmoides*, by the acanthocephalan *Neoechinorhynchus cylindratus* were examined by Eure and Esch (1974). Parasite densities were significantly higher in fish from heated water during the winter months, a possible reflection of greater densities of larval parasites and intermediate host populations in the effluent. River pollution from domestic and industrial sources was considered to be a contributing factor in increased parasite burdens found in fish from areas of heaviest pollution in Poland (Dabrowska 1974).

For marine species, good evidence relating pollutants with changes in parasite abundance is scarce. Results of an extensive survey of external parasites and disease conditions in North Sea fish (Möller[17]) did not disclose clear-cut relationships between parasitism and pollution, although the higher prevalence of vibriosis and lymphocystis in southern sectors which are most polluted indicated a possible influence of pollution. Other factors seemed responsible for differential abundances reported for the larger external parasites.

Several parasites of estuarine fishes from the Gulf of Mexico were examined by Overstreet and Howse (1977) in a search for associations with environmental pollution. Samples of Atlantic croaker were collected in 1970-72, and again in 1975. Large variations in prevalences of helminth parasites occurred, but clear associations with pollutants and changes in pollutant levels were not established. A myxosporidan protozoan seemed to be more promising. Infections of sheepshead minnows by *Myxobolus lintoni* were very abundant in one polluted bayou of Mississippi, but were absent in seemingly healthy habitats.

The stalked peritrich ciliate *Epistylis* sp., mentioned in an earlier section in connection with fin erosion and red sores, seems to be related to high organic content and possibly other stresses in freshwater and brackish water habitats. The ciliate, together with secondary bacterial invaders (principally *Aeromonas liquifaciens* (= *A. hydrophila*), produces a hemorrhagic hyperplastic condition beneath the scales that is referred to as red sore (Overstreet and Howse 1977). The ciliate infests a wide range of fish species in low salinity waters of Mississippi, especially centrarchids, sheepshead, and black drum (the drum is a marine invader in brackish water). Secondary bacterial infections associated with the ciliate may become systemic, and mortalities may result.

In addition to field observations, there is some experimental evidence for a causal relationship between specific pollutant chemicals and fungus parasitization of fish and shellfish. In one study, oysters exposed to pesticides (DDT, Toxaphene, and parathion) became infected with a mycelial fungus that caused lysis of the mantle, gut, gonads, gills, visceral ganglion, and kidney tubules (Lowe et al. 1971). None of the control oysters became infected, indicating a role for one or several of the pesticides in altering the host-parasite relationships of the oysters and the fungus. Presence of fungus infections made it difficult to differentiate histopathological effects of pesticide exposure from those due to the parasite.

CONCLUSIONS

In considering pollution-associated diseases of fish and shellfish, a number of conclusions seem warranted:

1. Environmental stress from pollutants seems to be an important determining factor in several fish and shellfish diseases. Effects include direct chemical-physical damage to cell membranes or tissues, modification of physiological and biochemical reactions, increased infection pressure from facultative microbial pathogens, and reduced resistance to infection.
2. The multifactorial genesis of disease in marine species is becoming apparent, involving environmental stress, facultative pathogens, resistance of hosts, and latent infections.
3. Some circumstantial evidence for the role of environmental carcinogens in the etiology of neoplasms of fish and shellfish is accumulating, but at present definitive conclusions are not justified.
4. The presence of marginal or degraded estuarine/coastal environments may be signalled by the appearance of, or the increase in prevalence of a number of diseases, including fin erosion, "red sores," ulcers, and possibly lymphocystis in fish; by "shell disease" in crustaceans; and by certain neoplasms in bivalve molluscs, but an absolute cause and

[17]Möller, H. 1977. Distribution of some parasites and diseases of fishes from the North Sea in February, 1977. Int. Counc. Explor. Sea, Fish. Improv. Comm., Doc. CM1977/E:20, 16 p.

effect relationship has not yet been demonstrated for most of these diseases.

5. Among the most severe and persistent problems in establishing pollutant-disease relationships are: the absence of baseline information about the organisms and their habitats prior to pollution, the existence of multiple pollutants in many badly degraded waters, and the circumstantial nature of much of the evidence linking pollution and disease.
6. A number of viruses have been found in crustaceans and molluscs in recent years, and the pathogenic role of two of them (shrimp *Baculovirus* and oyster *Herpesvirus*) has been demonstrated by exposure to increasing environmental stress. Other latent virus infections of invertebrates may be identified by similar experimental methods.

The evidence for an association of pollution and disease presented in this paper (except for results of experimental studies) is largely circumstantial. When confronted with the hard question "Can you state positively that the disease condition seen in natural populations is caused by specific environmental contaminants?", the answer at present has to be "No." However, the weight of this circumstantial evidence, particularly for diseases such as fin erosion and ulcers, is such that it leads to the conclusion that associations do exist between pollutants and disease.

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VERTICAL DISTRIBUTION, DIEL VERTICAL MIGRATION, AND ABUNDANCE OF SOME MESOPELAGIC FISHES IN THE EASTERN SUBARCTIC PACIFIC OCEAN IN SUMMER[1]

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ABSTRACT

Vertical distributions of myctophid fishes and other components of the mesopelagic micronekton were determined during the summers of 1973-75 at two stations in the eastern subarctic Pacific Ocean. Stratified samples were collected with a multiple net Tucker trawl so that the entire water column extending to between 385 and 460 m could be sampled during a daytime or nighttime period; two to four day and night vertical series of samples were obtained each summer. Four species of myctophids made up 87% of the total fish catch: *Stenobrachius leucopsarus* and *Diaphus theta*, which performed diel vertical migrations of 300 m vertical extent; and *Protomyctophum thompsoni* and *S. nannochir*, which exhibited only slight diel variation in vertical distribution. Populations of each myctophid species tended to be vertically stratified by age or size with larger individuals occurring in samples taken progressively deeper. Two other major components of the micronekton were euphausiids and decapod shrimps, chiefly *Euphausia pacifica* and *Sergestes similis*; both species were conspicuous diel vertical migrators. Samples collected in horizontal hauls immediately following sunset showed that three migratory species, the two migratory myctophids and *E. pacifica*, were closely associated with the single migratory sound-scattering layer (12 kHz); *S. similis* lagged the ascent of the migratory scattering layer. A single, deep, nonmigratory sound-scattering layer corresponded closely to the distribution of *P. thompsoni* during both day and night. As in other subpolar oceanic waters, abundance and standing stock of myctophids were high—0.9 fish/m^2 and 0.37 g dry weight/m^2.

In 1973 we began a field study of some small mesopelagic fishes of the family Myctophidae, commonly known as lanternfishes or myctophids, in the eastern subarctic Pacific Ocean. The objectives of the study were to determine the vertical distribution and migration characteristics of the numerically dominant species, to document their feeding behavior, and to ascertain if the distributions of fish were in any way influenced by the distribution of their preferred prey. Myctophids are major components of the mesopelagic fauna throughout the world ocean, and in most areas they are sufficiently abundant and stratified in the water column to cause deep sound-scattering layers (Baird et al. 1974; McCartney 1976). Indeed, study of these fishes has been heavily oriented toward aspects of their distribution in relation to sound-scattering layers (e.g., Tucker 1951; Barham 1966; Taylor 1968; Holton 1969; Farquhar 1971; Baird et al. 1974), although some investigations emphasized aspects of biological and ecological significance, such as individual growth rates, seasonal changes in abundance, and association among species (e.g., Pearcy and Laurs 1966; Harrisson 1967; Lavenberg and Ebeling 1967; Smoker and Pearcy 1970; Badcock 1970; Clarke 1973; Pearcy et al. 1977). Much of the research on myctophids has, in addition, stressed description of the prominent diel vertical migrations which are apparently undertaken by almost all species.

In the few species studied in detail, both the occurrence and pattern of vertical migration vary with age or ontogeny. Larval myctophids are nonmigratory, spending day and night in near-surface waters (Ahlstrom 1959). Diel vertical migration is first evident at or shortly after metamorphosis and usually persists throughout the remaining life of the fish, although in very old fish, migrations may differ substantially in character from those of younger fish and may even be supressed (Nafpaktitis 1968). Apart from this variation with age, diel vertical migrations of myctophids seem to be relatively regular, on a day-to-day basis, and exhibit little or no seasonal variation (Pearcy and Laurs 1966; Halliday 1970; Pearcy et al. 1977). Among some species, however,

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there may be a portion of the population which does not migrate, while other members of similar size and age do migrate (Clarke 1973; Badcock and Merrett 1976; Pearcy et al. 1977).

Virtually nothing is known about the biological causes or consequences of these diel vertical migrations, either with respect to the myctophids or their environment. Marshall (1954) suggested that myctophids migrate into the surface layer each night in order to feed on zooplankton, which is usually most abundant in surface waters (Vinogradov 1968). As pointed out above, larval myctophids spend both day and night in the zooplankton-rich surface layer, but as the larvae grow they perhaps become more conspicuous to visual predators and, after metamorphosis, they descend to greater depths,returning to the surface layer only at night, if at all. Vertical migrations may indeed have evolved as a means of avoiding or minimizing predation, but it is unlikely that this hypothesis can be tested in the ocean.

On the other hand, it is practicable to investigate the feeding ecology of myctophid fish in relation to their migrations; for example, what types of prey the fish utilize, when and where in the water column the fish feed, and whether the vertical distributions of the fish are affected by the vertical distribution and abundance of their preferred prey. As necessary background for such a study, in this paper we present details of the vertical distributions of the numerically dominant species of myctophids in the eastern subarctic Pacific Ocean.

METHODS

Study Area

We conducted the investigation during three summer cruises in areas centered at lat. 50°N, long. 145°W (July-August 1973 and July-August 1975; Station P in Figure 1) and at lat. 51°N, long. 137°W (July 1974; Station Q in Figure 1). These stations lie within the hydrographic province designated the Central Subarctic Domain by Dodimead et al. (1963). We chose the subarctic region for ease of sampling and identifying the fish and zooplankton. For example, in an earlier meridional cruise from Kodiak, Alaska, to Honolulu, Hawaii (August-September 1972), we found that deep sound-scattering layers are fewer in number, shallower, and more intense in the subarctic region than in transition and subtropical waters (Frost unpubl. data). Apparently related to this, the subarctic myctophid fauna is a simple one; only a few species are abundant, and they are relatively shallowly distributed in the daytime (Taylor 1968). Further, the study area is an open ocean environment, outside the potentially complicating influences of coastal and transitional waters (cf. McGowan 1971) and is roughly in the middle of the latitudinal range of several species of myctophids. Finally, the zooplankton assemblage in subarctic waters is also less diverse than in lower latitudes, it is well known taxonomically, and relatively few species are abundant.

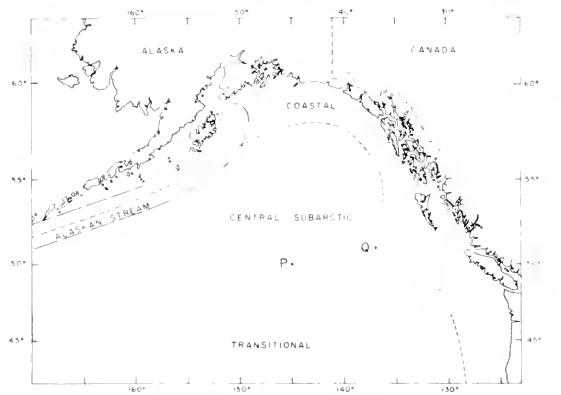

FIGURE 1.—Sampling stations in the eastern subarctic Pacific Ocean. Representative hydrographic domains for summer conditions after Dodimead et al. (1963).

Sampling Gear

Nekton samples were collected with a modified Tucker trawl (Tucker 1951) described by Frost and McCrone (1974). Briefly, the trawl had a rigid rectangular mouth with a 4-m^2 area when inclined forward at a 45° angle from vertical, and carried five separate nets (6.35-mm stretch mesh, knotless nylon ace netting) stacked one on top of another (much like fig. 4 in Harding et al. 1971). The net shape followed the design of Clarke (1969). The trawl carried an electronics package containing a strain gage pressure transducer (range 0-1,500 lb/in^2) for determination of depth and a precision pendulum-type tilt transducer (range 0°-90° from vertical) for determination of angle of inclination of the trawl mouth. A TSK (Tsurumi-Seiki Kosakusho)[3] flowmeter fitted with a magnetic

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

reed switch was mounted on the top beam of the trawl.

The trawl was towed on a two-conductor coaxial cable and its depth, angle of inclination of the mouth, and revolutions of the flowmeter were monitored continuously during trawling by means of a shipboard display unit. The nets were opened and closed at the mouth by means of a net-tripping assembly which was controlled electronically from the ship. The bottom net (without cod end) was left open during deployment to eliminate kiting of the trawl when a net was first opened (Clarke 1969; Badcock and Merrett 1976); thus, four sequential samples could be collected in one haul. The volume of water filtered by each net (assuming 100% filtration efficiency) was calculated from flowmeter revolutions and average angle of inclination of the net mouth.

To determine vertical distributions of fish and other components of the nekton, we towed the trawl obliquely and collected samples on the upward leg of a haul. We monitored the speed of the ship during trawling by reference to a Doppler ship's speed indicator.

Recordings of deep sound-scattering layers were obtained using an Edo-Western transducer operating at 12 kHz (pulse length 3-10 ms, beam width about 33°) and a Precision Depth Recorder (PDR) operating on the 0-400 fm (0-732 m) depth range scale. At the beginning of each cruise, echosounder characteristics (pulse length, power output) and recorder gain were set to give optimal resolution of the sound-scattering layer and were not varied thereafter.

Sampling Program

Taylor (1968) found a close correlation between distribution of abundant species of myctophid fishes and distribution of deep sound-scattering layers in the eastern subarctic Pacific near the Queen Charlotte Islands. Relying on this correlation, at each station we designed our sampling program after observing the depth and migrations of deep sound-scattering layers. The number, depth, and migration of scattering layers were virtually identical at Stations P and Q. We observed no differences between years at Station P, and our observations do not differ substantially from those of Bary (1967) who also used a 12-kHz echosounder in summer at Station P. In the daytime, a single, diffuse, sound-scattering layer extended from about 275 to 375 m depth (Figure 2A). In the late afternoon and early evening, this scattering layer became broader, chiefly by upward movement of the top of the layer, and it persisted with relatively little further change throughout the night. At about 2130 h (local time), a single, upwardly migrating layer became evident, and within half an hour it merged completely with the surface reverberation (Figure 2B). This migratory scattering layer began descent at about 0530 h and merged with the deep nonmigratory layer shortly after 0600 h. Slight variations in times of ascent

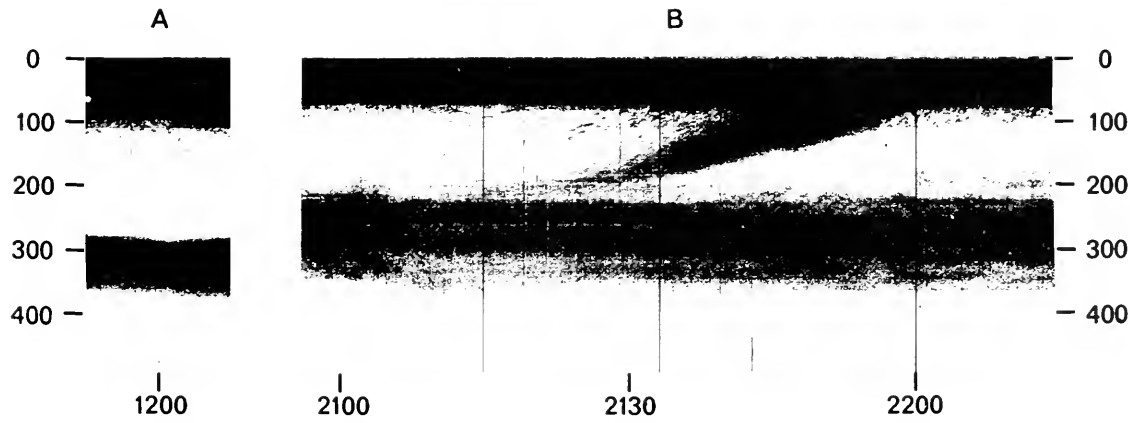

FIGURE 2.—12-kHz echograms typical of the summer period (July-August) in the sampling areas in the northeastern Pacific Ocean. A. Daytime record about noon, local time. B. Evening record taken on the same day showing the upward movement of the migratory sound-scattering layer and the persistence of the nonmigratory layer at depth. Local time, depth in meters. The dark areas above 100 m are due to surface reverberation.

and descent of the migratory sound-scattering layer depended on weather conditions; also, year-to-year differences are attributed to slight variations in time of cruises. We usually set the lower limit of nekton sampling at least 50 m below the depth of the deep nonmigratory scattering layer. With the exceptions noted below, nighttime sampling was confined to the time period between ascent and descent of the migratory scattering layer.

Somewhat different sampling programs were carried out in different years (Table 1). At Station P in 1973 the objective was to obtain information on vertical distributions of fish and zooplankton to aid in developing an optimal sampling strategy for studying diet and feeding behavior of myctophids. The 0-440 m water column was sampled in 55-m depth strata, and seven successive vertical series of samples, 4 night and 3 day series, were obtained. A shallow haul (0-220 m) and a deep haul (220-440 m) were required for each complete vertical series. The first nighttime series was not completed before the descent of the migratory sound-scattering layer. In order to obtain both the shallow and deep hauls during one night, the hauls were of relatively short duration, and consequently the nekton samples were relatively small.

At Station Q in 1974, the objectives were to confirm the vertical distributions found in 1973 at Station P and to document the feeding chronology of the common myctophids. The sampling for vertical distributions (Table 1) extended from the surface to between 400 and 460 m, depending on the depth of the deep sound-scattering layer, and usually included one sample collected below the scattering layer. Complete daytime vertical series (both shallow and deep hauls) of samples were collected on 2 days; as no fish were collected in the upper 200 m, two additional daytime vertical series were made with only one haul extending from below the depth of the sound-scattering layer to about 200 m. In order to achieve adequate sample size, the duration of each haul was long, but because there were so few hours of darkness, only one nekton haul could be made each night. Data from a shallow haul and a deep haul on successive nights were therefore combined to give a single, complete, night vertical series; two such night series were obtained, and all sampling was performed between ascent and descent of the migratory sound-scattering layer.

In addition to vertical series of nekton samples taken at Station Q, we utilized two types of horizontal hauls. To identify components closely associated with the migratory sound-scattering layer, on two evenings the trawl was launched near sunset and towed horizontally at 125 m. The 12-kHz echosounder was operated continuously during the hauls. Approximately 30 min before the scattering layer began to ascend from its daytime depth, a trawl net was opened and sampling began. The second net was opened just as the scattering layer reached 125 m, and the net was closed after the layer had passed that depth. The trawl was towed at 125 m for an additional 30 min, taking a third sample, then closed and retrieved. As part of the study of diel variations in feeding intensity of myctophids, a series of three horizontal hauls, each yielding four samples of 30 min duration, was made in the upper layer (40-m depth) throughout one night.

The sampling program at Station P in 1975 was similar to that at Station Q, although the nekton sampling for vertical distributions (Table 1) was much less extensive than in the previous two cruises. We obtained only one complete nighttime vertical series (400-0 m) and two deep daytime vertical series (385-220 m) to check on vertical distributions of myctophids. We collected one shallow vertical series in the 0-60 m layer in 15-m depth strata to examine the vertical distribution of myctophids within the surface layer at night, and we took one very deep daytime vertical series (782-440 m) to determine the distribution of myctophids below our usual sampling depths.

All samples obtained with the nekton trawl were preserved in a 4% formaldehyde seawater solution buffered with sodium borate.

TABLE 1.—Sampling data for vertical series of nekton samples in the northeastern Pacific. The three lower entries for Station P (1975) represent data for: first, the routine day-night vertical series (0-400 m); second, a single shallow (0-60 m) night vertical series; and, third, a single deep (440-782 m) daytime vertical series.

Stn.	Dates	Ship speed (km h)	Mean (range) duration of samples (min)	Mean (range) volume filtered per sample (m^3)	
P	5-9 Aug 1973	7.2±0.5	29 (16-45)	8,412	(4,863-13,357)
Q	18-22 July 1974	6.2±0.5	45 (24-66)	14,229	(6,833-20,361)
P	26-28 July 1975	6.9±0.5	32 (19-43)	10,984	(7,664-14,731)
	27 July 1975	6.9±0.5	21 (16-29)	7,638	(6,184-10,052)
	31 July 1975	6.9±0.5	68 (58-79)	23,232	(20,012-28,614)

Analysis of Samples

All organisms in the nekton samples were counted. Fish were identified from descriptions in Hart (1973) and Wisner (1976). The standard length (SL) (distance from the tip of the snout to the end of the vertebral column) of each fish was measured to the nearest millimeter. Among the invertebrates collected in nekton samples, only euphausiids and decapod shrimps were consistently captured in substantial numbers. The numbers of fish and shrimp were standardized to number per 10,000 m^3 of water.

Myctophid fish, preserved for about 3 yr, were sorted from samples for determination of body length and dry body weight. Intact, undamaged specimens were dried to constant weight at 65°C on glass slides in a drying oven. Drying usually took 3-4 days, but up to 10 days for some of the largest fish. Dried fish were weighed to the nearest milligram. The relationship between standard body length and dry body weight for each species of myctophid was determined by linear regression analysis of logarithmically transformed measurements.

RESULTS

The vertical series of nekton samples collected at Stations P and Q yielded nine species of myctophids, one abundant species of chauliodontid, and one relatively rare melanostomiatid. All other families combined made up only 2-6% of the total catch by number (Table 2). In addition to fish, the samples contained considerable numbers of euphausiids and decapod shrimps. Other invertebrate groups, such as siphonophores and squids, were only sporadically captured. The more common fishes had similar relative abundances at the two stations. More than 80% of the myctophids consisted of three species (*Stenobrachius leucopsarus*, *Protomyctophum thompsoni*, and *Diaphus theta*) whose vertical distributions were generally well bracketed by the sampling. The other species of myctophids were either rare or appeared to be distributed below the usual range of sampling; therefore, emphasis in this study was placed on the above three, abundant, relatively shallowly distributed species.

Vertical Distribution of Fish

The most abundant fish in our samples was *S. leucopsarus*. Its only congener, *S. nannochir*, was rarer (Table 2). As discussed later, with the exception of the very deep vertical series (782-440 m) in 1975, only small specimens (<35 mm) of *S. nannochir* occurred in the vertical series. The fish caught at Station P in 1973 were in such poor condition that it was not possible to discriminate the smaller specimens of the two species of *Stenobrachius*. However, there is evidence (presented below) that *S. nannochir* was extremely rare at Station P in 1973, much rarer than at Station Q or Station P in 1975 (Table 2). Redesign of the cod ends, after the 1973 cruise, provided us with good specimens which permitted discrimination of the two congeners.

TABLE 2.—Composition of the total fish catch in vertical series of nekton samples in the northeastern Pacific. Data for each station combine all vertical series.

	Station P, 1973		Station Q, 1974		Station P, 1975	
Family and species	No.	%	No.	%	No.	%
Myctophidae:						
Stenobrachius leucopsarus	720	63.8	1,038	45.4	461	49.3
S. nannochir	(1)	(1)	268	11.7	92	9.8
Protomyctophum thompsoni	125	11.1	413	18.1	210	22.5
Diaphus theta	111	9.8	304	13.3	61	6.5
Tarletonbeania crenularis	16	1.4	26	1.1	3	0.3
Lampanyctus regalis	9	0.8	11	0.5	0	0
L. ritteri	3	0.3	11	0.5	0	0
Notoscopelus japonicus	1	0.1	0	0	0	0
Symbolophorus californiense	1	0.1	0	0	0	0
Chauliodontidae:						
Chauliodus macouni	57	5.0	147	6.4	84	9.0
Melanostomiatidae						
Tactostoma macropus	21	1.9	15	0.7	3	0.3
Others	64	5.7	55	2.4	21	2.2
Totals	1,129		2,288		935	

(1) Due to the poor condition of the fish caught at Station P in 1973, it was impossible to discriminate the smaller specimens of the two species of *Stenobrachius*. It is possible that some of the fish listed here as *S. leucopsarus* were in fact *S. nannochir*, but for reasons described in the text, we do not believe this to be the case.

At Station P in 1973, *S. leucopsarus* occurred in largest numbers in the surface layer (0-55 m) at night and at 275-330 m during the day (Figure 3A). This pattern could occur if most specimens undertook a diel vertical migration over a depth range of 250-300 m. To be certain that the data reflect a vertical migration and not simply light-aided avoidance of the net by fish in the daytime, it was necessary to compare day and night total catches of fish integrated over the water column sampled (Table 3). Assuming that the entire vertical range of *S. leucopsarus* was sampled (this assumption is qualified below), then it is clear that, since the total catches for day and night series were statistically indistinguishable (Table 3), there was no evidence of daytime avoidance of the trawl by fish. Further, judging from the results of replicate sampling of zooplankton with nets (Wiebe and Holland 1968), the day and night totals in Table 3 are well within the range of variability expected for repeated samples from a pelagic population. Thus, the observed diel differ-

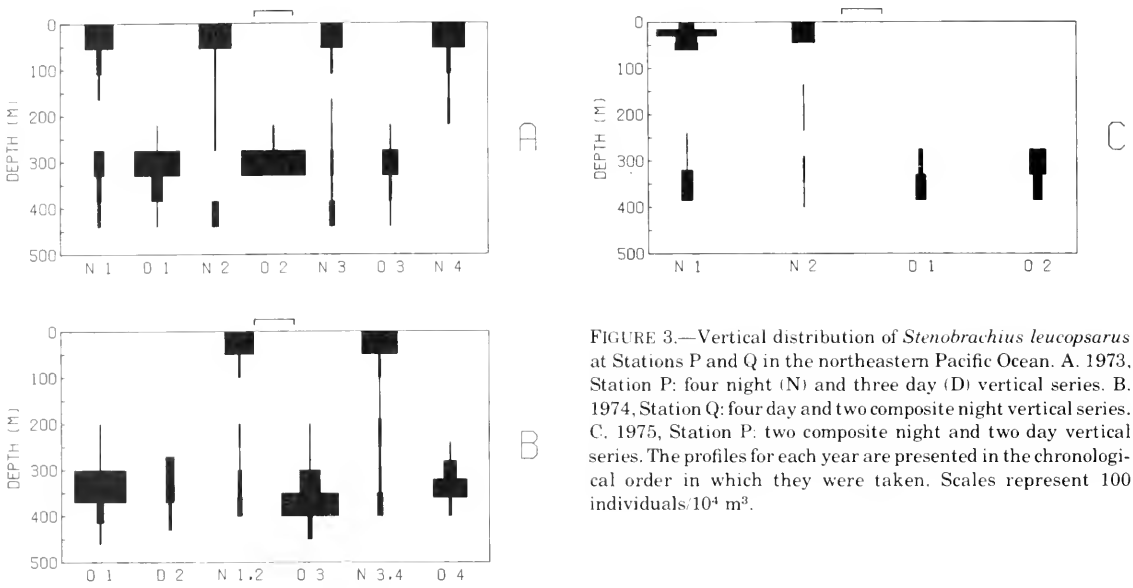

FIGURE 3.—Vertical distribution of *Stenobrachius leucopsarus* at Stations P and Q in the northeastern Pacific Ocean. A. 1973, Station P: four night (N) and three day (D) vertical series. B. 1974, Station Q: four day and two composite night vertical series. C. 1975, Station P: two composite night and two day vertical series. The profiles for each year are presented in the chronological order in which they were taken. Scales represent 100 individuals/10^4 m^3.

TABLE 3.—Day and night total catches for the water column sampled, of selected fish and crustacean species at Stations P and Q in the northeastern Pacific; means and ranges (parentheses) as number/100 m^2. Ratios given of largest to smallest estimate of abundance for a station.

Species	Station	Day		Night		Ratio
Stenobrachius leucopsarus	P, 1973	67.7	(28.6-82.0)	59.8	(47.3-73.7)	2.9
	Q, 1974	101.1	(48.4-153.6)	62.1	(56.5-67.7)	3.2
	P, 1975	28.0	(20.3-35.8)	37.6	(29.2-46.1)	2.3
Diaphus theta	P, 1973	6.8	(1.1-13.8)	12.4	(3.9-18.2)	16.5
	Q, 1974	22.6	(15.2-34.4)	[1]11.5	(11.0-12.0)	3.1
	P, 1975	3.6	(3.1-4.0)	5.4	(3.6-10.4)	3.4
Protomyctophum thompsoni	P, 1973	15.6	(12.7-20.9)	7.9	(0.0-13.8)	[2]4.8
	Q, 1974	26.7	(21.6-39.1)	23.6	(20.0-27.3)	2.0
	P, 1975	17.3	(17.2-17.3)	47.0	(28.9-65.2)	3.8
Chauliodus macouni	Q, 1974	10.1	(3.2-15.7)	8.2	(7.5-9.0)	4.9
Euphausia pacifica	P, 1973	169.7	(24.2-323.9)	[1]1,075.3	(214.5-5,825.0)	240.7
	Q, 1974	417.4	(272.0-531.5)	154.0	(17.5-290.5)	30.4
	P, 1975	322.5	(223.8-421.3)	423.7	(294.5-532.9)	2.5
Sergestes similis	P, 1973	19.8	(0.5-31.3)	[1]50.3	(28.0-80.8)	161.6
	Q, 1974	33.0	(14.0-47.6)	[1]72.9	(57.5-88.3)	6.3
	P, 1975	10.2	(9.3-11.0)	11.1	(9.6-12.6)	1.4

[1]Day and night abundance significantly different ($P < 0.1$) by rank test (Tate and Clelland 1957).
[2]Estimate based on smallest nonzero catch.

ences in the vertical distribution of *S. leucopsarus* (Figure 3A) indicate that the majority of individuals do perform a diel vertical migration.

The occurrence of some *S. leucopsarus* in the deepest samples at night (Figure 3A) indicates that the entire population was not participating in the vertical migration described above. Differences in migratory pattern appear to be largely a function of size or age of individual fish. The length-frequency histogram for our entire catch of *S. leucopsarus* at Station P in 1973 (Figure 4A) indicates that several size classes of fish were sampled. Since *S. leucopsarus* metamorphoses to the juvenile stage at 18 mm (Smoker and Pearcy 1970), the abundant 19-35 mm size class (Figure 4A) probably represented the youngest juvenile fish. The largest specimens caught at Station P attain the maximum size expected for *S. leucopsarus*, 85-111 mm (Kulikova 1957; Smoker and Pearcy 1970).

To determine the effect of size on vertical migration, we examined the three obvious size classes of *S. leucopsarus*: 19-35 mm, 38-82 mm, and 90-112 mm. The smallest size class (19-35 mm) performed a clear diel vertical migration from 275-330 m in the daytime to 0-55 m at night (Figure 5A). The anomalously low density of fish on the third day must be attributed to horizontal patchiness of fish. Note especially that only on one night (N3, Figure 5A) was one small-sized *Stenobrachius* captured below 275 m. The medium size class (38-82 mm) shows a similar migration (Figure 5B), though these fish seemed to be more dispersed vertically, both at night and in the daytime, than the smallest size class. The high density of medium-sized fish at 275-330 m on the first night, not apparent on the other three nights, probably reflected the fact that this sample was collected between 0554 and 0613 h, a time period when the migratory sonic scatterers, and presumably myctophids, were descending. Some of the medium-sized fish probably had already descended into the 275-330 m layer at the time this sample was collected. The largest size class of *S. leucopsarus* (90-112 mm) had a pattern of vertical distribution totally different from those of the two smaller size classes. Individuals of the largest size class were not captured at all in the first two daytime series and were caught only in the two deepest samples in the third daytime series (Figure 5C). They were captured in all four night series, but never in the surface layer (0-55 m), and in three of the four night series, the greatest density of large-sized fish occurred between 330 and 440 m. It is tempting to conclude from these data that the individuals of the largest size class also perform a diel vertical migration, moving from daytime depths below our lower limit of sampling (440 m) into our sampling range at night. Of course, a similar vertical distribution pattern could be obtained if the largest fish avoid the trawl in the daytime, although it seems unlikely that all fish of this size class could effectively do so. Nevertheless, with the data from Station P (1973), it is impossible to discriminate between these two possibilities for the largest fish.

Stenobrachius leucopsarus had a very similar pattern of distribution and diel vertical migration at Station Q (Figure 3B). The length-frequency distribution of the species was strongly skewed to juvenile fish (19-31 mm), which made up 88.7% of the total catch of the species. There was only one relatively distinct secondary mode, consisting of very large fish (81-108 mm), which composed 3.9% of the total catch (Figure 4B). Fish in the smallest mode and also the rarer intermediate sizes of fish (32-79 mm) were clear vertical migrants, closely following the pattern described above for Station P, and there was no difference in vertical distribution between the small- and medium-sized fish. Also, as at Station P, representatives of the largest size class of fish were captured, with the exception of 1 fish (out of 45 caught) in the deepest sample on day 4, only in the night hauls and almost always (43 out of 44 fish) below 50 m.

At Station P in 1975, the same patterns of diel vertical migration (Figure 3C) and size-dependent variation in vertical distribution of *S. leucopsarus* were evident, though far fewer fish were collected, both because of the fewer vertical series taken and an apparent decrease in abundance of the species compared with the previous 2 yr (Table 3). This decrease appears due partly to reduced abundance of the smallest size class (17-32 mm) which made up only 47.2% of the total catch in 1975 (Figure 4C), compared with 62.6% at Station P in 1973 and 88.7% at Station Q. In the one deep daytime vertical series (782-440 mm) at Station P, large *S. leucopsarus* were captured between 440 and 740 m (Table 4), thus supporting our earlier hypothesis that the largest fish caught at night above 440 m migrated in the daytime below our usual range of sampling. However, extensive day and night sampling over the entire vertical range of the large fish is required to completely rule out daytime avoidance of the trawl.

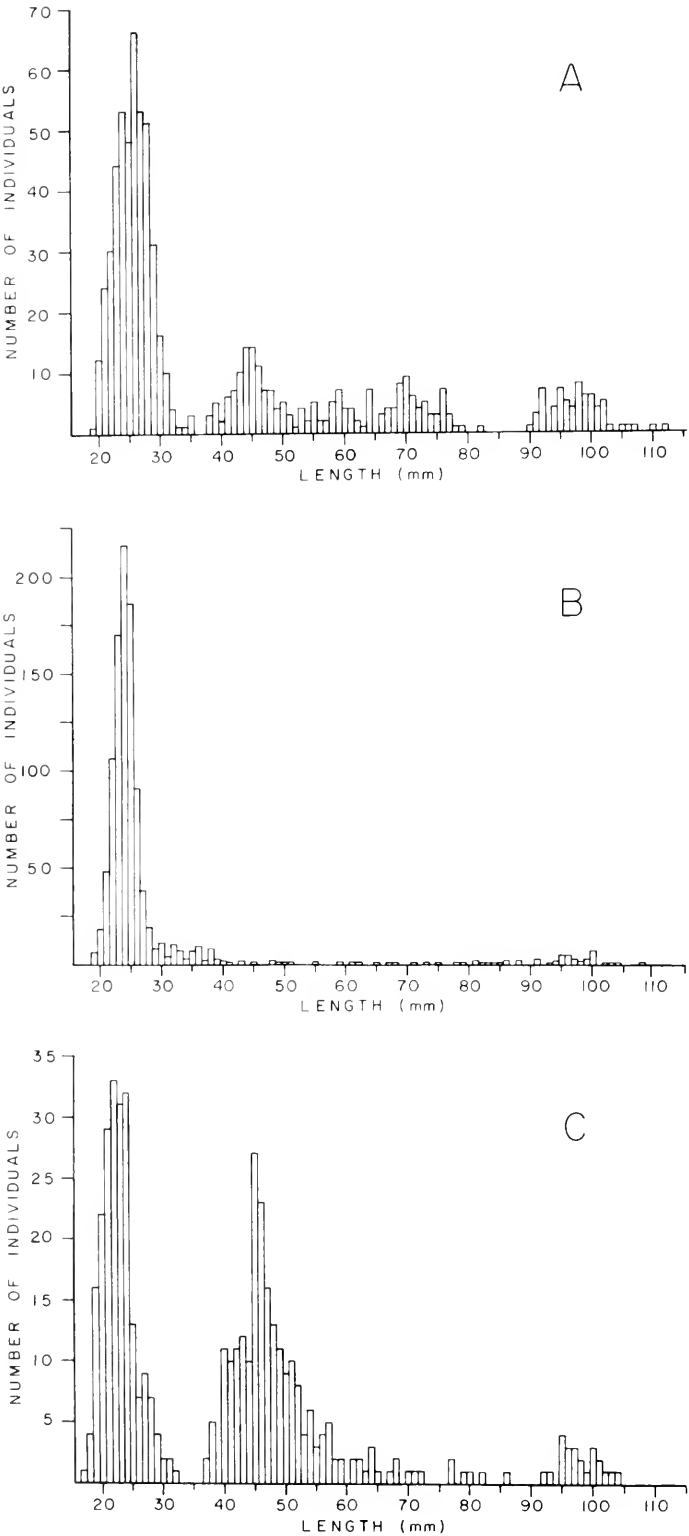

FIGURE 4.—Length-frequency distributions of *Stenobrachius leucopsarus* from all vertical series. A. 1973, Station P, N = 720. B. 1974, Station Q, N = 1,038. C. 1975, Station P, N = 461.

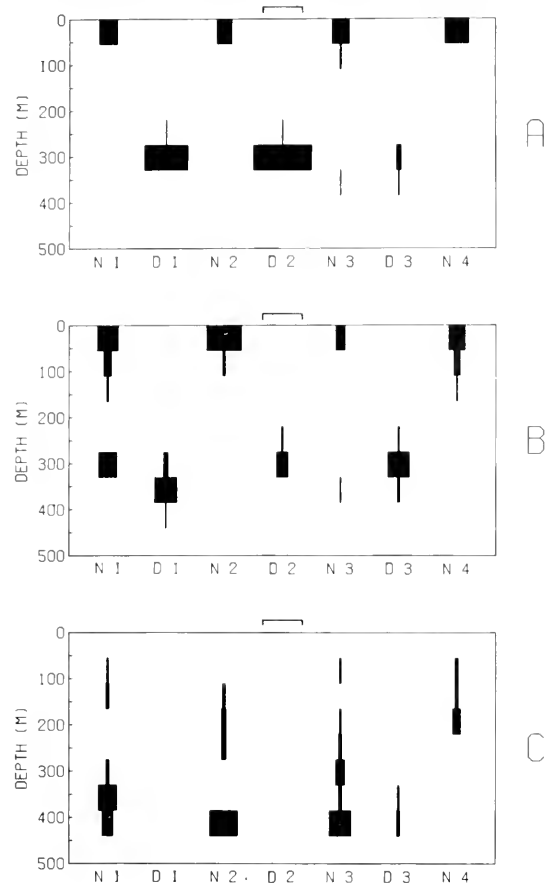

FIGURE 5.—Vertical distribution of three sizes of *Stenobrachius leucopsarus* at Station P, 1973. A. 19-35 mm, scale represents 100 individuals/10^4 m^3. B. 38-82 mm, scale represents 50 individuals/10^4 m^3. C. 90-112 mm, scale represents 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3A.

The one shallow night vertical series (60-0 m) at Station P indicated that *S. leucopsarus* were distributed throughout the surface layer but were concentrated between 15 and 30 m (Figure 3C). Examination of sizes of fish caught in this series suggested very fine-scale vertical stratification by age or size (Table 5). Recall that in all other vertical series taken at night very large fish (>80 mm) were always captured (except for one fish) below 50 m. Because we took only one such shallow vertical series, we cannot evaluate the frequency of occurrence or temporal persistence of this apparent stratification of fish by age in the surface layer at night.

The third most abundant myctophid in our samples, *Diaphus theta*, also performed a diel vertical migration (Figure 6); there was no consistent difference between day and night catches (Table 3). At night, *D. theta* ranged over the upper 165 m but was concentrated near the surface (0-55 m), while during the day most of these fish were collected below 275 m. As stated above for *S. leucopsarus*, the occurrence of *D. theta* at 275-330 m the first night at Station P (1973) is misleading because the sample was probably collected after the downward vertical migration of myctophids had begun.

The size range for the total catch of *D. theta* was 36-88 mm in 1973 and 46-84 mm in 1975 at Station P, and 33-76 mm at Station Q. The size-frequency distributions were similar in all 3 yr. Considering only Station Q, for which we have the largest collection, the size-frequency distribution (Figure 7A) was quite different from *S. leucopsarus* (Figure 4B). Small and large fish were rare and the samples contained primarily intermediate sizes (45-58 mm). Distinguishing, somewhat arbitrarily, three classes in the size-frequency distribution, there is indication of size-dependent

TABLE 5.—Vertical distribution of size classes of *Stenobrachius leucopsarus* in the shallow night vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m^3. Data based on a single haul with a single sample at each depth.

Depth (m)	17-32 mm	37-82 mm	85 mm
0-15	37.2	1.6	0
15-30	140.5	13.6	0
30-45	7.8	46.8	0
45-60	15.9	42.8	1.0
Total no. captured	138	89	1

TABLE 4.—Deep daytime vertical distribution of selected species of micronekton at Station P (1975) in the northeastern Pacific, as number/10,000 m^3. For *Stenobrachius leucopsarus*, the numbers in parentheses are abundances of large fish (91-112 mm SL). Data based on a single haul with a single sample at each depth.

Depth (m)	*Stenobrachius leucopsarus*	*Stenobrachius nannochir*	*Protomyctophum thompsoni*	*Lampanyctus ritteri*	*Chauliodus macouni*	*Sergestes similis*
440-540	4.5 (3.5)	49.6	0.7	0	2.4	10.8
540-640	8.5 (7.5)	7.0	0	0	0	7.5
640-740	4.4 (1.3)	4.9	0	0.9	0.4	0
740-782	0	2.7	0.5	0.5	0	0
Total no. captured	40 (28)	173	3	3	8	45

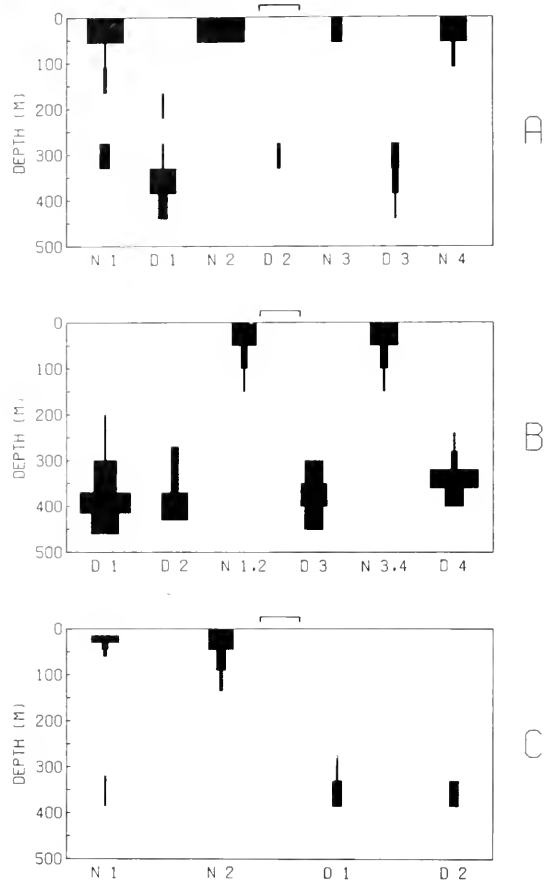

FIGURE 6.—Vertical distribution of *Diaphus theta*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

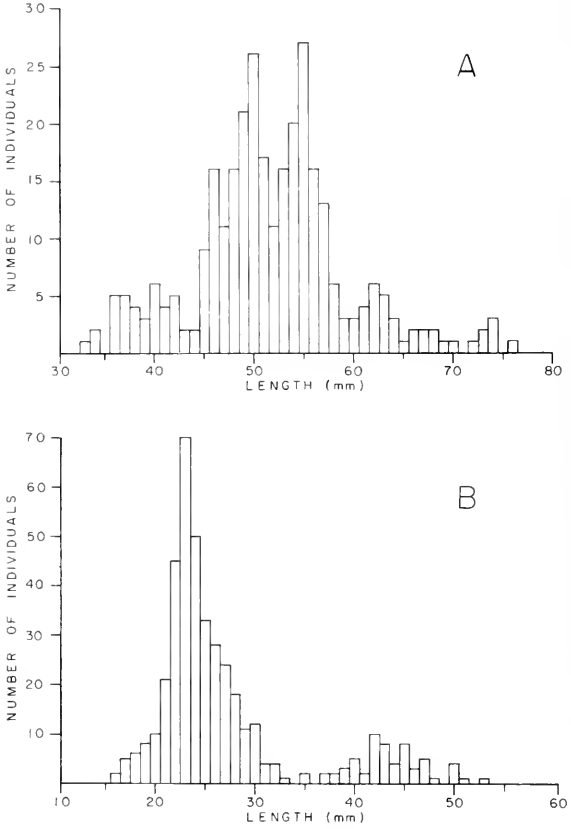

FIGURE 7.—Length-frequency distributions of *Diaphus theta* (A), $N = 304$, and *Protomyctophum thompsoni* (B), $N = 413$, from all vertical series at Station Q, 1974.

variation in vertical distribution and vertical migration. The smallest sizes (35-44 mm) of fish were consistently shallower than larger sizes both during the day and at night (Table 6); although the numbers of fish are small, they do indicate a possible trend. *Diaphus theta* was not captured in the very deep (782-440 m) daytime vertical series at Station P in 1975.

The second most abundant myctophid, *Protomyctophum thompsoni*, did not perform an extensive diel vertical migration similar to that of *S. leucopsarus* or *D. theta*; it remained below about 200 m both day and night (Figure 8). Nevertheless, the species tended to be somewhat more shallowly distributed at night than in the daytime. This is best demonstrated by the data from Station Q where the largest catches of this species were made. At Station Q, *P. thompsoni* ranged from 16 to 53 mm SL and the length-frequency distribution of the population was bimodal (Figure 7B). Calculations of mean depths of the two size classes showed that the smaller fish were always slightly more shallowly distributed that the larger fish (Table 6). Moreover, both size classes tended to be deeper in the daytime than at night, although the average change in depth (30-40 m for both size classes) was relatively small (Table 6). *Protomyctophum thompsoni* was rare below 440 m at Station P in 1975 (Table 4). The size range of the species at Station P was 18-51 mm (1973) and 16-50 mm (1975), and the size-frequency distribution was similar to that of Station Q.

The above three species of myctophids had vertical distributions which were, with the possible exception of the rare large specimens of *S. leucopsarus*, well bracketed by our vertical series of samples. Two other relatively abundant species of fish seemed to have vertical distributions which

TABLE 6.—Mean depth (meters) of size classes of *Diaphus theta* and *Protomyctophum thompsoni* in day (D1-D4) and night (N1, N2) vertical series at Station Q in the northeastern Pacific. Mean depth D was calculated from the equation $D = \Sigma n_i \bar{Z}_i / \Sigma n_i$, where n_i is the population density (number/10,000 m^3) of a size class in sample i and $\bar{Z}_i$ is the midpoint of the depth range of sample i.

Size class (mm)	D1	D2	D3	D4	N1	N2	Total no. captured
Diaphus theta							
35-44	342	357	325	336	25	25	40
45-58	394	382	377	351	32	30	224
58	390	400	404	344	76	69	40
Protomyctophum thompsoni							
16-35	332	316	330	301	294	257	354
36-53	381	338	340	340	307	309	59

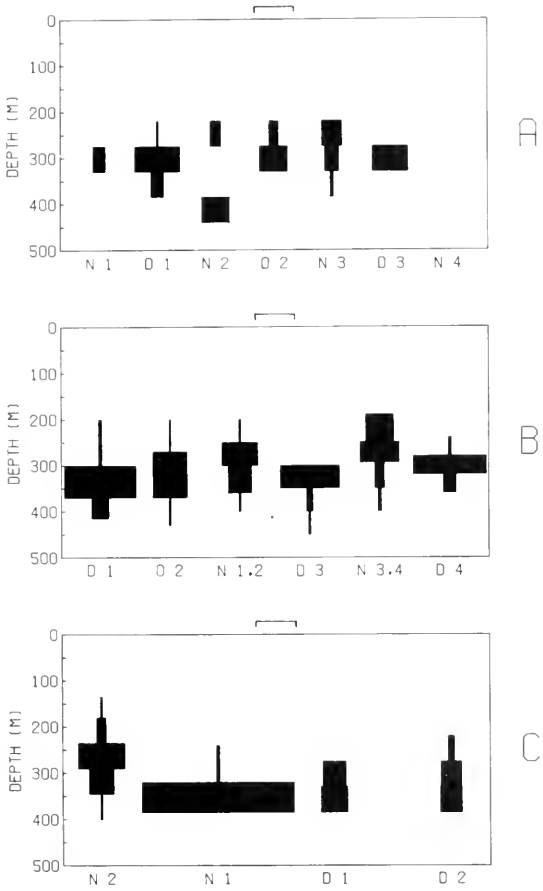

FIGURE 8.—Vertical distribution of *Protomyctophum thompsoni*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

extended deeper than our usual range of sampling. *Stenobrachius nannochir* was only captured below 275 m in the routine vertical series at Stations Q (1974) and P (1975). As noted earlier, due to the poor condition of the catch, small specimens of *S. nannochir* and *S. leucopsarus* were not distinguished in samples from Station P (1973). Half of the total catch of *S. nannochir* was from below 400 m, and all of the specimens caught above 440 m were <35 mm SL. It is for this reason that we think that the species must have been extremely rare in the 0-440 m layer at Station P in 1973, for we caught almost no small *Stenobrachius* in the deep samples at night (Figure 5A). The virtual restriction of catches of *S. nannochir* to our deepest samples, day and night, indicates that its distribution probably extended below our range of sampling. Indeed, it was the most abundant fish in the one very deep daytime vertical series at Station P (1975); it occurred down to 782 m and was concentrated in the 440-540 m layer (Table 4). Furthermore, an interesting vertical stratification by size was evident in this series, with the smallest fish dominating the shallowest sample and largest fish dominating the deepest two samples (Table 7). Note that we captured only small specimens (<35 mm) in all of the other, shallower vertical series. *Stenobrachius leucopsarus* and *S. nannochir* of similar body size tended to be vertically well separated in the water column at all times (Tables 4, 7; Figure 5).

TABLE 7.—Vertical distribution of size classes of *Stenobrachius nannochir* in the deep daytime vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m^3.

Depth (m)	22-37 mm	38-70 mm	85-113 mm
440-540	37.0	12.2	0.3
540-640	0.5	6.5	0
640-740	0	2.2	2.7
740-782	0	0.9	1.8
Total no. captured	107	55	11

The only other moderately abundant fish was the chauliodontid *Chauliodus macouni*, and only at Station Q was it captured in sufficient numbers to warrant description. *Chauliodus macouni* always occurred below 150 m, and there was no conclusive evidence of change in its vertical distribution during the day-night cycle (Figure 9, Table 3). However, in contrast to *P. thompsoni*, whose range of vertical distribution apparently was well sampled day and night (Figure 8B, Table 4), it appears from the abrupt truncation of histograms in Figure 9 that the deepest portion of the population of *C. macouni* was not sampled either in the daytime or at night. Indeed, in the very deep vertical series at Station P (1975), a number of *C. macouni* were captured in the 440-540 m layer

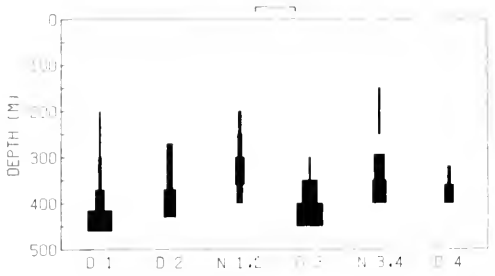

FIGURE 9.—Vertical distribution of *Chauliodus macouni* at Station Q, 1974. Scale represents 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3B.

TABLE 8.—Abundance (number/10,000 m^3) of *Stenobrachius leucopsarus* and *Diaphus theta* in three series of half-hour samples collected in horizontal tows at 40-m depth during one night at Station Q in the northeastern Pacific. Sampling commenced after the migratory scattering layer had merged with the surface reverberation and terminated after the scattering layer had descended below the surface reverberation (0425). Time is when net was opened.

Time	*S. leucopsarus*	*D. theta*	Time	*S. leucopsarus*	*D. theta*
2200	157	31	0130	262	42
2230	89	15	0200	329	36
2300	102	10	0300	188	72
2330	109	8	0330	178	66
0030	80	21	0400	146	28
0100	197	54	0430	8	0

(Table 4), indicating that the distribution of this fish probably extended below the normal limit of sampling in the routine vertical series. At Station Q, specimens of *C. macouni* ranged from 29 to 189 mm SL. Very large fish (>100 mm) were usually captured at night in the deepest samples, but for fish <100 mm there was no clear trend of size-dependent variation in vertical distribution.

Other fish species (Table 2) occurred sporadically in the samples and were caught primarily at night: the only daytime catches were below 300 m (e.g., *Lampanyctus ritteri* in Table 4). Included in the category "Others" in Table 2 were members of the families Bathylagidae, Gonostomatidae, Melamphaeidae, Opisthoproctidae, Paralepididae, and Scopelarchidae.

Variability in Abundance of Myctophids in Replicated Samples

With a few exceptions, the estimates of abundance of myctophids integrated over the water column sampled did not vary by more than a factor of 4 between vertical series within cruises (Table 3). At Station Q, three series of half-hour horizontal hauls were made at 40 m throughout one night (Table 8). Excluding the sample (0430) collected after the scattering layer had descended, concentrations of *S. leucopsarus* varied by a factor of about 4, those for *D. theta* by a factor of about 9. For both species, there was a significant trend (P = 0.05, run test, Tate and Clelland 1957) toward increased abundance during the night, and their abundances were strongly correlated (rank difference correlation coefficient 0.74, $P \sim 0.01$, Tate and Clelland 1957). Myctophids were abundant in the surface layer until the migratory scattering layer descended.

Estimated Abundance and Standing Stock of Fishes

Our data for mean abundance of all fishes captured for the 3 yr ranged from 0.78 to 1.61/m^2 for the water column extending to between 385 and 460 m (Table 9). The three most abundant species of myctophids combined accounted for 77-85% by number of all fish collected. There was no consistent difference between day and night estimates of concentrations of fish.

Equations for the regression of dry body weight on body length (Table 10) were used in conjunction with the lengths and abundance of fish from each sample to calculate the population standing stocks of *S. leucopsarus*, *D. theta*, and *P. thompsoni* for

TABLE 9.—Estimated mean abundance and standing stock of mesopelagic fishes at Stations P and Q in the eastern subarctic Pacific Ocean. Myctophids includes only the three most abundant species, *Stenobrachius leucopsarus*, *Diaphus theta*, and *Protomyctophum thompsoni*. Estimated mean abundance and standing stock are based on average of all day and night vertical series; values in parentheses are means for night vertical series only.

Station	Abundance (no./m^2)		Standing stock (g dry wt/m^2)
	Myctophids	All fishes	Myctophids
P, 1973	0.85	1.00	0.53 (0.77)
Q, 1974	1.24	1.61	0.27 (0.39)
P, 1975	0.61	0.78	0.34 (0.55)

TABLE 10.—Equations for the regression of dry body weight, W (grams), on body length, L (centimeters), for three species of myctophids.

Species	Regression equation	Range of SL (cm)	N
Stenobrachius leucopsarus	$W = 0.00125\ L^{3.546}$	2.0-11.8	92
Diaphus theta	$W = 0.00537\ L^{2.943}$	3.0-7.4	79
Protomyctophum thompsoni	$W = 0.00212\ L^{3.391}$	1.7-4.9	54

each vertical series of nekton samples at each station. A slight (<1%) bias toward underestimation of weight was corrected using the approximation for minimum variance unbiased estimator of the mean given by Beauchamp and Olson (1973). Mean standing stock, averaged over day and night series, ranged from 0.27 to 0.53 g dry weight/m² of sea surface (Table 9). Variations in standing stock did not closely follow variations in abundance because of large year-to-year variations in the size-frequency distribution of the most abundant species, *S. leucopsarus* (cf. Figure 4). For example, the low standing stock at Station Q is due to the relative scarcity of medium-sized (40-80 mm) *S. leucopsarus* in the catch at that station (Figure 4B). This also accounts for differences between years in the composition by species of the standing stock of the three myctophids. At Station P in both years, *S. leucopsarus* represented, on the average, 63.4-75.7% of the standing stock of myctophids, but at Station Q it contributed only an average of 32.4%. At Station Q, the rarer, but relatively larger, *D. theta* made up 59.3% of the standing stock; however, at Station P it made up only 21.2-24.3%. *Protomyctophum thompsoni*, because of its small body size (Figure 7B), averaged <13% of the standing stock at all stations (range of means for the three stations, 4.2-12.3%). Estimates of mean standing stock based only on night vertical series tended to average more than those based only on day series (Table 9) because of the contribution from the relatively rare (Figure 5), but very large (>90 mm), specimens of *S. leucopsarus* which were caught chiefly at night.

Vertical Distribution of Crustaceans

The most abundant organisms in the vertical series of nekton samples were euphausiids, predominantly large individuals (>12 mm total length). At Station P in both 1973 and 1975, *Euphausia pacifica* made up more than 80% of the euphausiid catch by number. At Station Q, 51% of the total euphausiid catch was *E. pacifica*; other species were *Thysanoessa spinifera* (30%), *Tessarabrachion occulatum* (9%), *Thysanoessa longipes* (8%), and *Stylocheiron maximum* (2%). All of these species also occurred at Station P, but were rare. Consequently, only the data for *E. pacifica* are presented here.

During the day, large *E. pacifica* occurred in greatest concentration between 275 and 400 m, while at night they were usually concentrated in the upper 55 or 60 m (Figure 10). No consistent difference between day and night total catches was evident, but sporadic, extraordinarily large or small catches of *E. pacifica* were obtained in both 1973 and 1974. Variations such as these are common in euphausiid catches (Brinton 1962b) and are usually attributed to horizontal patchiness. Our ranges of estimated abundances were consequently very large (Table 3). The other four species of euphausiids were too rare to draw definite conclusions about their distributions.

The penaeid decapod shrimp, *Sergestes similis*, was the only other abundant invertebrate in our nekton samples. At Station P (1973) and Station

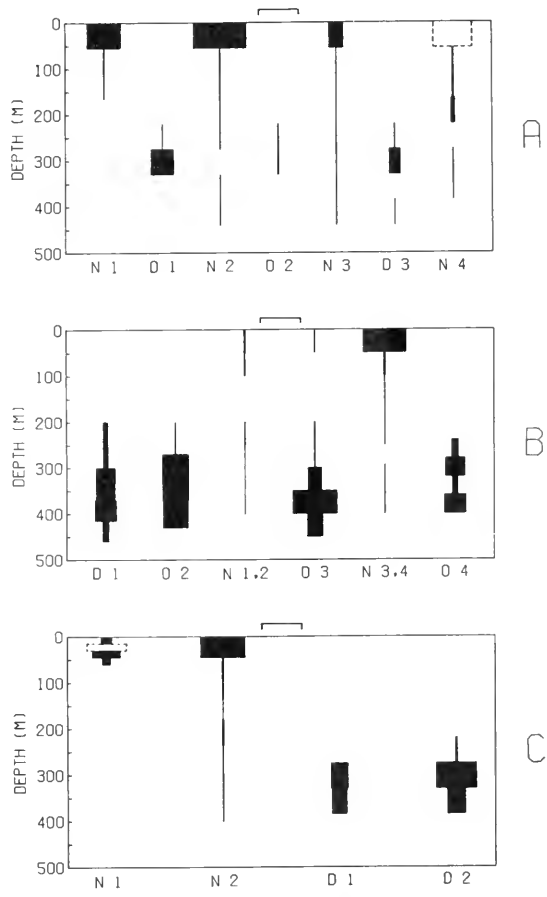

FIGURE 10.—Vertical distribution of *Euphausia pacifica*. A. 1973, Station P. Scale represents 1,000 individuals/10^4 m³. (The 0-55 m sample on the fourth night represents 10,447 individuals/10^4 m³.) B. 1974, Station Q. Scale represents 500 individuals/10^4 m³. C. 1975, Station P. Scale represents 500 individuals/10^4 m³. (The 15-30 m sample on the first night represents 3,086 individuals/10^4 m³.) Sequence of vertical series as in Figure 3.

Q, the species appeared to be performing an extensive diel vertical migration (Figure 11A, B); however, the average daytime catches at both stations were a bit less than half the average nighttime catches, though only in 1973 and 1974 were there statistically significant differences (Table 3). Except for the largest size class of *Stenobrachius leucopsarus* (Figure 5C), *Sergestes similis* is the only species for which we found such a prominent, repeated, day-night difference in catches. Either *S. similis* is a diel vertical migrator and descends below our usual range of sampling in the daytime or it is capable of avoiding the nekton trawl in the daytime. Our very deep daytime vertical series taken at Station P (1975) bears on this question. Although the species seemed considerably less abundant in 1975 (Table 3), this was probably partly due to the shallower depth to which the routine vertical series extended in the daytime. In the very deep daytime vertical series, *S. similis* occurred in considerable numbers between 440 and 640 m (Table 4). Thus it probably was a migrator and in the daytime ranged well below the greatest depth of sampling on routine vertical series.

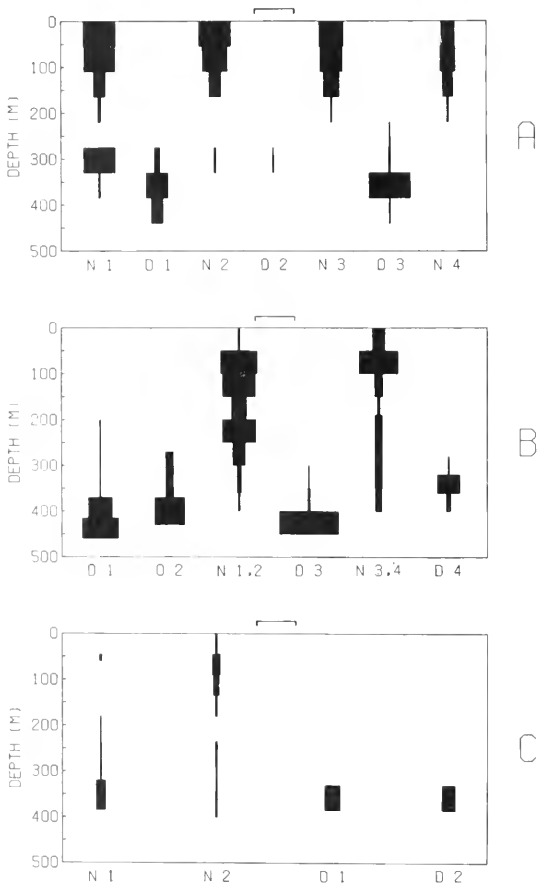

FIGURE 11.—Vertical distribution of *Sergestes similis*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 50 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

At both stations, *S. similis* tended to be rather broadly distributed over the 0-150 m layer at night and often was more abundant below 50 m than above (Figure 11). In this respect its diel migration differs from that of the two migratory myctophid fishes and *E. pacifica*, which tended to aggregate strongly above about 60 m at night.

In addition to *S. similis* several other types of malacostracans were collected in the samples: the caridean decapods *Hymenodora frontalis*, *Notostomus japonicus*, and *Pasiphaea* sp.; the penaeid decapod *Bentheogennema borealis*; and the mysids *Gnathophausia gigas*, *Boreomysis* sp., and *Eucopia* sp. All were rare, were collected only at night, and almost always occurred below 200 m.

Micronekton Associated With Sound-Scattering Layers

In the daytime, the position of the scattering layer corresponded closely with the daytime depth of occurrence of the smaller size classes of *Stenobrachius leucopsarus* and the populations of *D. theta* and *Protomyctophum thompsoni* (Figure 12A). For example, in the profiles shown in Figure 12A, the 300-400 m stratum contained an average concentration of 136 fish/10,000 m^3 of the three species combined. *Sergestes similis* is distributed too broadly and deeply in the daytime to contribute to the observed scattering layer (Figure 11B, Day 3). Excluding euphausiids, in our samples no other potential sound-scattering organism (e.g., physonect siphonophores) consistently had its center of abundance between 275 and 400 m in the daytime. The large *E. pacifica* collected with the nekton trawl had a pattern of vertical distribution (Figure 10B, Day 3) very similar to that of the migratory myctophid fishes.

Comparison of the vertical distribution and diel migration of *Stenobrachius leucopsarus* with the echosounder trace indicates a correlation between the fish and the migratory sound-scattering layer (Figures 2, 3). The correlation is best for individuals of the small and medium size classes (Figure 5). Similarly, the vertical distribution and diel mi-

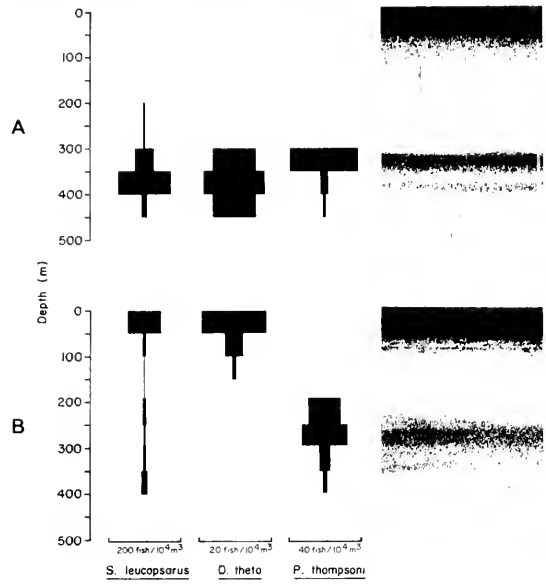

FIGURE 12.—Vertical distribution of three species of myctophids relative to a sound-scattering layer recorded with the 12-kHz echosounder. A. Midday distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Day 3 at Station Q). B. Nighttime distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Nights 3, 4 at Station Q).

gration of *D. theta* closely parallel the behavior of the migratory sound-scattering layer (Figures 2, 6). To examine this relationship more closely, at Station Q two series of three horizontal samples each were collected at 125 m in the periods preceding, during, and after ascent of the migratory sound-scattering layer past that depth. In the first series (Table 11, 17 July) both *S. leucopsarus* and *D. theta* were most abundant in the sample collected as the scattering layer was passing 125 m. Euphausiids (predominantly *E. pacifica*) and *Sergestes similis* were also abundant in the samples; however, maximum concentrations of each were obtained either in the sample collected before or after the scattering layer had passed 125 m (Table 11). Results from the second series (Table 11, 18 July) were similar except that euphausiids were not as abundant in the first sample of the series, and *Stenobrachius leucopsarus* was most abundant in the sample collected after the scattering layer had passed 125 m. The results, therefore, indicate that both migratory myctophids and euphausiids are associated with the migratory sound-scattering layer, whereas sergestid shrimps are not.

TABLE 11.—Occurrence of migratory myctophids and crustaceans (number/10,000 m³) in two series of three samples collected in horizontal hauls at 125 m depth before, during, and after ascent of the migratory sound-scattering layer past that depth.

	17 July			18 July		
Species	Before	During	After	Before	During	After
Stenobrachius leucopsarus	0	38	1	0	13	27
Diaphus theta	1	37	5	0	25	0
Euphausia pacifica	87	64	1	5	68	2
Sergestes similis	3	13	53	0	4	82

Position of the nonmigratory portion of the deep sound-scattering layer which was present at night was strongly correlated with the distribution of *P. thompsoni*, particularly the small size class. The scattering layer was broader and more diffuse at night, and so was the distribution of *P. thompsoni* (Figures 2, 8, 12B). Over the 200-300 m stratum, the average concentration of *P. thompsoni* was 16.3 fish/10,000 m³ for the profile shown in Figure 12B. The day-to-night persistence of the nonmigratory scattering layer (Figure 2) cannot be explained by reference to the distribution of either *S. leucopsarus* or *D. theta*. The two smaller size classes of *S. leucopsarus* and all *D. theta* have migrated into the surface layers at night, and the largest *S. leucopsarus* are not only rare but broadly distributed over 50-450 m. There are no other abundant potential sound-scattering organisms concentrated in the 200-300 m stratum at night.

DISCUSSION

Previous work on myctophids in open waters of the subarctic Pacific dealt chiefly with systematics and biogeography (Wisner 1976). However, Aron (1962) and Taylor (1968) considered aspects of the distribution of myctophids in eastern subarctic waters. Aron's (1962) results are qualitative due to the nature of the sampling gear used (unmetered, nonclosing nets of variable mesh size). Differences between results of our study and those of Taylor's (1968) comprehensive investigation are probably attributable to the different sampling gear employed rather than to fundamental variations in behavior of fish in different parts of the subarctic Pacific. For example, Taylor's use of very course-meshed nets probably accounts for both his finding of different relative abundances of myctophid species and for somewhat different patterns

of vertical distribution of species. Thus in Taylor's study, carried out not far from Station Q, *P. thompsoni* and *D. theta* were more abundant than *S. leucopsarus*, but this was probably because Taylor's net either did not efficiently catch juvenile (<35 mm) *S. leucopsarus* which were the numerically dominant size class of that species in our samples (Figure 4), or they were much less abundant during the time he sampled. Further, Taylor obtained some of the largest catches of *D. theta* and *S. leucopsarus* below 90 m at night. This probably also reflects the sampling bias of his net for larger sizes of fish, which at night tend to be more broadly spread over the water column than smaller fish (Figure 5C; Table 6, night series). Unfortunately, Taylor did not report the sizes of fish captured. Except for probable sampling bias toward larger sizes of fish, Taylor's results on vertical distribution of the nonmigratory *P. thompsoni* and other species of fish agree with ours.

Pearcy et al. (1977) described patterns of vertical distribution of mesopelagic fishes and crustaceans off the coast of Oregon. The mesopelagic assemblage there is essentially subarctic in faunistic affinity and the vertical distributions of species are similar to those observed at Stations P and Q. The only notable departure from our results was the finding by Pearcy et al. that significant numbers of all sizes of *S. leucopsarus* did not participate, at least on a regular basis, in the diel vertical migrations. Our observations at both Stations P and Q indicate that virtually all *S. leucopsarus* smaller than about 80 mm performed extensive diel vertical migrations (Figure 5). However, in our studies, *S. leucopsarus* was also very rare below 400 m (Figure 5, Table 4), whereas Pearcy et al. found large concentrations below that depth. Thus there may be major differences in the vertical distribution and migration behavior of *S. leucopsarus* in different parts of its geographical range (Paxton 1967). Significantly, Pearcy et al. (1977) detected no seasonal variations in vertical distributions and migrations for any species, which may also be true for subarctic waters to the north (Taylor 1968).

Perhaps the most remarkable feature of the mesopelagic fauna of the area sampled was its simplicity. Only four species of myctophid fishes were abundant in the upper 700 m. Two of these species, *S. leucopsarus* and *D. theta*, undertook diel migrations of substantial vertical extent; the other two, *P. thompsoni* and *S. nannochir*, did not. Other taxonomic groups also showed low diversity. Among the micronektonic crustaceans there were single species of abundant euphausiid, *E. pacifica*, and decapod shrimp, *Sergestes similis*, and both were vertical migrators. The contrast between this relatively simple mesopelagic micronekton fauna and that, for example, in the subtropical North Pacific (Brinton 1962a; Clarke 1973; Walters 1977) or subtropical North Atlantic (Badcock 1970; Foxton 1970a, b) is striking, but not atypical. Low taxonomic diversity of the mesopelagic micronekton is found in other subpolar oceans, such as the Boreal Atlantic (e.g., Backus et al. 1971; Zahuranec and Pugh 1971).

Associated with the taxonomic simplicity of the mesopelagic fauna herein reported, was a relatively simple structure of the sound-scattering layers. Generally, both the number and depth of sound-scattering layers change with latitude in the deep ocean; fewer and shallower layers are found in subpolar oceans than in tropical-subtropical oceans (Haigh 1971; Cole et al. 1971; Donaldson and Pearcy 1972; Tont 1976). Our unpublished observations on deep sound-scattering layers (12-kHz echosounder), taken in September 1972 along long. 155°W between Alaska and Hawaii, showed this trend. Subarctic waters had the relatively simple sound-scattering structure illustrated in Figure 2, with single migratory and nonmigratory layers occurring shallower than 400 m. In the subtropical waters near Hawaii, at least three sound-scattering layers were observed in the daytime at depths ranging from 260 to 625 m, and three to four migratory layers were recorded.

It is unlikely that the correlation between taxonomic diversity of the mesopelagic micronekton and complexity of the sound-scattering structure in the water column was fortuitous. Attempts to causally relate deep sound-scattering layers to aggregations of mesopelagic organisms were stimulated by hypotheses advanced more than three decades ago (for a review see Hersey and Backus 1962). However, field studies based on net samples taken simultaneously with echosounder records tend to be inconclusive for a variety of reasons. A major difficulty is that different taxonomic groups tend to occur together at the same depths and may even show similar migratory behavior. For example, all four of the migratory mesopelagic species in our study (*Stenobrachius leucopsarus*, *D. theta*, *E. pacifica*, and *Sergestes similis*) ascended towards the surface layer after

sunset, and only from fine temporal spacing of samples did it become apparent that some species were more closely associated with the scattering layer than others (Table 11). Similarly, in the daytime some of these migratory species cooccurred at the depth of the sound-scattering layer together with the nonmigratory *P. thompsoni*, and any or all could have contributed to the daytime sound-scattering layer. Despite extensive cooccurrence of several types of potential sound-scattering organisms, the most reasonable hypothesis is that myctophids were primarily responsible for both the migratory and nonmigratory sound-scattering layers in the eastern subarctic Pacific.

Taylor (1968), also working in the subarctic Pacific, found the best correlation between deep sound-scattering layers and those mesopelagic fish which possessed gas-filled swim bladders. Although Taylor grouped *Stenobrachius leucopsarus* and *D. theta* among fish with fat-invested swim bladders, gas is present in the swim bladders of immature individuals (<30 mm SL) of both species (Capen 1967). Taylor made no mention of the size of the fish caught in his study; however, in view of the very coarse-meshed nets he used, it is probable that he did not quantitatively sample immature fish. At Stations P and Q, some individuals of *S. leucopsarus* and *D. theta* were theoretically the right size to resonate at 12 kHz while at their daytime depths (Capen 1967), and the abundance of either species was probably sufficient to produce deep sound-scattering in the daytime (Hershey and Backus 1962). This presumably holds also for *P. thompsoni*, which has a gas-filled swim bladder throughout life (Taylor 1968; Butler and Pearcy 1972). Indeed, concentrations of either *D. theta* or *P. thompsoni* alone in Figure 12 were comparable with the concentration of *D. taaningi*, which Baird et al. (1974) believe was responsible for the migratory sound-scattering layer over the Cariaco Trench.

As pointed out above, *Sergestes similis* may be excluded as a potential sound scatterer; it was distributed too broadly and deeply in the daytime and lagged the ascent of the migratory sound-scattering layer at sunset (Figure 11, Table 11). Although *E. pacifica* (Figure 10) was about five times more abundant in the depth of the daytime sound-scattering layer than all myctophid fishes combined, it did not approach concentrations necessary for it to be an effective scatterer of 12-kHz sound (Hersey and Backus 1962; Bary 1966; Beamish 1971).

In conclusion, we suggest that the nonmigratory deep sound-scattering layer (Figure 2B) in the vicinities of Stations P and Q in the eastern subarctic North Pacific was caused by *P. thompsoni*, and that the migratory sound-scattering layer (Figure 2B) recorded the migrations of smaller size classes of *Stenobrachius leucopsarus* and *D. theta*. *Protomyctophum thompsoni* may have been largely responsible for the deep scattering layer observed in the daytime, with possible lesser contributions from the two migratory myctophid species. Pearcy (1977) found similar general correspondence between vertical distributions of the same three species of myctophids and deep sound-scattering layers off Oregon, but he pointed out that quantitative correlation between abundance of potential sound-scatterers and distribution of volume scattering was not always strong. A more definitive analysis, similar to that of Baird et al. (1974), is required; that is, simultaneous observations should be obtained on distribution of volume scattering and abundance and acoustical properties of suspected sound-scatterers.

In single hauls, we observed concentrations of myctophids, all species combined, which regularly exceeded 100 fish 10^4 m^3 in the region of the deep sound-scattering layer in the daytime and in the surface layer at night. Similar concentrations of myctophids are found in other oceans (e.g., Kashkin 1967). Further, the maximum concentrations of myctophids observed by us in the surface layer at night (365 fish/10^4 m^3, Table 8) and at depth in the daytime (874 fish/10^4 m^3, horizontal haul at 327-333 m, Station Q) equal or exceed maximum concentrations inferred from the apparently high catch rates of single hauls reported by Halliday (1970) and Backus et al. (1971) for the western Boreal Atlantic, where one species of myctophid, *Benthosema glaciale*, predominates. The very low concentrations of myctophids found by Pearcy et al. (1977), using a 2.4 m Isaacs-Kidd midwater trawl, are puzzling and seem to indicate that myctophids are about $^1/_{10}$ as abundant off the Oregon coast as in the open subarctic Pacific. However, the data of Pearcy et al. (1977) differ from the earlier results of Pearcy and Laurs (1966), in which reported concentrations of myctophids were much higher and similar to concentrations observed by us; the difference could be due to year-to-year variability (Pearcy 1977).

There is relatively little variability between years in our estimates of abundance of myctophid fishes (the three most abundant species, Table 2)

in the water column extending to 385-460 m. We estimate 0.61-1.24 myctophid fish/m² based on averaged day and night series (Table 10). No quantitative study comparable to ours has been made in the open subarctic Pacific, but Pearcy and Laurs (1966) provided data on the abundance of mesopelagic fish near the Oregon coast. In two cruises (August 1963), Pearcy and Laurs found about 0.78 myctophid fish/m² in the 0-500 m water column at night; this estimate is based upon the three numerically dominant myctophid fish captured (Pearcy and Laurs 1966, fig. 4), two of which ranked 1 and 3 in abundance among myctophids in our study. The average standing stock of all mesopelagic fish found by Pearcy and Laurs (1966) was 2.9 g wet weight/m² in the 0-500 m water column at night. Using a factor of 0.3 to convert wet weight to dry weight, the average nighttime standing stock is 0.87 g/m², a value probably not significantly different from our estimates based on night samples (Table 9), especially since the Pearcy and Laurs estimate is based on all mesopelagic fish captured. Similar concentrations of myctophids (about 0.6-0.8 fish/m²) are found in the subtropical Pacific near Hawaii (Clarke 1973; Maynard et al. 1975). However, many more species of myctophids (47) occur there, and the standing stock of myctophids (about 0.3-0.7 g wet weight/m²) is somewhat less than our estimates (0.23-0.53 g dry weight/m², Table 9), probably because the fish are considerably smaller in average size (Clarke 1973).

With regard to sampling bias, we found no evidence of light-aided avoidance of the nekton trawl by either myctophids or other types of micronekton occurring in the upper 385-460 m during the daytime (Table 3). Consistent day-night differences in catches of organisms, such as those observed for the largest size class (>80 mm SL) of *S. leucopsarus* and for *Sergestes similis*, were probably due to migration of these organisms below the depth range of daytime sampling. The results of the single very deep vertical series at Station P (Table 4) support this interpretation. Furthermore, very deep vertical migrations of both species are well documented in other parts of their geographical ranges in the North Pacific (Omori et al. 1972; Pearcy et al. 1977).

In addition to determining vertical distributions and vertical migrations of myctophid fishes, on each cruise we also sampled zooplankton with a smaller trawl (Frost and McCrone 1974). Analyses of the zooplankton samples, together with data on stomach contents of the three most abundant myctophids, are the subject of a report (in preparation) on the feeding behavior of myctophids in relation to their vertical distribution and the vertical distribution of their zooplankton prey.

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ANALYSIS OF A SIMPLE MODEL FOR ESTIMATING HISTORICAL POPULATION SIZES

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ABSTRACT

Estimates of historical abundance of animal populations are important in many management decisions. Historical estimates based on a simple model of population growth have been made for several populations of dolphin involved with the yellowfin tuna purse seine fishery. We used the data for the bridled dolphin, *Stenella attenuata*, to investigate the behavior of the model by which these historical estimates were calculated. For populations with low net reproductive rates, the effect of bias in the estimates of the input parameters on the estimated historical abundances was approximately linear and additive. When all the input parameters were independently estimated, the variances of the historical abundance estimates were dominated by the variance of the initial abundance estimate and the coefficient of variation of the historical estimate was less than the largest coefficient of variation of any parameter.

Many decisions about the management of animal populations are based on the estimates of abundance of the population relative to its historical or preexploitation size. These estimates are basic to any application of the theory of maximum sustained yield as incorporated in several international marine mammal management agreements such as the North Pacific Fur Seal Treaty and the International Whaling Convention. Similarly, the concept of "optimum sustainable populations" as specified in the recent Marine Mammal Protection Act of 1972 (MMPA) has been defined in terms of comparing the present size of a population with its original size (Southwest Fisheries Center[3]). Schools of dolphin of several species (primarily *Stenella attenuata* and *S. longirostris*) have been used by purse seine fishermen in the eastern tropical Pacific to locate yellowfin tuna, *Thunnus albacares*, since 1959, as described by Perrin (1969). Significant numbers of dolphin have been killed by becoming entangled in the purse seines. In order to make management decisions under the MMPA about these dolphin populations, the National Marine Fisheries Service (NMFS) needed estimates of the preexploitation abundance of the various populations. The NMFS convened a workshop of scientists to obtain the estimates based on a simple model of population change (see footnote 3). This paper evaluates the behavior of estimates of abundance obtained from their approach. This is important in order to be able to evaluate the degree of confidence to be placed in such estimates, and hence in management plans based on them.

METHODS AND MATERIALS

The model used to estimate preexploitation abundance is based on a common discrete model of population growth:

$$N_{\tau+1} = N_\tau - K_\tau + (N_\tau - K_\tau)(b-d) \qquad (1)$$

where N_τ = the abundance at time τ
b = the birth rate
d = the natural death rate
K_τ = the number of animals killed, assumed to occur at the beginning of time interval τ
$N_{\tau+1}$ = the abundance 1 time unit later.

Reversing the procedure (i.e., solving the above equation for N_τ) results in the expression

$$N_\tau = \frac{N_{\tau+1}}{1+R_\tau} + K_\tau \qquad (2)$$

where N_τ now is the estimate of abundance 1 yr

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earlier and R_τ is the net reproductive rate $(b-d)$. The above model was modified in the procedure used by NMFS to account for situations when the kills occur throughout the time interval instead of instantaneously at the end of the interval, as:

$$N_\tau = \frac{N_{\tau+1} + 0.5K_\tau}{1+R_\tau} + 0.5K_\tau \,. \qquad (3)$$

This equation can be repeatedly applied to give estimates any number of years (t) into the past. When rearranged to explicitly display the population size t years earlier, and relabeling so that the initial abundance is N_0, one obtains

$$N_t = \frac{N_0}{\prod_{j=1}^{t}(1+R_j)} + \sum_{j=1}^{t} \frac{K_j(1+R_j/2)}{\prod_{i=j}^{t}(1+R_i)} \,. \qquad (4)$$

Note in this form that the time-index t runs backwards from zero. As is apparent in this form, the estimation of abundance t years earlier involves $2t+1$ parameters. The sequences of annual kills and net reproductive rates can be termed the kill and the net reproductive rate vectors, each composed of t elements.

The data used here to explore this estimation procedure is from the report of NMFS Workshop discussed above (see footnote 3).[4] From existing unpublished data and reports the Workshop participants used estimates of the population size in 1974 and the annual incidental kills and reproductive rates from 1959 to 1974. Several sequences of estimated annual kills and reproductive rates were considered, incorporating the uncertainty in the data.

In the present paper the sequences of annual kills and net reproductive rates given in Table 1 are used to illustrate several general aspects of the behavior of Equation (4). These correspond to the "high kill" and "central reproductive rate" sequences for the bridled dolphin, *Stenella attenuata*, in the Workshop report. The estimate of 1974 abundance used by us and the Workshop was 3.5 million.

Estimation of Bias

A sensitivity analysis was done to examine the effects of biased parameter estimates on the backcalculated abundance. A new population size 1 yr earlier, from Equation (3), when each parameter is changed by a specified amount is

$$N_1'(n, k, r) = \frac{N_0(1+n)+0.5K_1(1+k)}{1+R_1(1+r)} + 0.5K_1(1+k) \qquad (5)$$

and in general for t years earlier,

$$N_t'(n, k, r) = \frac{N_0(1+n)}{\prod_{j=1}^{t}(1+R_j(1+r))} + \sum_{j=1}^{t} \frac{K_j(1+k)\ (1+(R_j(1+r)/2))}{\sum_{i=j}^{t}(1+R_i(1+r))} \qquad (6)$$

where N_0, R_t, and K_t are defined as above, and

- n = the proportion that N_0 deviates from its estimate
- r = the proportion that all elements of the net reproductive vector deviate from their estimates
- k = the proportion that all elements of the kill vector deviate from their estimates.

$N'_t\,(n,k,r)$ was then compared with N_t from Equation (4) or equivalently $N'_t\,(0,0,0)$. As a measure of the sensitivity of the basic model, $S_t\ (n,k,r)$ is defined to equal the percent that $N'_t\ (n,k,r)$ deviates from N_t

[4]It should be noted that the estimates used here are based on a number of assumptions currently under investigation and that these estimates are subject to significant change in the near future (I. Barret, Director, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1978).

TABLE 1.—Estimates used for kill and reproductive rate vectors of *Stenella attenuata* in the eastern Pacific.

t	Year	Kill (thousands)	Net reproductive rate
1	1973	120	0.040
2	1972	273	.040
3	1971	185	.040
4	1970	308	.036
5	1969	331	.032
6	1968	164	.028
7	1967	194	.024
8	1966	281	.020
9	1965	297	.016
10	1964	255	.012
11	1963	133	.008
12	1962	106	.004
13	1961	446	.000
14	1960	534	.000
15	1959	129	.000

$$S_t(n, k, r) = \left(\frac{N_t(n, k, r) - N_t}{N_t}\right) \cdot 100 . \quad (7)$$

Estimation of Variance

The variance of the backcalculated estimate of N_t from Equation (4) was approximated using the delta method (Seber 1973). This method is based upon a Taylor series expansion for a function in which quadratic and other higher order terms are ignored. If f is a function of the random variables $x_1, x_2, x_3 \ldots, x_n$ then the expression for the variance of f by the delta method is

$$V(f(X_1, X_2, X_3 \ldots, X_n)) = \sum_{i=1}^{n} V(X_i)\left(\frac{\partial f}{\partial X_i}\right)^2 + 2\sum\sum_{i<j} \mathrm{Cov}(X_i, X_j)\left(\frac{\partial f}{\partial X_i} \cdot \frac{\partial f}{\partial X_j}\right) . \quad (8)$$

In applying this expression to Equation (4), it is necessary to be able to define which of the parameters should be considered as random variables, and to give reasonable estimates for value of the variances and covariances of these variables. For the purpose of exploring the behavior of Equation (4), we assumed that the estimates of all the parameters in Equation (4) are independent random variables. The covariance terms in Equation (8) are then zero. This approach provides a picture of the variance of the back estimate of abundance if in fact independent estimates of the kills and the net reproductive rates were available for each year. A generalized expression for the variance using this approach is

$$V(N_t) = V(N_0)\left(\frac{\partial N_i}{\partial N_0}\right)^2 + \sum_{j=1}^{t} V(K_j)\left(\frac{\partial N_i}{\partial N_j}\right)^2 + \sum_{j=1}^{t} V(R_j)\left(\frac{\partial N_j}{\partial R_j}\right)^2 \quad (9)$$

where all parameters are defined as for the basic model [Equation (4)]. For detailed expressions for each of the right hand terms see Appendix I.

As noted the method used for approximating the variance of a function depends on the higher order terms in the Taylor's series expansion being small. The higher order terms in the delta method expression for the variance of N_t are composed of the second and higher order derivatives of N_t with respect to N_0, K_t, and R_t, and the higher order central moments of the probability distributions of the estimates of N_0, K_t, and R_t (i.e., skewness, kurtosis, etc.). The second and higher derivatives with respect to N_t and K_t are zero. Thus the terms involving R_t are the only higher order terms not equal to zero. The higher order derivatives of N_t with respect to R_t involve R_{t+1} to increasing negative powers. The three higher order moments of R_t are always decreasing since R_t is much less than one. Thus each of the higher order terms in the delta method expression for the variance of N_t are each less than the first order term in R_t (iii of Appendix I). The contribution of this first order term in R_t to the variance of N_t is small, as shown below. Thus the error induced by ignoring the higher order terms in the Taylor's series appears small.

The objective in doing the variance calculations was to understand the behavior of the variance of the population size when estimated by the basic back projection model [Equation (4)]. Thus a range of variances was calculated for a range of reasonable values of the variances of the estimated parameters. However, in our example of bridled dolphin estimates of the variance of many of the parameters were not available. Many of the kill estimates were not independently estimated and hence have large unknown covariances (Smith and Polacheck[5]). Estimates of net reproductive rate were obtained by extrapolation from other populations and from assumptions about density dependence. It is not clear that the uncertainty in these estimates can adequately be described by the notion of variance. Thus, the variances that we used and that we calculated for N_t should not be interpreted as actual estimates of variance for this population.

RESULTS

Bias

The results of the sensitivity analysis of the basic model will be presented by examining the effects of varying each of the variables n, k, and r of Equation (7), separately, and then in combinations.

The sensitivity of the back projected estimates

[5]Smith, T. D., and T. Polacheck. 1977. Uncertainty in estimating historical abundance of porpoise populations. Contract Rep. MM 7A C006, 39 p. Marine Mammal Commission, 1625 Eye Street, Washington, DC 20006.

(S_t) for a fixed number of years t into the past is linear with respect to n or k (Figure 1). This linearity can be seen in Equation (6) since n and k enter only as linear terms in the numerator. Positive values of either n or k yield positive deviations in the back estimates. However, the farther back the population is projected in time, the smaller the contribution of N_0 to the back estimate becomes relative to the contribution of the kills. Thus the effect of bias in the estimate of the initial numbers (n) becomes progressively smaller the farther back in time the population is projected, while the consequence of a consistent bias in the kill estimates (k) becomes larger (Figure 2). Since the annual kills have no simple relationship to time, the effect of a particular value of n or k over time (Figure 2) cannot be described by any simple function. This trade off in the sensitivity of the back projected estimates between n and k is exact in the sense that for any decrease over time in the slope of S with respect to n there is an equivalent increase in the slope of S with respect to k. This can be seen by evaluating the partial derivates of S with respect to n and with respect to k and noting that they sum to 1.

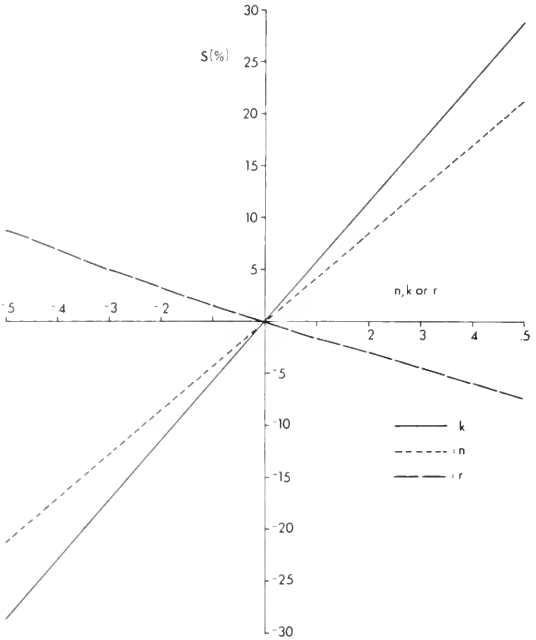

FIGURE 1.—Sensitivity of the model $S_t(n,k,r)$ in 1959 for a range of deviations in the initial number (n), for a range of deviations in the kills (k), or for a range of deviations in the net reproductive rate (r), for *Stenella attenuata* in the eastern tropical Pacific.

The effects of bias in the estimates of the net reproductive rate vector are more complicated than for the other two factors. Positive deviations in the net reproductive rates (r) yield negative deviations in the back projected estimate (Figure 2). The effect of r tends to increase over time (Figure 2). S approaches being linear with respect to r for any particular year, but unlike the relationship for k and n, this result is not exact (Figure 1). The approximate linearity of the sensitivity of N_t

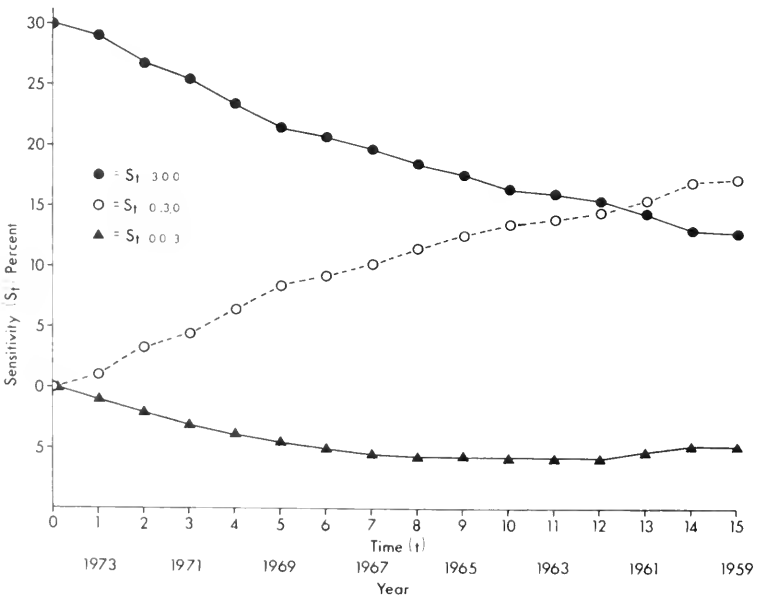

FIGURE 2.—Sensitivity of the model $S_t(n,k,r)$ over time to a 30% deviation in the initial number (n = 0.3), in the kill vector (k = 0.3), and in the net reproductive rate vector (r = 0.3) when all factors are held constant for *Stenella attenuata* in the eastern tropical Pacific.

to r appears to be a general feature of this procedure when r is small. This can be seen by examining S_t expressed as a function of r, which can be obtained explicitly by substituting the definitions of N_t [Equation (4)] and N'_t[Equation (6)] into Equation (7) and simplifying.

The consequences of having two factors varying simultaneously are shown in the series of contours of equal values of S from Equation (7) (Figures 3-5). These contour plots present a visual picture of the sensitivity of the back projection to the different factors. From this set of contour maps, it can be seen that the surface generated by S [Equation (7)] tends to be nearly linear. Since S has no nonlinear terms with respect to n and k, the surface described by S in these two dimensions is simply a plane (Figure 4). There are nonlinear effects between the net reproductive rate and both initial abundance and the sequence of kills. For the example examined here, the nonlinearity between k and r is insignificant. For instance, if r and k both equal 0.50, S deviates from a linear model by $<1\%$. In general the nonlinearity between k and r will be insignificant as long as the kills in any one year do not represent a large proportion of the population and as long as r is relatively small. Also, for the data considered here, the nonlinearity between the net reproductive rates and initial abundance is small but not insignificant. For example, if both n and r equal 0.50, S deviates from a linear model by as much as 5%. This interaction effect is negative, resulting in a surface's bending downward from a strictly linear model when n and r have the same sign.

If all three factors vary together, the surface

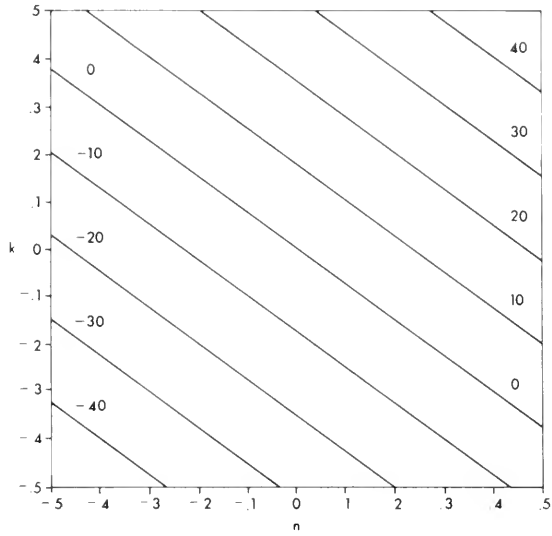

FIGURE 4.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the kill vector (k) when the net reproductive rate vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

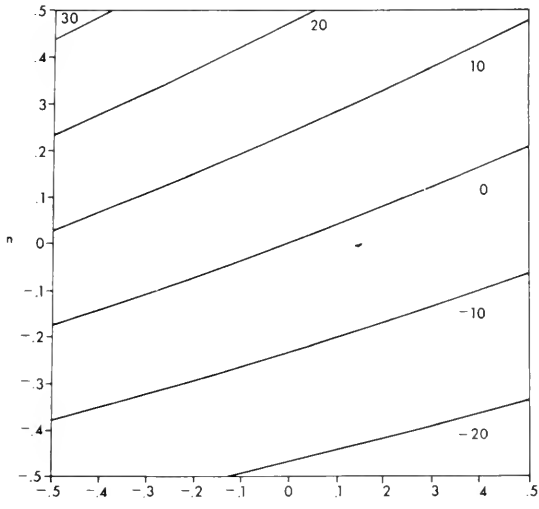

FIGURE 3.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the net reproductive rate (r) when the kill vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

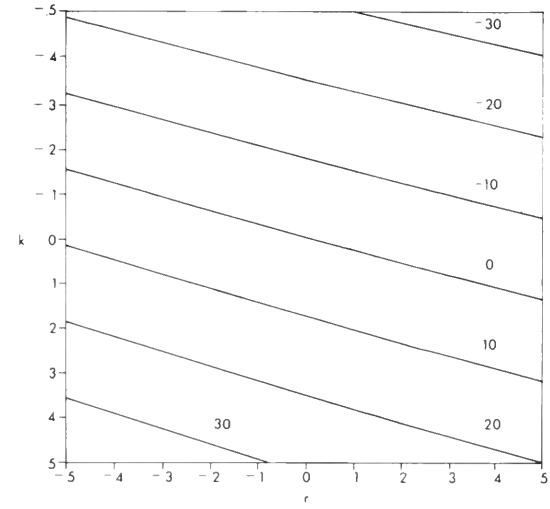

FIGURE 5.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the kill vector (k) and the net reproductive rate vector (r) when the initial number is held constant for *Stenella attenuata* in the eastern tropical Pacific.

generated by S is still relatively linear as there are no terms in S containing n, k, and r and the pairwise nonlinear effects are small as discussed above. Table 2 provides examples of points on this three dimensional surface when n, k, and r are equal in absolute values. It can be seen there, for the example examined, that if the absolute values of n, k, and r are 0.10, the sensitivity of N_{15} ranges from -12 to $+12$.

An empirical equation can be fitted to the sensitivity surface (S) by fitting a linear function for each factor considered independently and by determining a nonlinear term for n and r. The general form of this fitted equation is

$$\hat{S}_t\,(n,k,r) = (b_1K+b_2n+b_3r+b_4nr) \times 100 \quad (10)$$

where the b's are constant. The exact value of the b's depends on the number of years the population is projected back in time. For the example considered here, projecting back from 1974 to 1959, the values of the b's are shown in Equation (11):

$$\hat{S}_{15}\,(n,k,r) = (0.573k+0.427n-0.164r-0.125nr) \times 100. \quad (11)$$

This empirical approximation [Equation (11)] deviates by <2 from the true values of S_{15} for values of n, k, and r <0.5. This emperical equation is useful as the magnitude of the b's provides a measure of the relative sensitivity of the different factors. Thus in Equation (11) it can be seen that for the example considered here the 1959 abundance estimate (N_{15}) is most sensitive to bias in the estimates of the kills. This empirical equation also provides an easy way to generate approximate values of S for any combination of values for n, k, and r.

Variance

The results of the variance calculations for the bridled dolphin are summarized in Tables 3 through 6. Calculated values of the variance of N_t from Equation (9), when all of the random variables are assigned a coefficient of variation of 30%, are given in Table 3, over all years from 1974 to 1959. It can be seen that both the variances and the coefficients of variation (CV) generally decrease. The reduction of the CV over time is due to the fact that the major contributions to the back estimates of the population size are the addition of the kills of the previous years, since the reproductive rate is small. The variance of a sum of independent random variables is the sum of their variances. This always results in a CV for the sum which is smaller than the greatest CV of any of the random variables when the expected values of the random variables are positive (Appendix II). As a generalization, it can be stated that when the net reproductive rate is small the CV of the back estimate will not be larger than the largest CV of any of the random variables, and will usually be smaller.

Table 4 shows the breakdown of the variances calculated in Table 3 into their major components. The variance of N_0 is the major factor in the variance of these back estimates. The contribution of

TABLE 2.—Values of $S_{15}\,(n,k,r)$ when the absolute values of n, k, and r are equal.

Absolute value $\lvert k\rvert=\lvert n\rvert=\lvert r\rvert$	Sign of k	Sign of n + Sign of r +	Sign of n + Sign of r −	Sign of n − Sign of r +	Sign of n − Sign of r −
0.10	+	9	12	0	3
	−	−3	0	−12	−9
0.20	+	16	23	0	5
	−	16	1	−22	−17
0.30	+	24	36	1	8
	−	−10	2	−33	−26

TABLE 3.—Calculated variance and coefficient of variation for the back estimate of dolphin abundance when all random variables have a CV of 30%.

Year	Variance ($\times 10^{11}$)	CV (%)	Year	Variance ($\times 10^{11}$)	CV (%)
1974	11.03	30.0	1966	7.04	19.1
1973	10.22	29.0	1965	6.9	18.0
1972	9.53	27.0	1964	6.8	17.1
1971	8.88	25.7	1963	6.71	16.7
1970	8.35	23.8	1962	6.67	16.3
1969	7.99	22.1	1961	6.71	15.7
1968	7.56	21.2	1960	6.75	15.2
1967	7.25	20.2	1959	6.75	15.1

TABLE 4.—Breakdown of the variance of N_t into the major components that contribute to the calculated variance.

Year	Contribution to the variance of N_t ($\cdot 10^{16}$) due to the variance in: The initial number	The kills	The net reproductive rate
1974	110.3	0.00	0.000
1973	101.9	.12	.156
1972	94.2	.76	.305
1971	87.1	.10	.452
1970	81.2	1.755	.568
1969	76.2	2.604	.664
1968	72.1	2.70	.735
1967	68.8	2.91	.784
1966	66.1	3.49	.816
1965	64.1	4.16	.835
1964	62.5	4.64	.843
1963	61.5	4.73	.843
1962	61.1	4.99	.840
1961	61.1	5.24	.840
1960	61.1	5.55	.840
1959	61.1	5.56	.840

TABLE 5.—Coefficients of variation (CV) for the back estimates of bridled dolphin in 1959 (N_{15}) for a range of CV for the parameters of the model. The ranges of CV's of the kills, net reproductive rate, and initial abundances were selected to illustrate particular aspects of the behavior of the variances of the back estimates.

CV of the kills	CV of the net reproductive rate	CV of N_0			
		0	10	20	40
0	0	0	4.7	9.5	19.2
	40	2.2	5.3	9.8	19.3
10	0	1.4	5.0	9.6	19.2
	40	2.7	5.5	10.0	19.4
20	0	2.9	5.6	10.0	19.3
	40	3.7	6.0	10.3	19.5
40	0	5.6	7.5	11.2	20.0
	40	6.2	7.8	11.4	20.2
60	60	9.3	10.5	13.4	21.3
100	100	15.5	16.2	18.2	24.7

the variance of N_0 tends to completely dominate the variance of N_t because of the assumed independence of the kill estimates. Table 5 gives the CV for the back estimated population size of dolphin in 1959 for a range of CV for the different parameters involved in the estimate of N_{15}. As can be seen in this table, unless the variance of N_0 is near zero or unless the CV of the kill and reproductive vectors are extremely large (>60%), the CV of the back estimate does not exceed the CV of N_0.

Comparison of Equations (2) and (3).

A comparison of the estimated back abundance as calculated by the simpler model [Equation (2)] and the basic model [Equation (3)] for the dolphin population examined here is given in Table 6. The simpler model always gives a slightly higher estimate for the size of the back projected population but the increase in the estimate is always <1%. The sensitivities of the two models are nearly equivalent. When the values for the parameters in these models deviate as much as 50% the difference between sensitivities of the two models is <1%. The approximate variances of the back estimates of the two models are also similar.

TABLE 6.—Comparison of the back estimate of the abundance of bridled dolphin as calculated by the basic model [Equation (3)] and the simpler model [Equation (2)].

Year	Simple model ($\times 10^6$)	Basic model ($\times 10^6$)	Simple/basic
1974	3.500	3.500	1.000
1973	3.485	3.483	1.001
1972	3.624	3.617	1.002
1971	3.670	3.659	1.003
1970	3.850	3.835	1.004
1969	4.062	4.0416	1.005
1968	4.115	4.093	1.005
1967	4.214	4.190	1.006
1966	4.412	4.386	1.006
1965	4.640	4.612	1.006
1964	4.840	4.811	1.006
1963	4.934	4.905	1.006
1962	5.021	4.991	1.006
1961	5.467	5.437	1.005
1960	6.001	5.971	1.005
1959	6.130	6.100	1.005

That the difference between the original and the simpler model is small can be shown by analytically comparing the two models. If the projections are made only 1 yr into the past, the ratio of the estimate from Equation (2) to the estimate from Equation (3) is

$$1 + \frac{0.5R_1K_1}{N_0+K_1+0.5R_1K_1}.$$

Only if the value of R_1K_1 is large relative to N_0+K_1 can this ratio deviate significantly from 1. This is only possible if R_1 is relatively large. The general formula for the ratio of the two models is

$$1 + \frac{\sum_{j=1}^{t} 0.5K_jR_j\left(\prod_{h=1}^{j}(1+R_{h-1})\right)}{N_0 + \sum_{j=1}^{t} 0.5K_j\left(\prod_{h=1}^{t}(1+R_{h-1})\right) + \sum_{j=1}^{t} 0.5K_j\left(\prod_{h=1}^{j}(1+R_h)\right)}.$$

As in the case for projecting back only 1 yr, it can be seen that unless the R_jK_j terms are large relative to N_0 and unless the net reproductive rate is also large, the ratio of the two models will be close to 1.

DISCUSSION AND CONCLUSIONS

The results of this analysis indicate that errors in the input parameters do not compound in this procedure for estimating historical abundance. In fact, a systematic bias in the procedure for the estimation of a single set of parameters (either N_0 or R_t's or K_t's) always induces a bias in the back projected estimate which is less than the bias of the estimated parameters. This conclusion follows directly from the linear or near linear relation between S_t and n, k, or r with small rates of change. Moreover, the effects of bias in two or more sets of parameters are nearly additive. The interaction effects of bias in estimates of kills, net reproductive rates, and the initial number tend to

be small or nonexistent. This will be globally true for the relationship between k and n, but will be true for the relationship between k, r, and n only when the net reproductive rate is small. The relative importance of bias in K_t's, R_t's, or N_0 on N_t depends upon the actual values of the parameter. In the bridled dolphin example, after 15 yr, the back estimates were most sensitive to bias in the kill estimate, slightly less sensitive to bias in N_0, and considerably less sensitive to bias in the net reproductive rate. However, the importance of bias in N_0 will diminish with the number of years in the back estimate with a proportionate increase in the importance of bias in the kills.

The sensitivity analysis developed in this paper will include the extremes of a complete sensitivity analysis of the model. The values for $S_t(0,k,0)$ are limiting values to a complete sensitivity analysis of the individual elements of the kill vector on N_t. Similarly $S_t(0,0,r)$ is a limit to complete sensitivity analysis of the individual elements of the net reproductive rate. Given the additivity of S_t with respect to n, r, and k, the surface $S_t(n,k,r)$ contains the extremes of a sensitivity analysis in all $2t+1$ dimensions. If in fact the elements within the kill vector and within the reproductive vector are highly interdependent (as is the case for the data used here), then the sensitvity analysis used to look at the effects of bias in this paper approaches a total sensitivity analysis of the back projected estimate given these constraints.

The variance approximations also indicate that variability in the parameter estimates does not result in compounding uncertainty in the back projected estimates. When estimates of the parameters are independent and the net reproductive rate is low, the CV of the back estimate will be smaller than the CV of the input parameters. In our example if all the CV's were equal, the variance of N_0 would make the largest contribution to the estimated variance of N_t. In general this will be true as long as the kills in any one year do not approach the initial abundance. This is a direct consequence of the basic additivity of the model when the net reproductive rate is small.

In Smith and Polacheck (see footnote 4), an alternative probability structure was considered in which the elements within the kill vector and within the net reproductive rate vector were highly interdependent. In this situation, the variance of N_t is not completely dominated by the variance of N_0. The variances of N_t calculated using this interdependent probability structure are larger than the variances presented here in which all the parameters are assumed independent. However, the CV of N_t for the dolphin data within this interdependent probability structure is still less than the CV of the parameters if all parameters have equal CV. It appears that even in the situation in which a high degree of interdependence exists within the kill estimate or the net reproductive estimates, the variability in the parameter estimates does not induce compounding uncertainty in the back projected estimate.

The comparison of the results from the basic model [Equation (3)] with the simpler model [Equation (2)] indicate that there are no significant differences between the two models as long as the net reproductive rate is small. Thus it appears that there is no reason to favor the more complex model over the simpler.

In conclusion, it appears that this back projection procedure (either model) has reasonable statistical properties, at least when the net reproductive rates are small. However, Equation (1) is a simplified description of how the abundance of a population changes through time, especially in not accounting for changes in age structure. The authors feel that caution should be used in applying estimates from this procedure to the management of long-lived species since changes in the age structure for long-lived species are likely to be important.

ACKNOWLEDGMENTS

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Appendix I.—Expressions for the variance components of N_t.

Expression for the right hand terms of Equation (9) are:

$$V(N_0)\left(\frac{\partial N_t}{\partial N_0}\right)^2 = V(N_0)\left(\frac{1}{\prod_{j=1}^{t}(1+R_j)}\right)^2 \tag{i}$$

$$\sum_{j=1}^{t} V(K_j)\left(\frac{\partial N_t}{\partial K_j}\right)^2 = \sum_{j=1}^{t} V(K_j)\left(\frac{1+0.5R_j}{\prod_{h=j}^{t}(1+R_h)}\right)^2 \tag{ii}$$

$$\sum_{j=1}^{t} V(R_j)\left(\frac{\partial N_t}{\partial R_j}\right)^2 = \sum_{j=1}^{t} V(R_j)\left(\frac{N_{j-1}+0.5K_j}{(1+R_j)^2\prod_{k=j+1}^{t}(1+R_k)}\right)^2. \tag{iii}$$

Appendix II.—Coefficient of variation of a sum of random variables.

The following is a proof that the coefficient of variation of a sum of two independent random variables is smaller than the greatest CV for either of the random variables if the expected value of the random variables is greater than zero.

If A and B are independent random variables such that

$$E(A) = a>0 \quad E(B) = b>0 \text{ and}$$

$$CV(A) = \frac{\sqrt{V(A)}}{a} \geqslant \frac{\sqrt{V(B)}}{b} = CV(B)$$

then

$$\frac{V(A)}{a^2} \geqslant \frac{V(B)}{b^2},$$

$$V(A)b^2 \geqslant V(B)a^2,$$

$$V(A)(b^2 + 2ab) > V(B)a^2,$$

$$V(A)(b^2 + 2ab) + V(A)a^2 \geqslant V(B)a^2 + V(A)a^2,$$

$$V(A)(a + b)^2 \geqslant [V(B) + V(A)]a^2,$$

$$\frac{V(A)}{a^2} > \frac{V(B) + V(A)}{(a + b)^2} = \frac{V(A + B)}{[E(A + B)]^2},$$

$$CV(A) > CV(A + B).$$

LARVAL DEVELOPMENT OF *GALATHEA ROSTRATA* UNDER LABORATORY CONDITIONS, WITH A DISCUSSION OF LARVAL DEVELOPMENT IN THE GALATHEIDAE (CRUSTACEA ANOMURA)[1]

ROBERT H. GORE[2]

ABSTRACT

The complete larval development of the western Atlantic anomuran crab, *Galathea rostrata*, consists of four or five zoeal stages, and a single megalopal stage, based on larvae cultured under laboratory conditions. Variation in the duration and number of zoeal stages appears to be temperature-dependent, with larvae reared at 15°C developing through five zoeal stages and attaining megalopa in 52 days, whereas larvae cultured at 20°C passed through four or five zoeal stages, reaching megalopa in 18 or 23 days, respectively. At 20°C some third stage zoeae molted to a "regular" fourth zoeal stage, without pleopods, which was followed by a subsequent fifth stage before reaching megalopa. Other zoeae molted to an "advanced" fourth stage, possessing pleopods, which subsequently molted directly to megalopa, bypassing stage V completely. The variation noted in larval development in other galatheid genera is briefly discussed, and a provisional synopsis of morphological characters of systematic value is provided for their identification.

The anomuran crab genus *Galathea* is presently represented in the western North Atlantic by two species, *G. agassizii* and *G. rostrata* (A. Milne Edwards 1880). *Galathea agassizii*, primarily tropical and insular in distribution, is a deepwater species known from 166 to 490 fm (304-897 m) off St. Augustine, Fla., and from Cuba, St. Vincent, St. Lucia, and Barbados in the Caribbean Sea. In the eastern Atlantic the species is found from 82 to 898 fm (150-1,643 m) in the vicinity of both the Cape Verde and Canary Islands, and off northwestern Africa (Chace 1942; Miyake and Baba 1970). Contrarily, *G. rostrata* appears to be a warm-temperate or tropical/subtropical species, primarily continental in distribution. The species is recorded from the North American continental shelf at Cape Hatteras, N.C., to southeastern Florida, and in the Gulf of Mexico from western Florida, the Mississippi Delta, and southward to Islas Jolbos, north of the Yucatan Peninsula. There is a questionable record from off Rhode Island (Williams 1965). *Galathea rostrata* is also found in shallower water than *G. agassizii* and has been collected from 10 to 50 fm (18-92 m), with the exception of the possible depth record of 1,178 fm (2,156 m) from off Rhode Island. The only distributional record of the species for the entire eastern Florida coast was that of Haig (1956) who reported a single specimen collected from 21 fm (38 m) off Hillsboro Lighthouse (Broward County) in southeastern Florida. However, recent collections show that the species is not uncommon in the Indian River region of the central eastern Florida coast, especially on deeper water (60+ m) coquinoid limestone ledges and reefs of the ivory tree coral, *Oculina varicosa* Leseuer.

The few studies made on the larval development of new world galatheid crabs (e.g., Rayner 1935; Boyd 1960; Fagetti 1960; Boyd and Johnson 1963; Fagetti and Campodonico 1971) have all been made on eastern Pacific species, and the larvae of Atlantic American galatheids, including the genus *Galathea*, remain undescribed.

This paper provides the first description and illustration of the complete larval development of *G. rostrata*, as well as the first report on any species of *Galathea* reared totally under laboratory conditions, from hatching to megalopal stage. The larvae and postlarvae are compared with larval stages known from other members of the Galatheidea throughout the world, and shared features are briefly summarized.

MATERIALS AND METHODS

Eight ovigerous females of *G. rostrata* were obtained on 15 April 1977 by lockout diver from the

[1]Scientific Contribution No. 100, from the Smithsonian Institution-Harbor Branch Foundation, Inc., Scientific Consortium, Link Port, Ft. Pierce, Fla. This report is Article IX. Studies on Decapod Crustacea from the Indian River Region of Florida.

[2]Smithsonian Institution, Ft. Pierce Bureau, Ft. Pierce, FL 33450.

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Research Submersible *Johnson-Sea-Link II*, of the Harbor Branch Foundation, Inc. The adult galatheids inhabited a large clump of ivory tree coral which grew in 80 m of water on Jeff's Reef, lat. 27°32.8'N, long. 79°58.8'W, located about 17 n. mi. (27 km) northeast of Ft. Pierce Inlet, Fla. The entire coral colony was collected and returned to the surface inside of a 500-μm mesh cloth bag. Ambient seawater temperature on Jeff's Reef was 12°C at time of collection. The galatheids were immediately placed in compartmented plastic trays containing recently collected neritic seawater previously chilled to 10°C. Upon return to the laboratory each adult specimen was transferred to individual 100 × 80 mm covered glass laboratory dishes filled with approximately 340 ml of seawater previously chilled to 15°C. Each isolated female was maintained at this temperature, provided a change of chilled seawater, and fed freshly hatched *Artemia salina* nauplii, daily. All specimens were exposed to a 12-h light-12-h dark illumination program in a controlled temperature unit (CTU) until hatching occurred. Five females survived in this regimen and yielded larvae over a period from 16 April to 6 May 1977.

Seven larval series were initiated. Using methodology previously described by Gore (1968), five such series were cultured in 24-compartmented plastic trays. These consisted of two series of 8 and 24 larvae, held in the CTU at 15°C (±0.5°C), and three series of 24 larvae each, maintained at cool laboratory room temperature (ca. 20°C, ±1°C). Two mass culture series of about 30 larvae each were also established in individual 100 × 80 mm glass dishes at cool laboratory room temperature, which was controlled by reverse-cycle air conditioning, and was monitored daily with a 7-day recording thermometer. Fresh surfzone seawater (35.5-36‰) was collected weekly, filtered through glass wool, stored in 14-gal (ca. 56-l) polypropylene carboys, and used throughout the rearing period.

All larval series were checked daily, and any molts or dead individuals were recorded and preserved in 70% ethanol. Specimens were examined microscopically, slides prepared, and drawings made as described in previous studies by Gore (1968). Measurements given below are the arithmetic average of all specimens examined in any particular stage. A complete series of larvae, or their molts, is deposited in the National Museum of Natural History, Washington, D.C. (USNM 170862); the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 1028-01); the British Museum (Natural History), London (BMNH 1978:103); and the Rijksmuseum van Natuurlijke Historie, Leiden (D 31735).

RESULTS AND DISCUSSION OF THE REARING EXPERIMENT

Galathea rostrata passes through four or five morphologically distinct zoeal stages and a single megalopal stage, before completing development in the laboratory. Culture temperature undeniably affects duration of development, and perhaps larval survival as well. While the duration of the zoeal and megalopal stages differed at each rearing temperature, it was nevertheless generally consistent within each of the temperature series, as will be discussed below.

At 15°C five morphologically distinct zoeal stages were observed for those larvae surviving to metamorphosis. The minimum time required to pass through these stages and attain megalopal stage was 52 days. Most larvae remained in each zoeal stage approximately 9-11 days through the first four stages. Only two stage V zoeae survived, and they remained as such 14 and 16 days before molting to megalopa. However, neither of these specimens survived longer than 6 or 7 days as megalopae, so the mean duration of the postlarval stage at 15°C remains unknown (Table 1). With the minimum noted period of 6-7 day duration for megalopae at this temperature, completion of development and metamorphosis to first crab stage

TABLE 1.—Duration of larval and postlarval development in *Galathea rostrata* under laboratory conditions at the indicated temperatures.

Temp and stage	Days required to attain next stage			
	Min	Mean	Mode	Max
15°C:				
I	10	10.8	10	14
II	8	9.7	10	[1]16
III	9	10.5	9	17
IV	8	9.4	9	11
V	14	—	—	16
Mg	6-7	(Both megalopae died in stage)		
20°C:				
I	5	5.8	6	7
II	4	4.2	4	5
III	4	4.1	4	5
IV (regular)	5	5.7	6	6
V (regular)	5	5.8	6	6
IV (advanced)	3	3.3	3	4
Mg (combined)[2]	12	12.6	13	13
III-IV (intermediate)	7	—	—	8 (Died in stage)

[1]One zoea remained 30 days in stage II, dying 13 days later in stage III.
[2]Combined megalopae data include stages obtained from both IV (advanced) and IV (regular).

is conservatively estimated to take well over 60 days (Figure 1).

At 20°C either four or five morphologically distinct zoeal stages occurred. The minimum time required to complete larval development and reach megalopa was 18 days. Most larvae remained in each zoeal stage from 3 to 6 days and as megalopae from 12 to 13 days. The total duration of development from hatching to first crab stage spanned a minimum of 30 days at 20°C, if only four zoeal stages were required, but took at least 37 days with five zoeal stages (Figure 1, inset).

The larvae generally fared well at both culture temperatures. Although the larvae at 15°C took longer to complete their development, they initially appeared to survive better than their counterparts at 20°C (Figure 1). At 15°C, at least 50% larval survival occurred through stage IV, before a rapid decrease occurred in stage V and megalopa. Larvae reared at 20°C exhibited a steep decline after stage 1, to about 35% survival, and showed a continual decline thereafter. The precipitous decline in larval survival at this temperature from stage I to stage II was the result of an almost complete mortality in one culture tray, for unknown reasons.

At 15°C ecdysis in the earlier zoeal stages (I-III) generally was a less critical period than at 20°C, although the larvae at the latter temperature were still able to complete most molts. The larvae at 20°C attained subsequent stages more rapidly than did those at 15°C, and some were able to complete zoeal development, although overall larval mortality was relatively higher. On the other hand, at 15°C larval survival may have been enhanced by lower temperature, but the major difficulty then seemed to be the attainment of stage V and megalopa. Only two megalopae were obtained in the 15°C program and neither was able to molt to the succeeding first crab stage. In contrast, four megalopae survived at 20°C, and molted to crab stage I; three of these specimens were maintained in the laboratory to crab stages XII and XIV.

Ecdysial and Sequential Variation in *Galathea rostrata*

Two modes of developmental variation were noted in *G. rostrata* at 20°C. In one mode, some zoeae III molted to an instar which, for purposes of discussion, is labelled "regular" stage IV. This stage was characterized, among other features, by a reduced number of antennular aesthetascs and was always without well-developed pleopod buds on the abdominal somites. Zoeae remained in this stage for 3-4 days before molting to stage V, an instar possessing distinct, well-developed, pleopod buds and an increased number of antennular aesthetascs. The duration of stage V lasted 5-6 days and was followed by the molt to megalopa. One of these postlarvae subsequently molted to first crab stage.

In the second mode of variation, some zoeae III molted to an "advanced" stage IV, with some, but not all, of the features as noted above for stage V. Zoeae remained longer in the advanced stage (5-9 days) before molting directly to megalopa. Three of these megalopae went on to attain first crab stage. The two types of development are compared in the inset of Figure 1.

Two other stage III zoeae, which remained in stage III 7-8 days (instead of the usual 4-5), molted to what appeared to be an intermediate stage IV. These zoeae exhibited some stage V zoeal features in size, maxillipedal setae numbers, and in possessing pleopod buds, although the latter were only rudimentary. A reduced number of antennular aesthetascs similar to that of regular stage IV zoeae was also seen. The two specimens survived only 4-5 days in this stage before dying. This mode of variation was not considered as important as the previous two modes and will not be discussed further.

Remarks

The regular and advanced fourth stages cannot be equated to an early and late fourth stage, nor to substages IVa and IVb, because no molt occurred from one fourth stage or substage to another. If the molt from stage III was to regular stage IV, this was invariably followed by an ecdysis to stage V, and then a subsequent molt to megalopa. If the molt from stage III produced an advanced stage IV, this in turn molted directly to megalopa, skipping stage V altogether. At 15°C the regular stage IV and stage V appear to be necessary plateaus in larval development, whereas at 20°C development may proceed in some zoeae without resorting to either of these instars.

The regular fourth zoeal stage (as defined above), therefore, appears to be a true sequential stage of development, inasmuch as it was seen in larvae at both 15°C and 20°C programs. However, it is also a stage which can occasionally be skipped

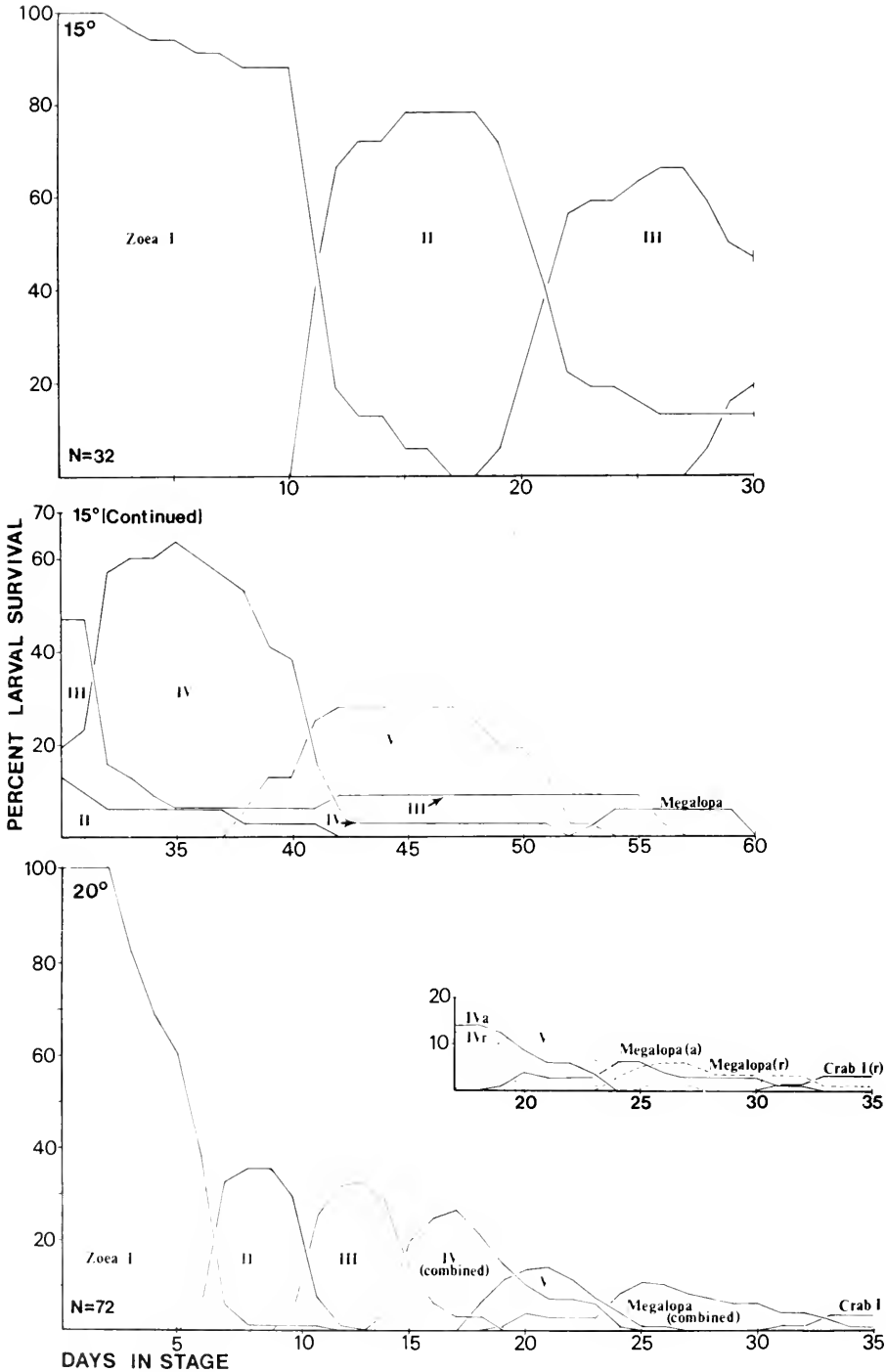


FIGURE 1.—Percentage survival and duration of stages in larvae of *Galathea rostrata* reared under laboratory conditions at 15°C (upper 2 graphs) and 20°C (lower graph). Inset at 20°C gives duration and survival of regular (IVr, dashed line) and advanced (IVa, solid line) stages; number of days the same as in larger graphs.

by some 20°C larvae, and thus could be thought of as an intercalated stage, if the advanced stage IV be considered more indicative of the developmental sequence. Other features shared between the advanced fourth and regular fifth zoeal stages (besides the presence of well-developed pleopod buds noted earlier) include increased numbers of antennular aesthetascs, a remarkable elongation of the antennal endopodite, the appearance of a mandibular palp, and slight changes in setae number on maxillulae, maxillae, maxillipeds, and telsonal uropods (see section on Description of the Larvae). Moreover, the advanced stage IV zoeae were always larger than the regular stage IV zoeae.

It will probably remain a question of semantics whether the regular stage IV is considered an intercalated stage or one that occasionally may be skipped. It could just as well be asked whether the advanced stage IV was an intercalated stage because it embodies many of the features of regular stage IV, plus some seen only in stage V zoeae in the developmental sequence. What is of more importance in the development of *G. rostrata* is that the substitution of an advanced stage IV and the subsequent elimination of the regular stages IV and V allows earlier postlarval metamorphosis. The resultant early benthic crab stages may be reached in a shorter period of time by the species, thereby reducing the time spent in the plankton.

Discussion

It is, of course, conjectural as to whether the larvae of *G. rostrata* skip stages in their development in the natural environment or are ever subject to constant low (e.g., 15°C) or intermediate (20°C) seawater temperatures. The adults of the species, found in deeper continental shelf waters, presumably are often exposed to cool seawater temperatures, as was noted, e.g., during the time the adult females for this study were collected. It is not unreasonable to assume that developmental stages may occasionally be subjected to relatively constant cool temperatures as well, either immediately after hatching or just prior to postlarval metamorphosis when the megalopae settle to the sea floor. In addition, should the larvae become entrained in cyclonic cold core rings of Gulf Stream origin (see Richardson 1976; Wiebe 1976; Wiebe et al. 1976), they would presumably be subjected to relatively constant cold water (at least 17°C) for at least part of their developmental period. Delayed metamorphosis provides an alternative hypothesis against the more traditional "stepping-stone" idea, to account for the rather extensive distribution of the species along the Middle and North American continental shelves.

There is some evidence that larvae of other species of *Galathea* may skip stages in the plankton (Lebour 1930, 1931) and that other galatheids may intercalate substages (e.g., Boyd and Johnson 1963). For example, the larvae of four of the five British galatheids described by Lebour, viz. *Munida rugosa* (Fabricius 1775 [as *M. banffica* = *M. bamffica* (Pennant 1777)]), *Galathea intermedia* Lilljeborg 1851, *G. squamifera* Leach 1814, and *G. strigosa* (Linnaeus 1767) developed through four zoeal stages, whereas *G. dispersa* Bate 1859, exhibited four or five stages. Lebour (1930) considered five stages in the latter species as "probably normal" but pointed out that the megalopa could be obtained from the fourth [numerical] stage, and "the normally fifth [numerical] stage has been seen to emerge from the third stage." She stated that the fourth or fifth stage may therefore be omitted in *G. dispersa*, but made no mention of intercalated stages or substages.

The developmental situation in *G. dispersa* is quite similar to that noted in this report for *G. rostrata*, in which an advanced fourth stage replaces the regular fourth and fifth stages, thereby causing them to be omitted from the developmental sequence. Lebour's (1930) "fifth stage. . . from third" is probably equivalent to what is termed in this report the advanced fourth stage. Her statement that long, unjointed pleopods appear in the "last" stage of *G. dispersa* indicates that either the fourth stage (or advanced) or fifth stage (or regular) possess these appendages, depending on whichever stage is "last." It also indicates that the molt to megalopa does not occur without the appearance of pleopods in the "last" larval stage. However, North Sea species of *Galathea* differ from *G. rostrata* in possessing pleopod primordia "in the third stage" which are "long but unjointed in the last stage" (Lebour 1930). In addition, Sars (1889) had also noted and illustrated pleopod development in the "last" stage of larvae attributed to *G. intermedia*, *Munida rugosa*, and *Munidopsis* [as *Galathodes*] *tridentata* (Esmark 1857). The latter species will be considered further below.

Rayner (1935), using planktonic stages from Argentinian waters, described the larvae he attributed to *Munida gregaria* (Fabricius 1793) and

M. subrugosa (White 1847). Rayner did not note any substages or skipped stages in the five instars he described for the two species, and was not certain whether additional stages followed. By analogy with *M. rugosa* [as *M. bamffica*] he thought it possible that the next stage would be postlarval. In this he was probably correct, but it seems strange in retrospect that Rayner did not attach importance to the well-developed pleopods on the larvae before him, a feature by which he earlier characterized the fifth zoeal stage. These appendages in other galatheid larvae are quite obviously developed at stage V (see Lebour, Sars, Boyd and Johnson, and others), and Sars (1889) even drew attention to them when describing his "last zoeal stage."

Intercalation of substages, however, is known in the genus *Pleuroncodes,* as was specifically discussed by Boyd and Johnson (1963) in the larvae of *P. planipes* Stimpson 1860.[3] Five zoeal stages had been initially noted in this species (Boyd 1960), but a sixth stage, apparently unnatural and not known to occur in the plankton, could be induced in the laboratory. Boyd and Johnson thought this stage was due to the presence of penicillin pills or to the $CaCO_3$ buffer in the pills, used to control bacterial growth in the cultures. These authors also stated that numerical stage IV could be subdivided into a complex of from four to nine substages, each represented by a molt, all without pleopods, but otherwise morphologically similar to each other. Although no sequential substages were skipped (e.g., a molt from substage IVa to IVh), one or more substages could be omitted terminally, with a subsequent molt to the morphologically discrete stage V, which possessed pleopods (Boyd 1960). Boyd and Johnson suggested that in *P. planipes* the number of substages in stage IV was probably influenced by temperature, with higher culture temperatures (e.g., 16°-20°C) producing faster development but causing more substages to occur before the molt to stage V. They noted, however, that other factors such as food supply or crowding of larvae might also exert an effect on the number of substage instars, but neglected to consider the possibility that the large number of induced substages in stage IV might also be due to the use of antibiotics in the cultures, as suggested by Fagetti and Campodonico (1971).

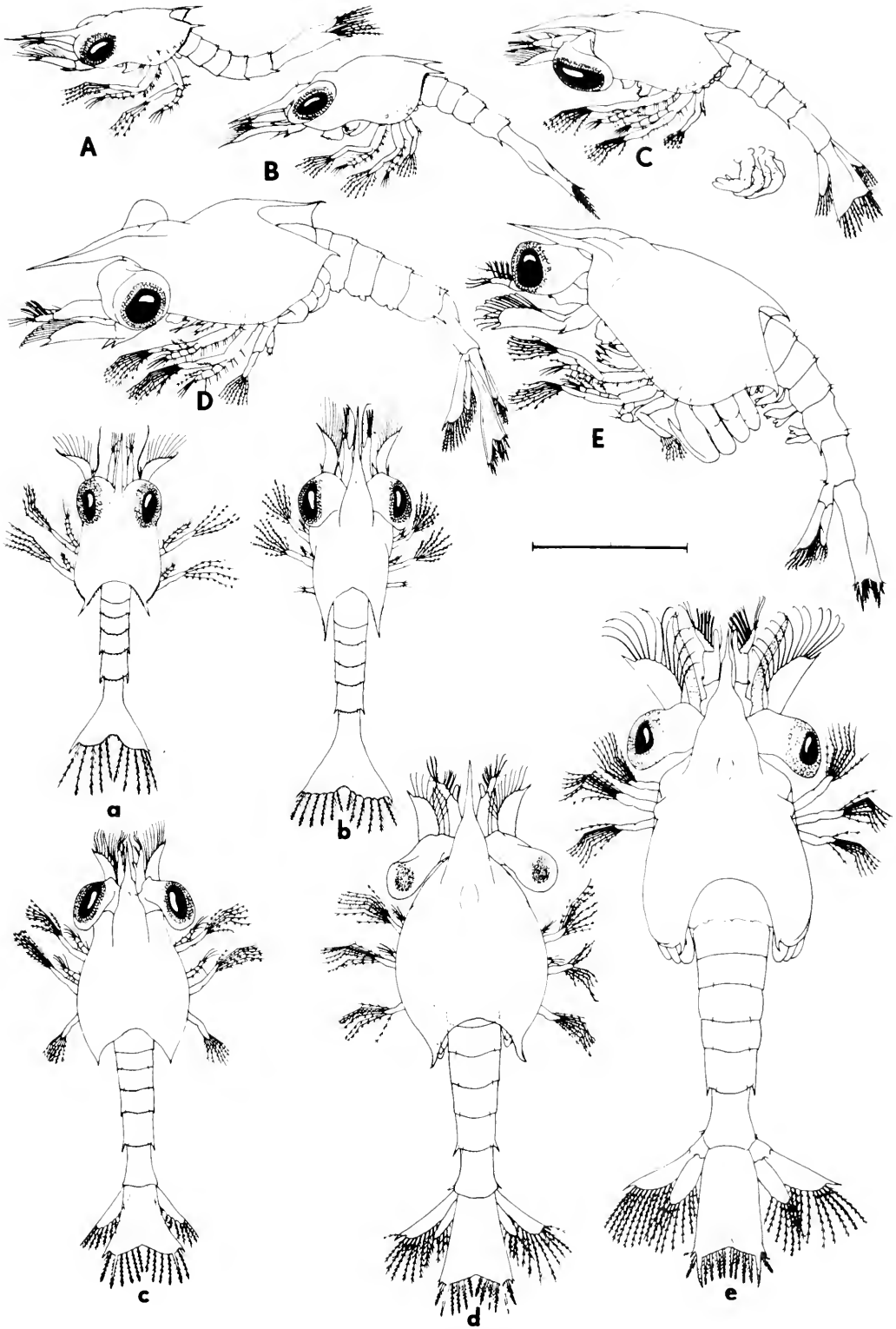
[3]Both Stimpson (1860) in his original description of *Pleuroncodes planipes* and Haig (1955) have suggested that the species may prove to be only a northern Pacific form of the Chilean *P. Monodon.*

FIGURE 2.—*Galathea rostrata*, zoeal stages in lateral and dorsal view: (A, a) First zoea; (B, b) second zoea; (C, c) third zoea; (D, d) fourth zoea (regular); (E, e) fifth zoea. Scale line equals 1.0 mm.

The Chilean congener, *Pleuroncodes monodon* Milne Edwards 1837, also was found to have intercalated substages (Fagetti and Campodonico 1971). At 15°C, substage IVa-d were followed by a molt to stage V, possessing pleopods; at 20°C a fifth substage (IVe) was attained instead of zoeal stage V. Whether stage IVe would be followed by ecdysial stage V is not known because all larvae in stage IVe died. However, the lack of pleopods in stage IVe implies that stage V should occur, with pleopods, before the molt to megalopa takes place. Whether such substages occur in the plankton is conjectural, but they certainly would present some difficulty in separation because of their great similarity to each other in samples collected from the plankton.

Abbreviated larval development is also known to occur in at least two galatheids. Sars (1889), in describing the prezoel, "first" and "last" zoeal stages of *Munidopsis tridentata* from Norwegian waters suspected that development time was shorter than that seen in *Galathea*, but came to no conclusion as to the total number of stages. He commented on the remarkably advanced features exhibited in the early zoea, an observation later supported by Samuelsen (1972). Samuelsen determined that only three zoeal stages exist for *M. tridentata* and further suggested that the megalopal stage followed stage III because the latter stage was in the same relative state of development as some fourth zoeae which preceded the megalopae in other galatheids. Samuelsen noted that the presence of a mandibular palp, pleopod primordia, antennular aesthetascs, antennal setae, and scaphognathite setae in the early zoeal stages were all advanced features usually restricted to later zoeae in other galatheid larvae. The relatively nonsetose feeding appendages and endopodites of the natatory appendages indicate that the larvae may not feed, although they can swim well.

Al-Kholy (1959) described and figured larvae attributed to a "*Galathea* sp." which apparently developed through only three zoeal stages. However, no methodology was given, nor indication as to whether the larvae were cultured in the laboratory or collected from the plankton. It is doubtful whether the species will ever be identi-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fiable based on his incomplete descriptions and rather stylized illustrations.

Advanced development[4] is implied in but one galatheid, the cave-dwelling *Munidopsis polymorpha* Koelbel 1892. This species is presently known only from a littoral cave formed by lava tunnels which connect to the sea in the Canary Islands (Fage and Monod 1936). These authors never found more than five, extremely large (1.5-1.8 mm in diameter) eggs on an individual female. No larval stages were described, but it was hypothesized that the young *Munidopsis* was well advanced in development inside the egg and probably hatched into a form nearly like the adult. Given the rather unique habitat for a *Munidopsis*, advanced development in *M. polymorpha* would not be surprising. The vast majority of other species of *Munidopsis* are deep-sea forms, most of which occur below 500 m (Mayo 1974) in the Atlantic Ocean, although some species occur in shallower waters on the continental shelf.

In summary, it is apparent that larval development in the Galatheidae is quite diverse, including advanced development (i.e., with imminent metamorphosis) in the cave dwelling *M. polymorpha*, abbreviated development with as few as three larval stages (*M. tridentata*, Al-Kholy's *Galathea* sp.?), to "normal" development of four-five zoeal stages (e.g., *Munida*, *Galathea*). Substage intercalation is known in the genus *Pleuroncodes*, but seems to be restricted to the fourth, or penultimate, ecdysial stage. Intercalation of a sixth zoeal stage, perhaps only a laboratory artifact, is also known in one species of this genus. Skipped stages appear only in two species of *Galathea*, and perhaps one of *Munida*, at present, and these result in the elimination of regular zoeal stages IV and V and their replacement by an advanced stage IV which subsequently molts directly to megalopa.

Developmental variation such as that just discussed allows some interesting speculation as to its evolutionary consequences in view of the fact that the phylogenetically closely related anomuran family Porcellanidae generally undergo a reduced developmental sequence of usually no more than two zoeal stages. These stages appear to be morphologically equivalent in most respects to *Galathea* stages I and IV, sensu lato. Substages have been postulated for some porcellanid larvae, notably Indo-Pacific species, but are not positively known to occur in Atlantic and eastern Pacific species. Previously postulated substages in Atlantic species have been shown to be the result of accelerated morphological development without an ensuing molt and have been seen primarily in larvae collected from the plankton (Gore 1968 and others). However, the larvae of the western Pacific genus *Petrocheles* apparently do reflect their galatheid ancestry by undergoing five zoeal stages during development. Morphological features of the telson, uropods, and antennal scale in these larvae all resemble, to a greater or lesser degree, their counterparts in larvae of *Galathea* and *Munida* (Wear 1965). Further studies along these lines should be most interesting and productive.

DESCRIPTION OF THE LARVAE

First Zoea

Carapace length: 1.0 mm.
Number of specimens examined: 10.

Carapace: (Figure 2A, a). Typically galatheid, somewhat inflated; rostral spine horizontal, little expanded proximally, straight, extending to level of scapherocerite spine, or slightly beyond, about 0.5× carapace length(CL), unarmed; posterolateral carapace margins armed with a series of about 15 small denticles placed before large, posterior spine; latter slightly more than 0.1× CL; dorsomedial carapace margin excavated, with about 13 small denticles along sinus margin. Two small setae medially above eyes; latter sessile.

Antennule: (Figure 3A). A simple rod, both endopodite and exopodite fused to protopodite; former with 1 elongate plumose seta, latter with 3 aesthetascs and 3 setae.

Antenna: (Figure 3B). Endopodite rodlike, about 0.4× scaphocerite length, fused to protopodite, a single distinct spine at its tip, plus a long plumose seta; scaphocerite usually with 9 setae along margin, tip produced into long daggerlike spine about 0.3× total scale length; protopodite

[4]The term "direct" development is restricted in this paper to those larvae which hatch from the egg in a form morphologically similar to the adult and undergo no further metamorphosis. Larvae exhibiting "advanced" development usually hatch in the penultimate or ultimate zoeal stage and thus may undergo additional ecdysis prior to metamorphosis. Larvae with "abbreviated" development hatch as early zoeae (often with a prezoeal or first zoeal stage present), but may dispense with one or more intermediate stages in completing their larval development.

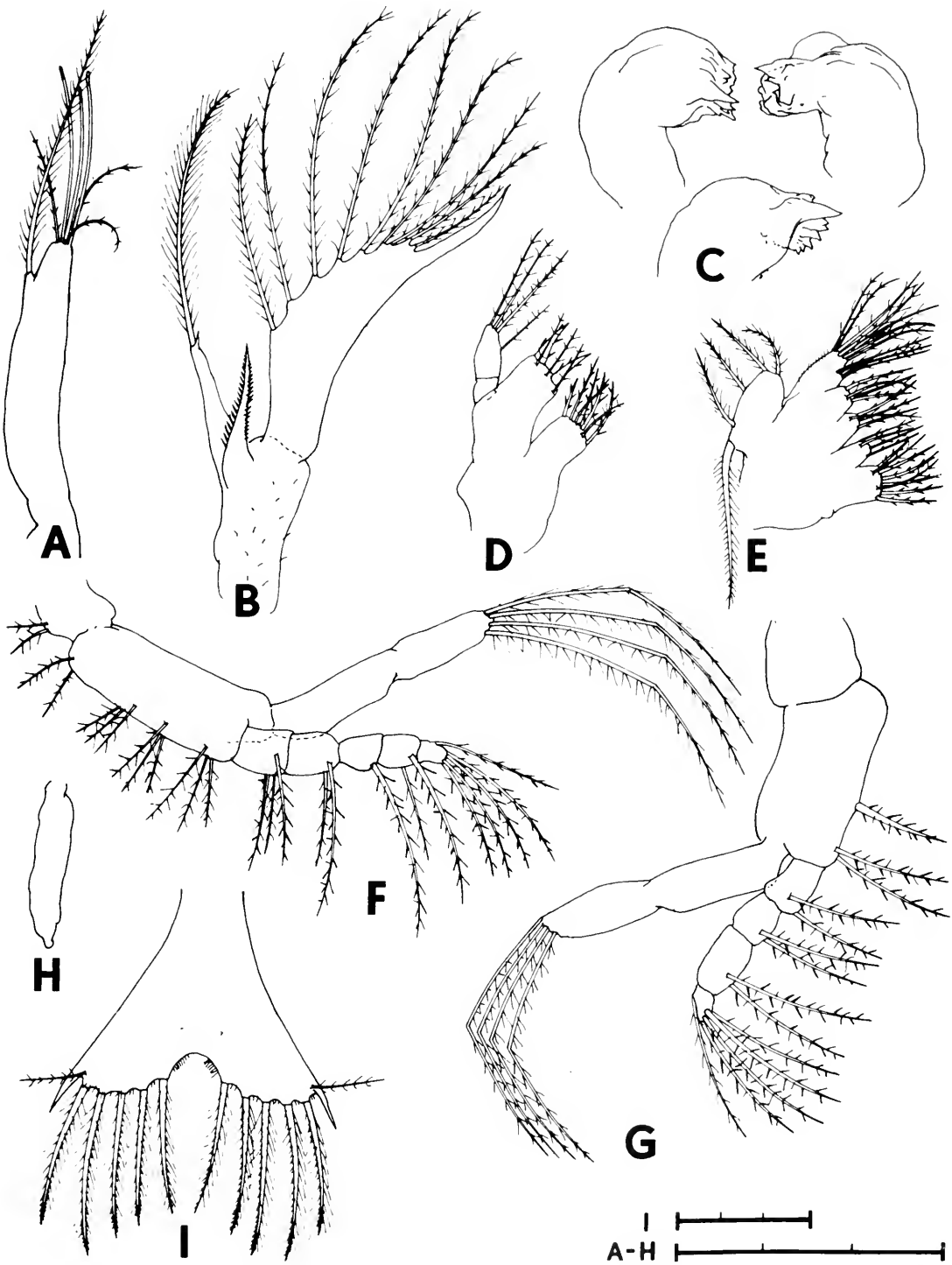


FIGURE 3.—*Galathea rostrata*, first zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated interiorad to zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxillped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

with sharply pointed spine ventrally, armed along either side with distinct acute spinules; this spine falling short of distal tip of endopodite; scattered setae basally on protopodite.

Mandibles: (Figure 3C). Asymmetrical dentate and spined processes, as shown.

Maxillule: (Figure 3D). Endopodite segmented, 3 terminal, 1 subterminal seta. Basal endite with 2 large, widely separated strong spines, plus 3 setae; coxal endite with 4 spines, 3 strong setae.

Maxilla: (Figure 3E). Endopodite setae, progressing subterminally, 3-4, 3, plus 3 laterally, and additional fine hairs as illustrated. Basal endite proximal and distal lobes each with 3 regular and 1 spinelike seta; coxal endite proximal and distal lobes with 8, and 4 spinelike setae, respectively. Scaphognathite with 4 lateral, 1 stout elongate apical seta.

Maxilliped 1: (Figure 3F). Coxopodite with 2 setae. Basipodite setae formula progressing distally 2, 3, 3, 3. Endopodite five-segmented, setae progressing distally 3, 2, 1, 2, 4 + I (Roman numeral denotes dorsal setae); all endopodal and basipodal setae heavy, spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 2: (Figure 3G). Coxopodite naked. Basipodite setae 1, 2, progressing distally. Endopodite four-segmented, setal formula 2, 2, 2, 4 + I; all spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 3: (Figure 3H). A small, unsegmented amorphous bud.

Pereiopods: Appear as small and undifferentiated buds, gradually enlarging as stage progresses.

Abdomen: (Figure 2A, a). Five somites; last 2 with large lateral spines; somites 2-5 each with paired setae dorsally, plus a series of small distinct spinules along posterior margin of somite; somite 6 fused to telson. Pleopods absent.

Telson: (Figure 3I). Setal formula on margin 7 + 7; all plumose setae (= processes 3-7) with small, hooklike spinules progressing down their length; other setae and hairs as illustrated. Anal spine absent.

Color: Zoea transparent; frontal region of carapace diffused with orange, brighter orange dorsally on midgut region. Chromatophores as follows: orange on protopodite of antennule, faintly orange on scaphocerite of antenna; red-orange around inner oral region; mandibles and labrum outlined in red, interiorly orange; basipodites of maxillipeds 1 and 2 red-orange along dorsal and ventral margins; red spiderlike chromatophores dorsally in longitudinal line on abdominal somites 3-5; orange chromatophores ventrally placed in a similar manner. Eyes black, with bluish highlights in reflected light.

Second Zoea

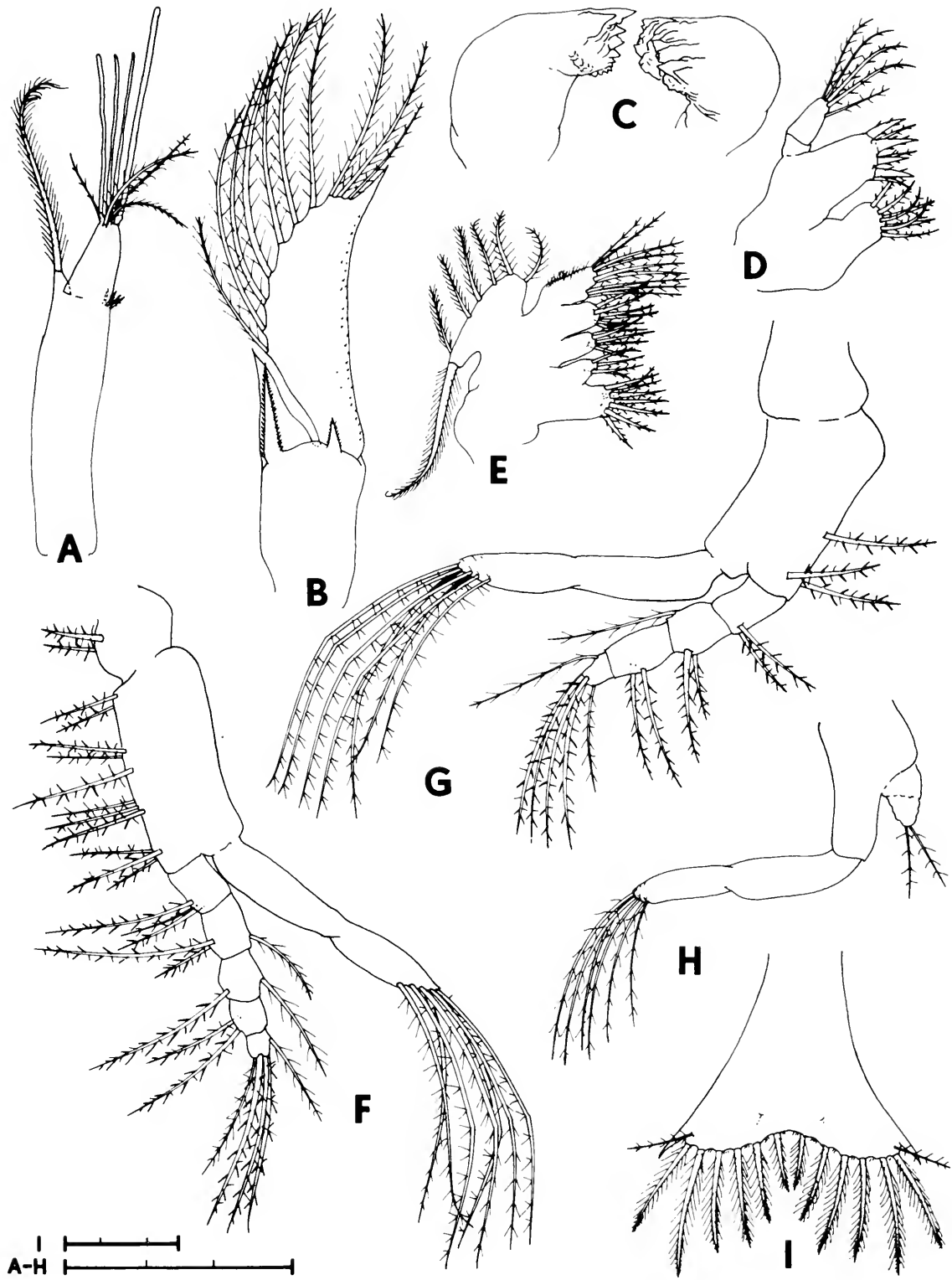
Carapace length: 1.2 mm.
Number of specimens examined: 8.

Carapace: (Figure 2B, b). More inflated; rostral spine more or less knifelike in lateral view, noticeably expanded proximally in dorsal view; about 0.5× CL, overreaching distal tip of antennal scaphocerite spine in several specimens, unarmed; posterolateral margins of carapace with about 14 small denticles or spinules, dorsomedial margin possessing only scattered nubs or with denticles totally absent; posterior spines remain slightly more than 0.1× CL; eyes now stalked.

Antennule: (Figure 4A). Incipient segmentation seen at junction of exopodite with protopodite; former usually carrying 4 aesthetascs and setae, with 4 small thick setules on junction with protopodite. Endopodite retains single long plumose seta.

Antenna: (Figure 4B). Endopodite thickened, drawn into point distally, appearing conical, about 0.3× scaphocerite length, incompletely fused to protopodite, now lacking elongate plumose seta seen in first stage. Scaphocerite usually with 10 marginal setae, plus numerous small spinules ventrally along outer margin; distal spine about

FIGURE 4.—*Galathea rostrata*, second zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.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0.2× scale length. Protopodite now carries second sharp spine ventrally, armed as first along outer margins; larger ventral spine now shorter than endopodite; ventral spinulelike setae inconspicuous or lacking.

Mandibles: (Figure 4C). Dentition now larger, more complex. No palp.

Maxillule: (Figure 4D). Endopodite unchanged from stage I. Basal endite with 4 large spines, 3 setae; coxal endite processes stronger, but number unchanged, from stage I, appearing to be 5 spines, 2 strong setae.

Maxilla: (Figure 4E). Endopodite setal formula progressing subterminally 4, 2, plus 3 laterally, and fine hairs as shown. Basal endite proximal and distal lobes with 4-5, 6 processes, respectively, former as 3-4 spinelike and 1 thin seta, latter as 1 strong and 1 regular spine, 4 thin setae. Coxal endite distal lobe with 3 spines, 1 strong seta, proximal lobe with 8 spines or strong spinelike setae. Scaphocerite with 6 lateral, plus usual elongate apical seta.

Maxilliped 1: (Figure 4F). Coxopodite and basipodite setae unchanged from stage I. Endopodite setal formula now 3, 2 + I, 1 + I, 2, 4 + I. Exopodite remains two-segmented throughout later development, now with 7 natatory setae.

Maxilliped 2: (Figure 4G). Coxopodite and basipodite as in stage I. Endopodite setal formula 2, 2 + I, 2, 5 + 1. Exopodite as above and for later stages, carrying at this stage 7 natatory setae.

Maxilliped 3: (Figure 4H). Remarkably developed; incompletely two-segmented exopodite with 6 natatory setae; endopodite poorly calcified, originating about half way up basipodite, two-segmented, with 2 terminal setae.

Pereiopods: (Figure 2B). Undifferentiated, but enlarging buds throughout stage.

Abdomen: (Figure 2B, b). Five somites, sixth still fused to telson; lateral spine on somite 5 distinct, that of somite 4 reduced, even vestigial; paired dorsal setae on posterior dorsal margins of somites 2-5 remain, and are present throughout later zoeal stages; posterior marginal spinules much reduced in size and number.

Telson: (Figure 4I). Marginal setal formula 8 + 8, additional pair added in medial sinus; latter reduced from distinct U-shaped notch seen in stage I. Armature on plumose processes as before, but distal tips with hooklike processes more distinct; other setae and hairs as shown.

Color: Similar to stage I, but with less diffusion of orange frontally; internal midgut region, mandibles and maxillipedal basipodites retain red-orange color, mandibles showing noticeable red outline, maxillipedal color appearing more diffused than stage I; abdominal somites 4-5 with red dorsal and lateral chromatophore lines, plus orange line ventrally, all connecting to single orange ring of spiderlike chromatophores around each anterior margin of somites 4 and 5. Eyes electric blue to black in reflected light.

Third Zoea

Carapace length: 1.3 mm.
Number of specimens examined: 8.

Carapace: (Figure 2C, c). Proximal margins of rostral spine more developed laterally when seen dorsally, in this and subsequent stages; length remains about 0.4-0.6× CL, distal tip reaches to about tip of scaphocerite spine or slightly beyond; posterolateral margins of carapace with denticles much reduced, becoming irregular nubs; dorsomedial margin with only poorly developed, ragged nubs, almost totally obsolete; posterior carapace spines considerably shortened, less than 0.1× CL. Eyes much enlarged, basal peduncles elongate.

Antennule: (Figure 5A). Exopodite segmented from protopodite, bearing 2 lateral aesthetascs in addition to 3 terminal, plus 3 or 4 setae, at tip. Endopodite slightly enlarged, retaining long plumose seta. Protopodite carries single long lateral seta distally, plus 2 short fine setae, placed medially, and basally, and 4 short stout setae distally.

Antenna: (Figure 5B). Endopodite continues to develop, but remains incompletely segmented from protopodite, now about 0.5-0.6× scaphocerite length, a thin seta just below spinous tip. Scaphocerite with 9-11 marginal setae, number somewhat variable on left and right appendages in same specimen, plus additional shorter spinules

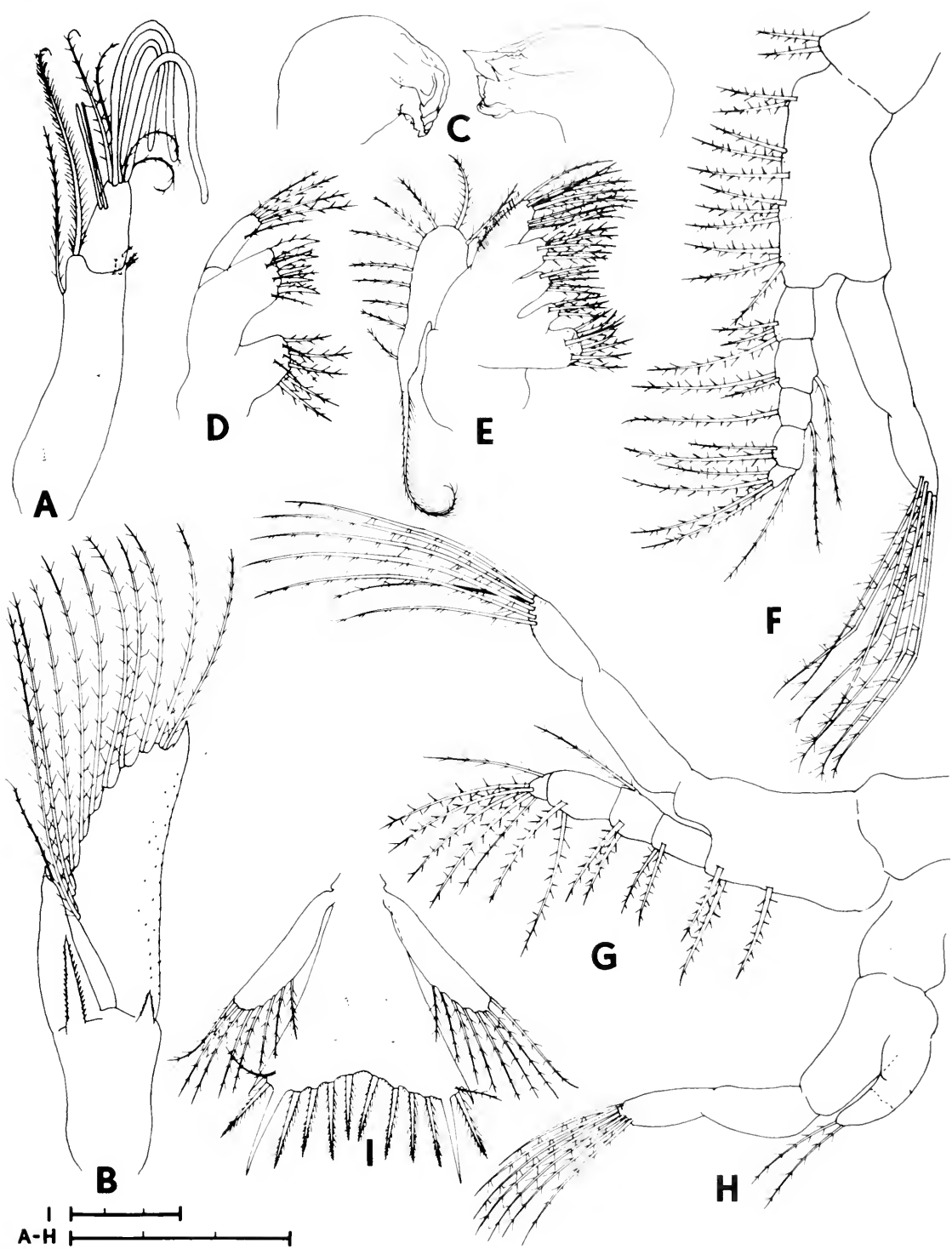


FIGURE 5.—*Galathea rostrata*, third zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

along ventral outer margin; distal spine shortened to about 0.1× scale length. Protopodite retains 2 sharp ventral spines, larger about 0.6× endopodite length, smaller about 0.3× length of larger.

Mandibles: (Figure 5C). Incisor and molar processes more developed; no palp.

Maxillule: (Figure 5D). Endopodite unchanged. Basal and coxal endites both with 5 spines, 3 setae.

Maxilla: (Figure 5E). Endopodite unchanged. Numbers and form of processes on either endite little changed from earlier stage, with exception of basal endite distal lobe; latter now with 1 spine, 4 strong setae, 1 thin seta. Scaphognathite with 10 marginal setae and usual thick apical seta.

Maxillipeds 1 and 2: (Figures 5F, G). Coxal, basipodal, dorsal and ventral endopodal, and exopodal natatory setae as in previous stage.

Maxilliped 3: (Figure 5H). Endopodite bud now subequal to basipodite length, incipient segmentation more prominent in some specimens than others; exopodite with 7 natatory setae.

Pereiopods: (Figure 2C, and detailed inset). More developed, many with incipient segmentation; partial chelation of protochela often visible.

Abdomen: (Figure 2C, c). Six somites present, sixth divided from telson; distinct lateral spine remains only on somite 5; spinules on dorsal posterior margins vestigial, ragged and irregular. In some specimens small, amorphous swellings occur ventrally on somites 2-5, signifying future position of pleopod buds.

Telson: (Figure 5I). Marginal setal formula remains 8 + 8; fourth pair of processes elongate spines fused to telson; processes 3, 5-8 retain noticeable hooklike spinules distally; other dorsal setae as illustrated. Uropods present at junction of abdominal somite 6 and proximal margin of telson; exopods of same well developed, with variable number of marginal plumose setae (usually about 8); endopods, if present, merely foreshortened naked buds.

Color: More distinctly colored than stage II. Orange chromatophores: dorsally on interior margin of eyestalks, a single orange spot on carapace laterally, just above each maxilliped 1, another small grouping laterally on abdominal somite 2; diffused orange on antennular peduncle, ventrolaterally on carapace below eyes, interiorly on mouthparts and within gut region, and on endopodites of maxillipeds 1-3. Red chromatophores: on cutting edge of mandibles, dorsomedially and laterally on abdominal somite 4, laterally on somite 5, the latter appearing as if small drops of blood.

Fourth Zoea (Regular)

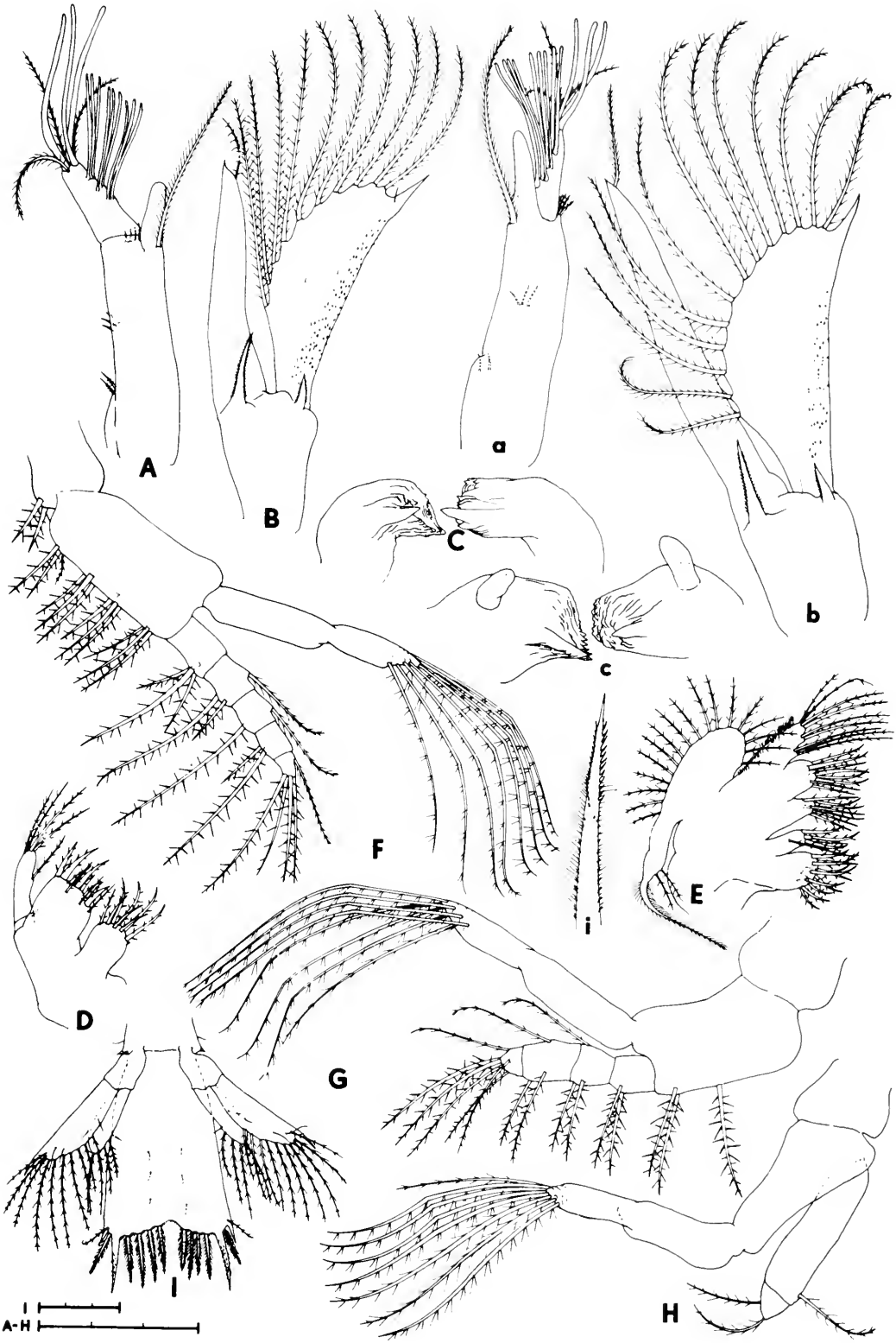
Carapace length: 1.4 mm.
Number of specimens examined: 10.

Carapace: (Figure 2D, d). Rostral spine with noticeably raised lateral margins, greatly expanded basally at point of attachment to carapace, slightly overreaching scaphocerite spine and antennular exopodite; carapace posterolateral and dorsomedial margins unarmed; posterior spines quite short, hooked downward. Eyes large, on elongated stalks.

Antennule: (Figure 6A). Exopodite with three rows of lateral aesthetascs, numbering distally 2-3, 3, 2-3, in addition to usual 3, plus 3 setae, at tip. Endopodite about 0.5× length of exopodite, plumose seta absent. Protopodite retains distal lateral setal, plus usual 4 stout setae at junction of exopodite; 3 medial, 2 basal setae now also present.

Antenna: (Figure 6B). Endopodite elongate subequal to scaphocerite length; latter bearing 10-12 (numbers variable on left and right appendages in same specimen) marginal setae plus numerous ventral spinules on outer margin. Larger protopodal ventral spine about 0.3× endopodite length, smaller about half size of larger; armature of both remains as in earlier stages.

FIGURE 6.—*Galathea rostrata*, fourth zoeal appendages: (A) Antennule, regular stage; (a) same, advanced stage; (B) antenna, regular stage; (b) same, advanced stage; (C) mandibles, regular stage; (c) same, advanced stage; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; all regular stage; (i) detail, fifth telsonal process, 40× objective. See text for discussion. Scale lines total 0.3 mm.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Mandibles: (Figure 6C). Molar and incisor processes acutely spinous, otherwise unchanged from earlier stages; no palp.

Maxillule: (Figure 6D). Endopodite unchanged, but may have small seta at base of segment. Basal endite with 7 stout spines, 3 setae; coxal endite with 5 or 6 long spines, 3 strong setae, and occasional small tooth.

Maxilla: (Figure 6E). Endopodite unchanged. Basal endite distal lobe with 6 spines, 2 setae, proximal lobe with 7 or 8 spines and strong setae intermixed; coxal endite distal lobe with 4 terminal spines, 1 lateral seta, proximal lobe with 11 spines, placed 5 terminally, 4 subterminally, 2 laterally. Scaphognathite with 17-20 marginal setae, including 2 or 3 anteriorly near base, plus usual long apical plumose seta, as shown.

Maxilliped 1: (Figure 6F). Basipodite adds a single small seta proximally, ventral formula now 3, 3, 3, 3. Endopodal and coxal setae unchanged; 8 exopodal natatory setae.

Maxilliped 2: (Figure 6G). Coxal and basipodal setae unchanged. Endopodite setal formula 2, 2 + I, 2 + I, 5 + I. Exopodal natatory setae 8.

Maxilliped 3: (Figure 6H). Endopodite overreaches basipodite, bearing 3 setae. Exopodite with 8 natatory setae.

Pereiopods: (Figure 2D). Chelation and segmentation more or less apparent, progressing rapidly throughout stage; entire pereiopodal mass hangs from beneath posterolateral carapace region in later stage.

Abdomen: (Figure 2D, d). Lateral spine present only on somite 5; dorsal spinulation on posterior margins of somites nearly absent; paired dorsal setae remain. A short, sharp spine on posterolateral margin of somite 6, just above insertion of uropodal basipodite. Pleopod primordia may be present in some specimens, but development is weak and occurs slowly, if at all, throughout stage.

Telson: (Figure 6I, i). Uropods completely developed, exopodite distal outer tip produced into long spine, 8-11 long marginal setae present; endopodites with 4 or 5 setae; with shorter setae on both rami. Telson marginal setal formula 8 + 8, fused fourth process now heavily spinulose, other movable processes (except process 2, which, as in other anomurans, remains a simple seta) carry distinctive, sharp, separated, spinules along their length (Figure 6i; 40× objective), these spinules much more hooklike distally, more spinous proximally. Other dorsal and ventral setae on telson as illustrated.

Color: Similar to stage III; quite developed and noticeable along anterior and internal margin of eyestalks; interiorly on midgut, and bases of maxillipeds; single red chromatophores now basally on antennular protopodite, on posterior margin of maxillipedal basipodites, and laterally on abdominal somites 3-5; eyes blue, reflecting green highlights.

Remarks: This stage, with limited aesthetasc numbers, reduced antennular endopodite and unsegmented protopodite, lacking mandibular palps, and with developing pereiopods and usually only pleopodal primordia, always molted to zoeal stage V.

Fourth Zoea (Advanced)

Carapace length: 1.6 mm.
Number of specimens examined: 12.

Carapace: Differs little from regular stage IV except being larger, more inflated; armature similar to regular stage zoea.

Antennule: (Figure 6a). Endopodite about 0.75× to nearly equal to length of exopodite; latter with four rows of aesthetascs laterally, as 1, 3, 3, 2, plus usual 3, plus 3 setae terminally. Other setae as illustrated.

Antenna: (Figure 6b). Endopodite distinctly overreaches (1.2×) scaphocerite; latter with 12-14 marginal setae; larger ventral propodal spine about 0.25× endopodite length, remaining half again as long as smaller propodal spine.

Mandibles: (Figure 6C). Large, heavily toothed processes, distinguished now by undivided simple palp.

Maxillule: May add one more process on basal endite; tooth on coxal endite usually distinct.

Pereiopods: Well formed, completely segmented and chelated, protruding almost totally from under posterolateral carapace margins.

Abdomen: Somites 2-5 each with a pair of undivided pleopod buds, gradually lengthening as stage progresses, but never becoming bifid.

Color: Similar to regular stage IV zoeae.

Remarks: The zoeae in this stage are much more developed morphologically, possessing a different arrangement of antennular aesthetascs, a well-developed antennal endopodite, mandibular palps, segmented and chelated pereiopods, and distinct (but undivided) pleopod buds. These zoeae molt directly to megalopae, bypassing stage V completely.

Fifth Zoea

Carapace length: 1.6 mm
Number of specimens examined: 8.

Carapace: (Figure 2E, e). Rostral spine with lateral margins appearing somewhat embossed at posterolateral angle of zoeal orbit; carapace lateral margins deeply rounded, convex posterolaterally, unarmed; posterior spine recurved ventrally in some specimens, nearly straight in others, inner margin of same curving regularly inward to deeply excavated dorsomedial margin of carapace; latter entirely without armature. Eyes large, ovoid, on well-developed elongate stalks.

Antennule: (Figure 7A). Exopodite with five rows of aesthetascs laterally: 2, 3, 3, 3, 2, plus 3 and 3 setae at tip. Endopodite from about 0.75× to just subequal in length to exopodite. Protopodite segmented into elongate basipodite and truncated coxopodite; former with a single long plumose seta distally, plus 4 stout setae terminally at exopodite junction, 3 more medially; latter with 2 stout setae ventrally near line of segmentation.

Antenna: (Figure 7B). Endopodite very noticeably longer than scaphocerite (1.3-1.4×); latter bearing 12-14 plumose marginal setae plus additional ventral marginal spinules as in earlier stages. Larger propodal ventral spine less than 0.2× endopodite length, smaller remains about half the size of larger, both armed similarly as illustrated. Toward end of larval stage transparent endopodite reveals distinctly segmented megalopal antennal flagellum within endopodal sheath.

Mandibles: (Figure 7C). Noticeably dentate, each with simple, distinct palp.

Maxillule: (Figure 7D). Endopodite unchanged from regular stage IV; basal setule may not be present. Basal endite with 8 stout spines, 3 setae; coxal endite with 6 long spines, 3 strong setae, and small tooth, placed as illustrated.

Maxilla: (Figure 7E). Endopodite unchanged. Basal endite distal lobe with 8 spines and strong setae, 2 thin setae terminally, one regular seta laterally; proximal lobe with 6 terminal, 2 subterminal, 2 lateral processes, most appearing to be strong setae and spines. Coxal endite distal lobe with 2 spines, 2 strong apical setae, 2 thinner subapical or lateral setae; proximal lobe with about 13 spines and strong setae, progressing terminally to laterally as 7, 4, 2. Scaphognathite with about 22-25 marginal setae, including enlarged plumose seta apically; 2 small setules present, positioned laterally.

Maxilliped 1 and 2: (Figures 7F, G). Little changed from previous stage.

Maxilliped 3: (Figure 7H). Little changed in form from previous stage, except endopodite now much larger, longer, extending well past distal margin of basipodite; 3 setae as before.

Pereiopods: (Figure 2E). Extremely large, appearing to be nearly functional, protruding beneath, and forcing posterolateral margins of carapace, outward; walking leg segmentation and cheliped chelation distinctly visible.

Abdomen: (Figure 2E, e). Lateral spine on somite 5, and that on posterodistal angle of somite 6, the only armature. Pleopods present as well-developed, bifid, buds.

Telson: (Figure 7I, i). Uropods well-developed, both endopodite and exopodite with variable number of marginal setae, usually 8-10, and 10-13 or occasionally 14, respectively. Telsonal fused and movable processes as illustrated; fourth process distinctly spinulose; occasionally an extra

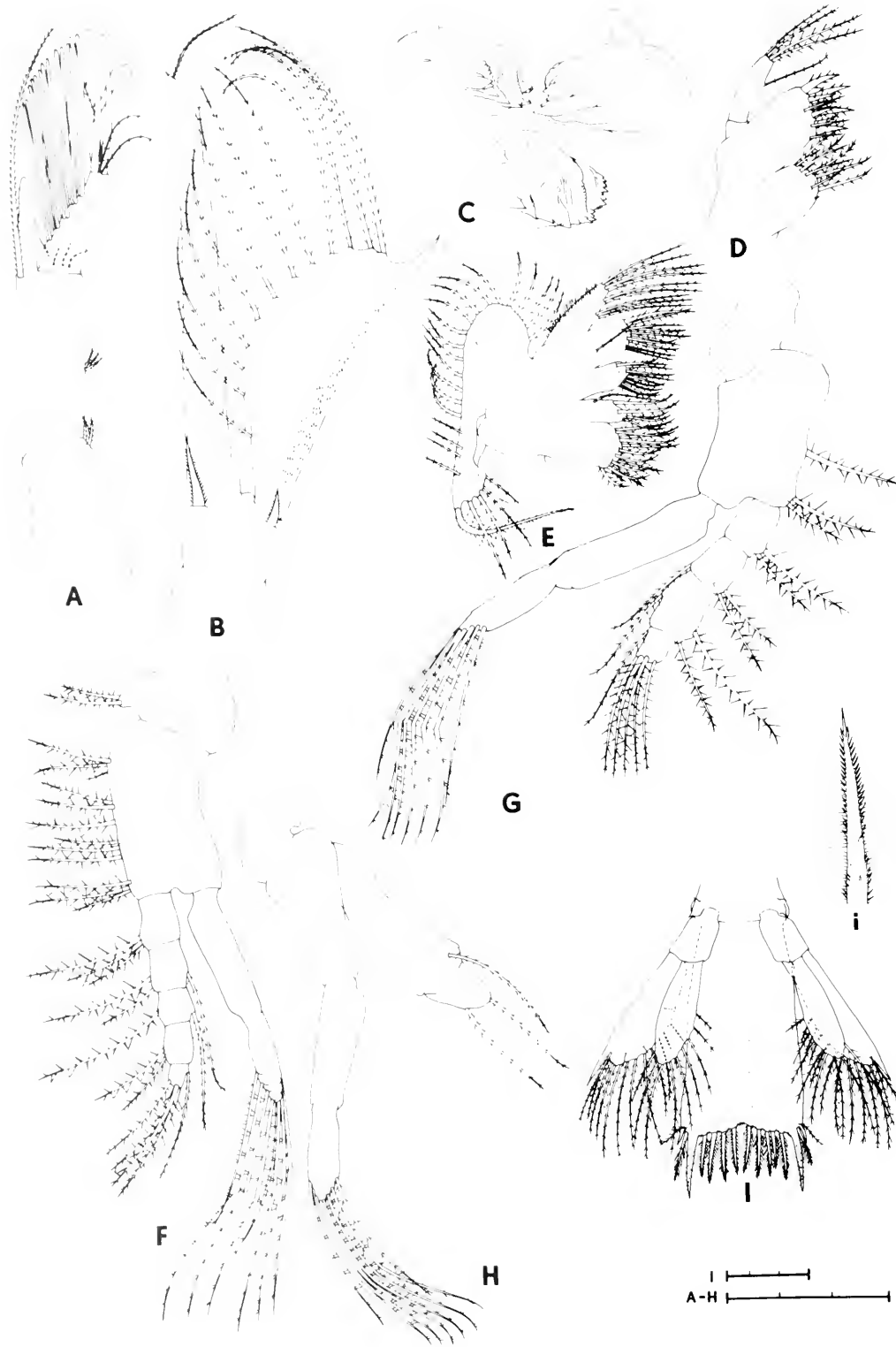
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FIGURE 7.—*Galathea rostrata*, fifth zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated exteriorad of zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; (i) detail (40 × objective), fifth telsonal process. Scale lines total 0.3 mm.

plumose process appears making telson marginal setal formula 8 + 9 as shown.

Color: Chromatophores as follows: Red, on anterior margin of eyestalks, paired on carapace dorsally just behind eyes on frontal region, single ventrolaterally beneath each eyestalk just above mandibular region, ventrally on both antennular and antennal peduncles at junction with carapace, laterally on carapace above insertion of maxilliped 2; interiorly on mouth region on outer margin of mandible, posterior to mandible on maxillule, and on midgut; abdominal somites 3-5 with several groups laterally, plus a reddish-orange line above hindgut of same. Orange chromatophores in elongate streaks longitudinally on basipodite of maxillipeds 1-3, more diffused on maxillipedal endopodites, and in lateral groupings on abdominal somites 3-5. Eyes blue-green in reflected light, corneas dark, probably black.

Remarks: This stage followed the regular stage IV and invariably molted to megalopal stage.

Megalopa

Carapace length × width: 1.7 × 1.2 mm.
Number of specimens examined: 4.

Carapace: (Figure 8A, B). Resembling miniature adult; rostrum triangular proximally, drawn into sharp point distally, armed along lateral margins with 4 distinct spines, some smaller spinules occasionally interspersed; frontal region with additional spinules as illustrated; 2 elongate thickened setae on gastric region, plus other setae and spinules as shown; lateral margins with 4 large spines, including 1 at epibranchial angle, 2 placed about equidistant behind, and the fourth at junction with cervical groove; a variable number, usually 3, smaller spines laterally between larger spines; a fifth large spine on posterolateral margin, followed by another, smaller, dorsally and posteriorly. Numerous small setae scattered over entire carapace; eyes each with 2 large, feathery setae on anterodorsal margin.

Antennule: (Figure 9A, a). Biramous; peduncle large, three-segmented; basal segment inflated, with 2 large forward-directed spines dorsally, another, smaller, distoventrally; other setae as shown; remaining two segments nearly smooth, sparsely setose. Lower ramus three-segmented, tip with 2 spinules (see detail, Figure 9a), other setae as shown. Upper ramus six- or occasionally indistinctly seven-segmented; aesthetascs on segments two through five in the following sequence of rows and numbers: one row (2), two rows (3, 3, + 2 setae), two rows (3, 2, + 1 seta), one row (2); sixth segment with a single elongate terminal seta plus other smaller setae.

Antenna: (Figure 9B). Peduncle three-segmented, heavily spined; flagellum with 2 or 3 fused segments plus a variable number (about 24) shorter segments each bearing 5 or 6 setae distally; terminal segment with 7 longer setae, as illustrated.

Mandible: (Figure 9C). Symmetrical, scoop-shaped process, chitinized along leading margin; a three-segmented palp, basal segment of which bearing 2 short, spinelike setae, third segment with about 13 or 14 stout, toothed spines.

Maxillule: (Figure 9D). Endopodite now possessing but a single short, terminal seta. Basal endite with 4 strong terminal setae, followed by 16 short, stout spines, 4 subterminal and 3 lateral setae; a single seta basally as shown; coxal endite lower portion extended into elongate, weakly chitinized, lobe fringed with fine hairs; 3 basal setae, 3 lateral setae, followed by 11 stout spines and 8 strong setae terminally.

Maxilla: (Figure 9E, e). Endopodite with a single, long subterminal seta. Coxal and basal endites heavily spinose and setose, numbers and position difficult to discern, but approximately as follows: basal distal lobe, about 14 terminally, 4 + 2 subterminally, 2 laterally; proximal lobe, about 6 terminally, 3 + 1 subterminally, 1 + 2 laterally; coxal distal lobe, about 3 each, terminally and subterminally, 2 + 8 in irregular row laterally; proximal lobe, about 11 placed more or less terminally, 8 subterminally, 22 in a row encircling lobe laterally, 1 + 2 beneath these; for exact positioning refer to outer (Figure 9E) or inner (Figure 9e) views of lobes. Scaphognathite with about 40

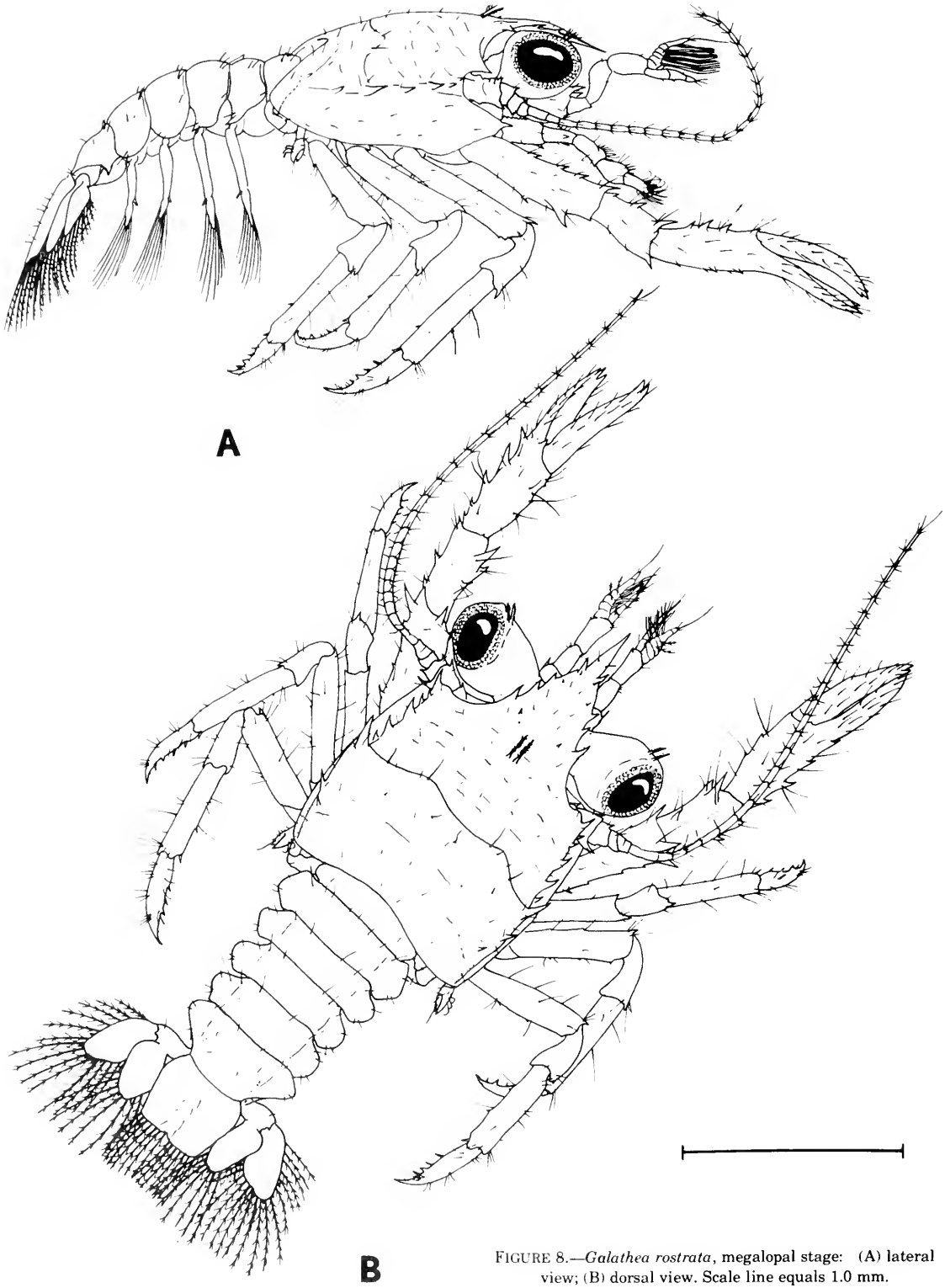

FIGURE 8.—*Galathea rostrata*, megalopal stage: (A) lateral view; (B) dorsal view. Scale line equals 1.0 mm.

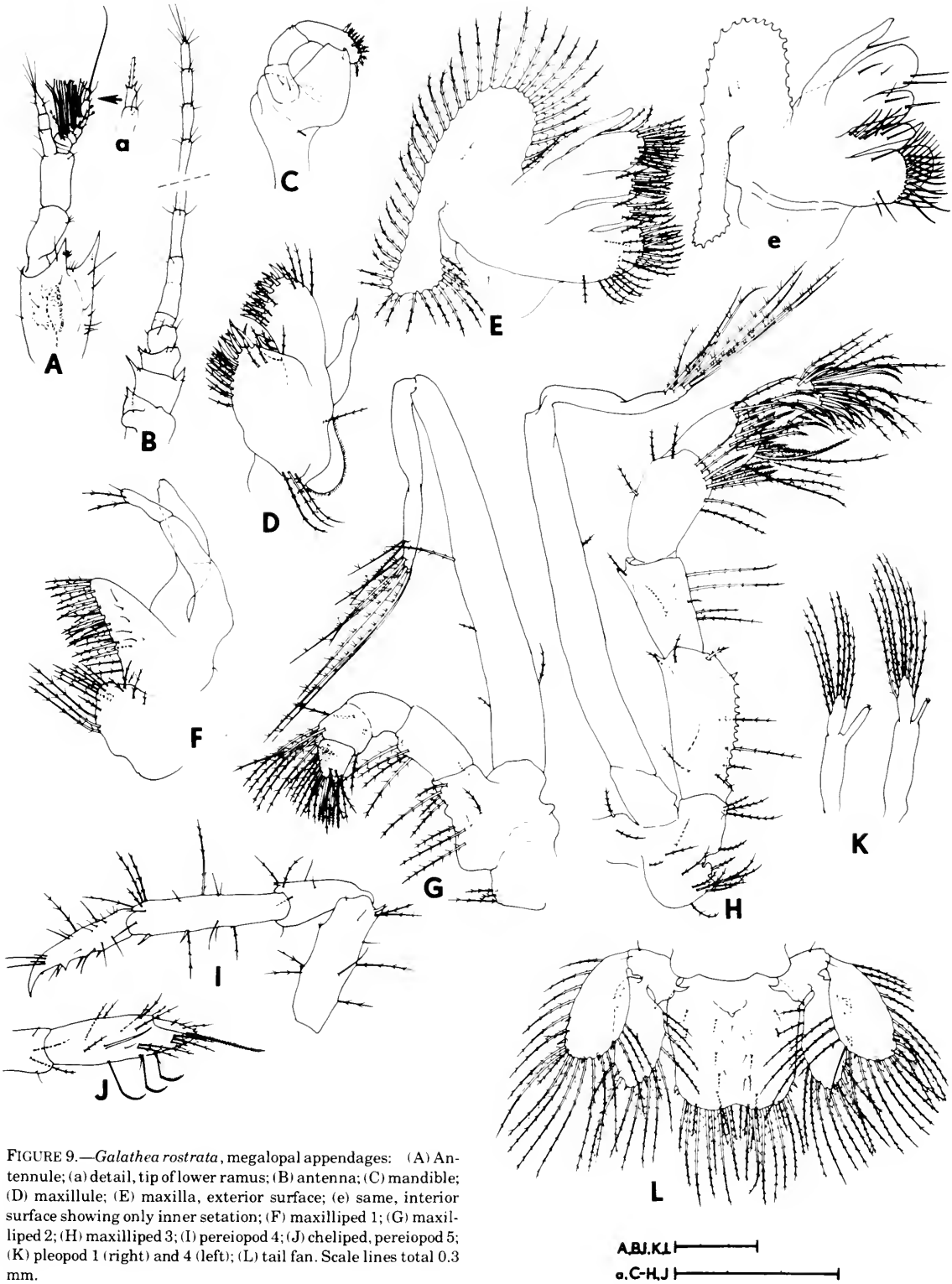

FIGURE 9.—*Galathea rostrata*, megalopal appendages: (A) Antennule; (a) detail, tip of lower ramus; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla, exterior surface; (e) same, interior surface showing only inner setation; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) pereiopod 4; (J) cheliped, pereiopod 5; (K) pleopod 1 (right) and 4 (left); (L) tail fan. Scale lines total 0.3 mm.

marginal setae plus finer setules on either side of upper lateral surface.

Maxilliped 1: (Figure 9F). Exopodite and endopodite weakly chitinized; former two-segmented, with 3 more or less terminal setae; latter naked. Protopodite with about 27 and 15 setae on basal and coxal endites, respectively, placed as illustrated.

Maxilliped 2: (Figure 9G). Exopodite two-segmented, 8 terminal, plus other setae, as shown. Endopodite four-segmented, proximal two with 4 and 2 setae, respectively, distal two each with about 12 processes, including 5 daggerlike spines terminally. Setae on basipodite and coxopodite as illustrated.

Maxilliped 3: (Figure 9H). Exopodite two-segmented, 8 terminal setae. Endopodite five-segmented; ischium and merus each with strong, sharp triangular spine, plus a shorter spine at anterodistal angle; ischium also with prominent crista dentata; last three segments (carpus, propodus, dactylus) with 3, about 15, about 18 long daggerlike spines plus numerous longer setae interspersed among them. Several setae on coxopodite and basipodite.

Pereiopods: (Figures 8A, B; 9I, J). Chelipeds rounded, equal, elongate, heavily spined, covered with long, stiff bristlelike setae, these more prominent in gape of fingers and on outer surface of manus; fingers of each hand trifid at tips. Merus and carpus with marginal spines. Walking legs thin, elongate; merus, carpus, and propodus covered with setae plus small spinules ventrally along margins, these often difficult to discern except under higher (40× objective) magnification; propodus with 2 larger spinules ventrally; dactylus with 3 large movable spinules plus one fixed triangular tooth on ventral margin; a second, very small, almost vestigial tooth may appear about midway between larger fixed tooth and dactylar tip. Pereiopod 5 chelate, 1 long serrated seta, 3 scythelike pectinate setae quite noticeable, plus additional numerous setules on manus; 2 very small, spinulelike teeth on distal tip of dactylus.

Pleopods: (Figures 8B, 9K). Occur on somites 2-5; biramous, greatly elongate; exopodal setae progressing toward telson 8, 8, 8, 7, with minor variation of 1 or 2 occasionally seen on left or right side in same specimen; endopodites not as long as exopodites, thin, naked, but each with appendix interna of 2 or 3 small hooks developed at tip.

Tail Fan: (Figure 9L). Telson with 6 or 7 long plumose setae, and several shorter marginal setae interspersed among these, numbers of latter inconsistent in same specimen; 1 or 2 small toothlike spines laterally, as shown. Uropods biramous, each with 4 widely separated marginal spines, that on outer lateral margin of endopodite the strongest; exopodite with about 18-20, endopodite blade with 11-14 plumose marginal setae, numbers again variable in same specimen. Smaller setae on dorsal and ventral surfaces of tail fan as illustrated.

Color: Megalopa beautifully colored. Carapace and abdomen overall red-orange, dorsolateral carapace margins and spines darker red; an irregular longitudinal white, or semitranslucent stripe extends dorsally from just behind frontal region along entire length of carapace and abdomen; this stripe bordered with darker orange-red chromatophores along its length; a similar white stripe appears laterally, below which carapace becomes translucent, but covered with numerous red spiderlike chromatophores; a third stripe appears ventrally on sternum, extending to junction of abdomen. Numerous pale blueish-white dots interspersed over dorsal surface of carapace, especially on either side of previously noted longitudinal stripe. Eyestalks orange-red, with regular white band longitudinally, this meeting second band which encircles distal margin of eyestalk just before cornea; latter black, overlain with dark red maculations. Chelipeds with distal margin of merus, entire carpus, propodus, and all but distal tip of dactylus ivory white; merus proximally red-orange; cheliped finger tips orange. Walking legs translucent, speckled with many red-orange chromatophores, these coalescing to form irregular bands on outer segments; dactyli of latter clear, or light horn color.

DISCUSSION

In the western North Atlantic Ocean the family Galatheidae is represented by four genera: *Galathea* (2 species), *Munida* (31 species), *Munidopsis* (48 species), and *Phylladiorhynchus* (1 species). With the exception of the present report, the larval development of the remaining 81

galatheid species known to occur in the western Atlantic is unknown.

The majority of our knowledge on galatheid larvae comes from studies conducted on species from the eastern Atlantic and Pacific Oceans, and associated seas such as the Red, Mediterranean, or North Seas. Lebour (1930) first characterized larvae in the family Galatheidae, and Gurney (1942) was the first to provide a synopsis of larval features based on Lebour's work and studies he made on western Pacific galatheid larvae. As might be expected, only some of the characters considered important by Gurney in 1942 remain valid today, and the lack of detailed descriptions in earlier studies on galatheid larval morphology prevents comparative statements to be made among most of the species for which the larvae are known. Nevertheless, morphological differences in rostral, carapacial, antennal, abdominal, and telsonal features continue to be of some value in distinguishing the larvae of at least five galatheid genera.

In general, the larvae so far described for species of *Munida* share several features with those known from *Galathea* and *Pleuroncodes*, and are thus somewhat indicative (as seems true for the adults) of close relationships among the three genera. *Pleuroncodes*, an eastern Pacific genus, is morphologically very similar to *Munida* in several larval features, more so than are larvae of *Galathea* as presently described. As noted in the following synopses, the larvae of the three genera can be easily separated. The adults, based on present taxonomic criteria, are distinct and generic status is undoubtedly warranted.

The genus *Munidopsis*, on the other hand, is a heterogeneous grouping of forms, some adults bearing little resemblance to others in the taxon (see Mayo 1974, for discussion). The larvae from the sole species so far described, however, are certainly distinctive and do not resemble those from other genera. The genus *Munidopsis*, as presently constituted, would seem to provide an ample example of a taxon wherein the relationships among the various species (and perhaps their elevation to generic status) might be clarified on the basis of morphological relationships among their larvae.

The first zoeal larvae of the eastern Pacific species *Cervimunida johni* (Fagetti 1960) are quite spinose but could perhaps be confused with either *Munida* or *Pleuroncodes* larvae (Fagetti and Campodonico 1971). It remains to be seen whether later larval stages would be more distinctive. The presence of a single ventral antennal spine (instead of two as seen in other genera) is of limited value, because *Galathea* and *Munida* exhibit a single spine in stage I and two spines in later stages (see below).

In the genus *Galathea*, larvae are principally known from northeastern Atlantic species described by Lebour (1930, 1931) and Sars (1889). Live specimens of these species may be separated from larvae of *G. rostrata* by chromatophore color and position, but unfortunately no further detailed comparison is possible until the former species are completely redescribed and illustrated. This holds true for most of the studies by the 19th and early 20th century authors which were listed in Gurney (1942). The "*Galathea* sp." briefly described and illustrated by Al-Kholy (1959) from the Red Sea agrees in several respects with "typical" *Galathea* larvae, but differs in others. Whether it may be equated with Gurney's (1938) *G. longimana* remains uncertain as the brief descriptions and illustrations of both authors prohibit meaningful comparison between the two studies, and those on other *Galathea* larvae.

In order to facilitate comparison between the two western Atlantic *Galathea* species a summary of larval features exhibited by *G. rostrata* is provided in Table 2. These may be applied both to *G. agassizii*, when its larvae become known, and to other *Galathea* larvae when expanded or more complete descriptions are provided. In addition, a provisional synopsis of larval characters for the five genera discussed above is also presented. The summaries have been extracted from the more reliable larval descriptions, as so noted, and may allow distinction among the more typical larvae in each genus. As our knowledge increases further modification may be required.

SYNOPSES OF GALATHEID LARVAE

In the following section, emphasis is placed on the setal-spinal formulae of the larval telson. Conventionally, this formula may be expressed thusly: 8 + 8, indicating that eight telsonal processes, consisting of fixed and movable spines, setae, and thin hairs, occur on each side of the telsonal midline. It is apparent now that the type of these processes may provide a useful reference feature in distinguishing between the various galatheid larvae. Accordingly, spines (whether movable or fixed) are herewith denoted by Roman

TABLE 2.—Summary of zoeal features in the larval stages of *Galathea rostrata*.

	Zoea I	Zoea II	Zoea III	Zoea IV (regular)	Zoea IV (advanced)	Zoea V
Rostral spine	Not expanded proximally	Expanded proximally	Expanded proximally	Raised lateral margins	As in regular stage	Expanded proximally
Posterior carapace spines	Elongate	Elongate	Reduced	Slightly hooked	Slightly hooked	Hooked
Eyes	Sessile	Stalked	Stalked, enlarged	Stalked, elongate	Stalked, elongate	Stalked, greatly developed
Antennule	Simple rod, no lateral aesthetascs Endopod reduced	As in stage I Endopod more developed Protopod lacks lateral seta	Exopodite segmented, 2 lateral aesthetascs Protopod with 1 lateral seta	3 lateral rows aesthetascs Endopod ½ exopod length Protopod unsegmented	4 lateral rows aesthetascs Endopod subequal to exopod	5 lateral rows aesthetascs Endopod subequal to exopod Protopod segmented
Antenna	Exopod with seta Scaphocerite spine elongate	Exopod lacks seta Scaphocerite spine reduced	Exopod ½ scaphocerite length, with apical seta	Exopod subequal to scaphocerite, with apical seta	Exopod longer than scaphocerite with apical seta	Exopod much longer than scaphocerite with apical seta
Mandibles	Without palp	Without palp	Without palp	Without palp	Palp present	Palp present
Maxillipeds				and thereafter		
Endopod (1)	3,2,1,2,4 + I	3,2 + I,1 + I,2,4 + I	As in previous stage	2,2 + I,2 + I,5 + I	As in previous stage	and thereafter
Endopod (2)	2,2,2,4 + I	2,2 + I,2,5 + I	2,2 + I,2,5 + I	Longer than basipod, 3 seta	As in regular stage	Much longer than basipod, 3 seta
Endopod (3)	Bud	Less than basipod, 2 seta	Subequal to basipod, 2 seta	8	8	8
Exopods (1, 2)	4	7	7	8	8	8
(3)	0	6	7	Amorphous buds	Developing buds	Developing buds
Pereiopods	Amorphous buds	Developing buds	Developing buds	6 somites, spine on 4 vestigial	Well-formed buds	Segmented, chelated buds
Abdomen	5 somites, lateral spines 4, 5 Pleopods absent	5 somites, spine on 4 reduced Pleopods absent	6 somites, spine on 4 vestigial Pleopods absent	6 somites, spine on 4 absent Pleopod primordia may be present	6 somites Pleopods present, undivided	6 somites Pleopods present, bifid
Uropods	Absent	Absent	Exopods present Endopods rudimentary	Exopods and endopods developed	As in previous stage	and thereafter
Telson	7 + 7 setae 4th process movable	8 + 8 setae 4th process movable	8 + 8 setae 4th process fused	8 + 8 setae As in previous stage	8 + 8 setae and thereafter	8 + 8 setae

numerals, setae by Arabic numerals, and fine hairs by lower case Roman numerals. It should also be remembered that previously movable setae may, in a subsequent stage, become fixed spines and the setal formulae will change accordingly. Thus, a setal configuration proceeding medially of a fixed spine (I), a thin hair (ii), a regular seta (3), a previously movable seta now a fixed spine (IV), followed by four movable setae (5-8) results in the telsonal formula of I + ii + 3 + IV + 5-8. While somewhat more ponderous than the previously used formula of 8 + 8, it does provide a clearer picture of the type of processes and their changes throughout subsequent larval development.

Cervimunida (Fagetti 1960)

Rostrum elongate, needlelike, noticeably denticulate; carapace posterolateral and posterior margins dentate; posterior spines extremely elongate, reaching fifth abdominal somite; antennal scaphocerite elongate, aciculate, distinctly spined along outer margin, and upper surface, basal segment with a single dorsal spine, unarmed ventrally (thus differing noticeably from other galatheids where the situation is exactly the reverse); abdominal somites spined dorsally, somites 4 and 5 with large lateral spines; telson deeply bifurcate, furcae heavily armed; setal formula I + ii + 3-7 (based on first stage zoeae). Presumably four or five larval stages.

Galathea (Sars 1889; Lebour 1930, 1931)

Rostrum acute, often expanded at base, may be armed distally; carapace posterolateral margin usually spinulate or denticulate, posterior spine rarely exceeding third abdominal somite; antennal scaphocerite broad, flattened, basal segment with single spine ventrally in stage I, two spines in all other stages; posterodorsal margins of abdominal somites minutely denticulate, but may become unarmed in later stages; distinct posterolateral spines on somites 4, 5, or both but may be absent later; no median dorsal spine on somite 6; telson triangular, not deeply bifurcate in early stages, becoming more elongate and truncately triangular in later stages; lateral spines may be denticulate; marginal setal formula in stages I and II of I + ii + 3-7, 3-8, respectively, and in all later stages I + ii + 3 + IV + 5-8. Four or five larval stages, pleopods present in last stage, as primordia in penultimate stage on occasion.

Munida (Sars 1889; Lebour 1930, 1931; Rayner 1935)

Rostrum elongate, needlelike, spinulate on dis-

tolateral margins and tips in early stages, but may be unarmed in later stages; a serrated posterolateral carapace margin with noticeable posterior spine, latter often extending to about fourth abdominal somite; antennal scaphocerite elongate, thin or even noticeably aciculate, often spined; basal segment with a single ventral spine in first stage, 2 in later stages; abdominal somites 2-5 with two or more spines or spinules dorsally, margin of somite 6 with a single larger median spine from stage III onward; telson originally deeply bifurcate in early stages of development, but becoming more triangularly truncate later, thus appearing similar to that in *Galathea* in later stages; telson furcae often spined; telson setal formula I + ii + 3-7, 3-7 or -8 in stages I and II and I + ii + 3 + IV + 5-9, 5-10, 5-11 or -12 in stages III-V, respectively. Four of five larval stages, pleopods present in last stage.

Munidopsis (Sars 1889; Samuelsen 1972)

Rostrum broad, flattened, nearly spatulate in all zoeal stages, profusely armed about outer margins; carapace with a large, forward-directed spine on anterolateral margin; entire ventral and posterolateral margins noticeably spinulate, posterior margin rounded, lacking elongate posterior spine otherwise typical of larvae in the family; antennal scaphocerite a flattened blade, two spines ventrally; posterodorsal margins of abdominal somites unarmed, a posterolateral spine present on somite 5; telson broadly spatulate, posterior marginal setal formula 1 + 2 + iii + IV + 5-15 in stage I, and I + 2 + iii + IV + 5-15 in stages II and III; other smaller hairs interspersed among setae 5-15. Three larval stages, pleopods present in each.

Pleuroncodes (Boyd 1960; Fagetti and Campodonico 1971)

Rostrum flattened basally, expanded similarly to that of *Galathea*, distal portion acute, margins noticeably spinulate, especially at tip; posterolateral carapace margins serrated, elongate posterior spines usually extending to fourth abdominal somite; antennal scaphocerite narrow, not as aciculate as in some *Munida*, basal segment with either 1 or 2 ventral spines; abdominal somites 1-5 heavily spined dorsally on posterior margins, becoming somewhat reduced in spination in later stages; somite 6 with a median dorsal spine in stage III and later; telson deeply bifurcate in stages I and II, becoming more truncately triangular in later stages as in *Munida* and *Galathea*; furcae may be denticulate; marginal setal formula I + ii + 3-7, 3-8 in stages I and II, and I + ii + 3 + IV + 5-9, 5-10, and 5-12 in stages III-V, respectively. Five larval stages, including up to eight substages in stage IV; stage VI in laboratory culture; pleopods present in stage V. The genus is presently restricted to the eastern Pacific Ocean.

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A THEORETICAL EXAMINATION OF SOME ASPECTS OF THE INTERACTION BETWEEN LONGLINE AND SURFACE FISHERIES FOR YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

This paper explores several aspects of a dual fishery (surface and longline) on yellowfin tuna, *Thunnus albacares*. The work is exploratory in nature and results, though indicative, are not conclusive for any specific fishery. Our results indicate that the yield per recruit is higher for the longline fishery than for surface gear if all fish are available to both gears and higher for the combined gears than for either gear fishing alone. The effect of fishing by one gear on yield to the other gear and the effect of the fishery on stock fecundity is shown to be greater for the often assumed 1:1 sex ratio than for the ratios usually observed. A simulation model was used to examine the interrelations of pattern of movement of fish, pattern of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either only along the coast or throughout the fishing area. The results indicated that either of these patterns of recruitment could allow for increased catch as the surface fleet moved offshore. However, location or pattern of recruitment is shown to be important when measuring natural mortality and for examining the potential of a localized fishery, primarily on younger fish, relative to a fishery exploiting the full range of the stocks or to one taking primarily older fish. Tagging and fecundity studies are suggested for further investigation of the questions examined in this paper.

An unsolved problem common to many of the tuna fisheries of the world is the nature of the interaction between longline and surface (i.e., seining, pole and line, and occasionally trolling and shallow handline) fisheries for the same species. Fisheries for yellowfin tuna, *Thunnus albacares;* albacore, *T. alalunga;* bluefin tuna, *T. thynnus;* southern bluefin tuna, *T. maccoyii;* and bigeye tuna, *T. obesus,* are prosecuted by both types of gear in the Pacific, Atlantic, and Indian Oceans. Although there can be considerable overlap of sizes of fish taken by the two types of gear, in general, longline gear takes larger (older) fish. Exploitation of a tuna stock by the two types of gear presents management with the problems of determining the effect of various combinations of fishing effort by the two gears on both yield per recruit to the two gears and recruitment to the stocks. In order to make these determinations, it is necessary to estimate 1) availability of the stock at each age to each of the two gears [The available portion of the stock is subject to both other mortality (any mortality not caused by gear of concern) and fishing mortality caused by the gear of concern. The unavailable portion of the stock is subject only to other mortality.], 2) fishing mortality of the available portion of the stock caused by each gear, 3) natural mortality, 4) growth, 5) fecundity, and 6) the relationship between egg production and recruitment.

The aim of this paper is to examine the interactions between longline and surface fisheries for yellowfin tuna and to determine the impact such interactions may have on the assumptions often made in assessment of yellowfin tuna fisheries and thus on the assessment calculations themselves. The paper is divided into three major sections. The first section examines the relationship between availability of the stock(s) of yellowfin tuna to surface and longline fishing and yield per recruit to the two gears. This is an important, and to our knowledge unexamined, aspect of all tuna fisheries exploited by both types of gear; the subsequent sections examine two asepcts of the biology of tuna that can affect the catch by each type of gear. The second section examines the effect of age specific sex ratios of yellowfin tuna on yield per recruit to the two types of gear and on egg production. The third section examines the effect of

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random migration or dispersal and location of recruitment of yellowfin tuna on estimates of mortality and yield per recruit to each gear. We have restricted our analysis to yellowfin tuna but believe that the concepts that we develop apply to the other species as well.

MATERIALS AND METHODS

While stocks of yellowfin tuna are subjects of important fisheries in all tropical oceans, information on vital parameters is sketchy and nonuniform. For example, tagging information available in the Pacific is lacking for the Atlantic stocks. On the other hand, regulation of the Pacific fishery makes interpretation of the catch information more difficult. Hence it is necessary to pick and choose from the available information that which is most relevant to the problems at hand. Although the parameters are likely to differ for fish from different oceans, if not fish from different areas of the same ocean, few studies have conclusively demonstrated that such differences exist. In addition, several (e.g., Lenarz et al. 1974) have found that conclusions from studies such as described in this paper are often insensitive to the likely range of values of parameters such as natural mortality, fishing mortality, and growth. In the first and second sections, we have used data primarily from the eastern Atlantic because historically catches have been more equally shared by longline and surface fisheries than in the eastern Pacific; in the third section we have modelled the eastern Pacific since information on migration patterns is more extensive. In both instances, the results are intended to be general rather than specific. Data extracted from one area and used in another is thought to be the best available and the question of real differences is left for further investigation.

With a noted exception, the growth equation $L = 194.8 \times (1 - e^{-0.42(t-0.67)})$ estimated by Le Guen and Sakagawa (1973) and length-weight equation $W = 0.0000214L^{2.9736}$ estimated by Lenarz (1974) are used for yellowfin tuna where L is fork length in centimeters, t is age in years, and W is weight in kilograms. Unless otherwise stated, we assumed that the annual instantaneous coefficient of natural mortality (M) is 0.8 (Hennemuth 1961). We estimated age-specific fecundity from two indices derived by Hayasi et al. (1972) (Table 1). Their index I was obtained from longline data and their index II was obtained from surface data. The fecundity indices were calculated by Hayasi et al. (1972) for fish caught in the Pacific by multiplying mean ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish. For much of our work, we used estimates of the 1967-71 average size (age) composition of the Atlantic yellowfin tuna fishery made by Lenarz et al. (1974) (Table 2). Use of length-age key assumes that length and age are equivalent. Sex composition shown in Table 2 is based on data from the Pacific.

TABLE 1.—Indices of fecundity of yellowfin tuna as interpolated from Hayasi et al. (1972), for fish caught in the Pacific calculated by multiplying average ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish.

Midpoint of size interval (cm)	Fecundity index I	Fecundity index II
80	0.04	0.07
85	0.04	0.14
90	0.05	0.21
95	0.08	0.27
100	0.15	0.36
105	0.23	0.42
110	0.33	0.51
115	0.42	0.61
120	0.55	0.70
125	0.70	0.81
130	0.88	0.92
135	1.12	1.04
140	1.40	1.15
145	1.80	1.26
150	2.30	1.37
155	2.77	1.50
160	3.20	1.62
165	3.57	1.76
170	4.05	1.91
175	4.42	2.06
180	4.82	2.23
	5.01	2.43

Estimates of the size- (age-) specific instantaneous coefficient of fishing mortality (F_t) on an annual basis were made using the Gulland (1965) and Murphy (1965) method. The computer program COHORT, written by W. W. Fox, Jr., of the Southwest Fisheries Center, was used to obtain estimates of F_t for each 5-cm size interval, beginning at 32.5 cm. The estimation procedure was initiated with a trial value of F_t for the largest size interval (Input F).

Estimates of F_t were obtained from the average 1967-71 catch composition data (Table 2) as was done by Lenarz et al. (1974). When feasible it is more desirable to estimate F_t from individual cohorts. This was not done because of the small number of years in the data series and belief that estimates from the average composition would adequately reflect conditions of the fishery. In a latter study, Fonteneau and Lenarz (1974) estimated F_t for individual cohorts from a longer time

TABLE 2.—Composite catch in numbers of yellowfin tuna by gear, sex, and size. Length composition by gear is based on data from Lenarz et al. (1974) on the Atlantic fishery. Sex composition is based on data from the Pacific (Murphy and Shomura 1972).

Age at beginning of interval (yr)	Midpoint of size interval (cm)	Male			Female		
		Surface	Longline	Total	Surface	Longline	Total
1.0579	35	1,179	0	1,179	1,179	0	1,179
1.1325	40	14,528	0	14,528	14,528	0	14,528
1.2039	45	61,563	0	61,563	61,563	0	61,563
1.2888	50	186,611	4	186,615	186,611	4	186,615
1.3710	55	237,622	11	237,633	237,622	11	237,633
1.4562	60	210,711	226	210,937	210,711	226	210,937
1.5445	65	121,824	324	122,148	121,824	324	122,148
1.6363	70	137,389	1,076	138,465	137,389	1,076	138,465
1.7317	75	102,046	2,718	104,764	102,046	2,718	104,764
1.8310	80	90,710	2,847	93,557	90,710	3,847	93,557
1.9348	85	67,060	6,013	73,073	67,060	6,013	73,073
2.0432	90	52,541	6,525	59,066	52,541	6,525	59,066
2.1568	95	51,366	5,833	57,199	51,366	5,833	57,199
2.2761	100	56,714	7,537	64,251	56,714	7,537	64,251
2.4017	105	52,752	17,036	69,788	52,752	17,036	69,788
2.5343	110	51,497	20,105	71,602	51,497	20,105	71,602
2.6748	115	35,981	22,017	57,998	35,981	22,017	57,998
2.8240	120	26,167	21,430	47,597	26,167	21,480	47,597
2.9832	125	30,779	28,679	59,458	30,779	28,679	59,458
3.1538	130	26,001	29,272	55,273	26,001	29,272	55,273
3.3376	135	21,975	22,345	44,320	21,975	22,345	44,320
3.5368	140	16,749	26,035	42,784	16,749	26,035	42,784
3.7542	145	26,919	38,782	65,701	11,661	16,800	28,461
3.9935	150	31,942	36,099	68,041	8,450	9,549	17,999
4.2595	155	24,727	33,933	58,665	3,767	5,170	8,937
4.5590	160	18,701	22,644	41,345	1,524	1,845	3,369
4.9017	165	14,497	13,140	27,637	573	519	1,092
5.3021	170	5,621	6,162	11,783	94	103	197
5.7838	175	3,703	240	3,943	21	1	22
6.3883	180	1,836	55	1,891	3	0	3
Total		1,781,711	371,093	2,152,804	1,679,858	254,020	1,933,878

span and obtained results similar to Lenarz et al. (1974).

The computer program MGEAR, written by W. H. Lenarz, was used to obtain estimates of yield per recruit using the Ricker (1958) yield equation. A description and listing of MGEAR is available from its author. The program was slightly modified to calculate indices of egg production using the following equation

$$E_{t_1,t_2} = 0.5\,(t_2 - t_1)\,N_{t_1}\,(FI_{t_1} + FI_{t_2}e^{-(F_{t_1} + M_{t_1})(t_2 - t_1)})$$

where E_{t_1,t_2} = index of egg production between age t_1 and t_2,
FI_{t_1} = index of fecundity for age t_1,
N_{t_1} = number of females in population of age t_1,
F_{t_1} = coefficient of instantaneous fishing mortality between age t_1 and age t_2, and
M_{t_1} = coefficient of instantaneous natural mortality between age t_1 and age t_2.

For this equation it is assumed that the estimates of FI are proportional to egg production per female, which is assumed to be continuous, and that the rate of egg production is linear over the interval (t_1, t_2).

A computer program MIGR was written by J. R. Zweifel to perform the calculations used for the third section of this paper. Since new methodology is developed, a description of the calculations will be given in that section.

AVAILABILITY OF THE STOCK(S) OF ATLANTIC YELLOWFIN TUNA TO SURFACE AND LONGLINE GEAR

In previous works on yield per recruit, yellowfin tuna of all ages in either the entire Atlantic (e.g., Hayasi and Kikawa 1970; Wise 1972; Hayasi et al. 1972; Lenarz et al. 1974), or in the eastern Atlantic (e.g., Fonteneau and Lenarz 1974) were assumed to be equally available to both longline and surface gear. However, since the surface fishery for yellowfin tuna occurs very close to the west African coast (Fox and Lenarz 1973) while the longline fishery for yellowfin tuna is distributed throughout the tropical Atlantic, it seems possible that the longline fishery is exploiting some fish that are not available to the surface fishery. It is

also possible that some stock(s) which are available to surface fishing are never available to the longline fishery. Since significant tagging efforts have begun only recently in the Atlantic and the results of these studies have not been published, data are not available to evaluate the availability of yellowfin tuna to both gears.

However, there is evidence from the Pacific that yellowfin tuna are not equally available to longline and surface gears. With the permission of W. H. Bayliff of the Inter-American Tropical Tuna Commission (IATTC), we examined yellowfin tuna tag return data from the eastern Pacific during 1963-66 in an attempt to evaluate the availability of fish to both gears in that area. We tabulated the number of tag returns for fish larger than 100 cm at return by 10-cm size groups (Table 3). All of the fish had been at liberty for at least 10 mo. Although all of the tagged fish were measured when released, not all were measured when recovered. Bayliff recommended the relationship

$$L = 167\,(1 - e^{-0.6(t-0.833)})$$

estimated by Davidoff (1963) for growth of yellowfin tuna in the eastern Pacific as the best equation to estimate the size of unmeasured fish. All of the returns were surface-caught fish, even though longliners captured a considerable number of yellowfin tuna in the eastern Pacific (east of long. 130°W) (Kume and Joseph 1969). In fact for many of the 10-cm size groups, the longliners caught more yellowfin tuna than the surface gear operators (Table 4).

TABLE 3.—Number of returns of tagged yellowfin tuna from the eastern Pacific Ocean by size interval and year (W. H. Bayliff, pers. commun.).

Size interval (cm)	1963	1964	1965	1966
101-110	2	16	3	3
111-120	1	7	1	1
121-130	2	0	2	0
131-140	0	0	0	1
141-150	0	0	0	0
151-160	0	0	1	0

Again at the suggestion of Bayliff, we estimated the expected return of tags from longline-caught fish when all fish are equally available to both gears. Assuming tag recoveries were independent of each other, recovered tags were reported at the same rate by both components of the fishery, and tagged fish were equally available to both gears: then the expected returns of tagged fish of size i by gear j in year k is given by

$$E(R_{ijk}) = R_{i\cdot k}N_{ijk}/N_{i\cdot k} \qquad (1)$$

$$i = \begin{cases} 1, \text{ when size is between 101 and 110 cm} \\ . \\ . \\ . \\ 6, \text{ when size is between 151 and 160} \end{cases}$$

$$j = \begin{cases} 1, \text{ when fish are caught by surface gear} \\ 2, \text{ when fish are caught by longline gear} \end{cases}$$

$$k = \begin{cases} 1, \text{ when fish are caught in 1963} \\ 2, \text{ when fish are caught in 1964} \\ 3, \text{ when fish are caught in 1965} \\ 4, \text{ when fish are caught in 1966} \end{cases}$$

where R_{ijk} = number of returns and
N_{ijk} = number of fish caught.

A dot in the position of a subscript signifies summation of the variable over the subscript, e.g., $X_{i\cdot k} = \sum_{j=1}^{2} X_{ijk}$.

Forty fish were returned by the surface gear during 1963-66 (Table 3). Using the statistics of Tables 3 and 4 and the three assumptions, a return of 5.4 of these tags would have been expected from the longline fishery and 34.6 from the surface fishery. The chi-square value, corrected for discontinuity, for the observed and expected returns (Equation 1) is 5.13, with probability slightly less than 0.025. The power of the test of the hypothesis of independence, equal reporting rate, and equal availability was reduced because we combined the year and size strata to avoid

TABLE 4.—Catch of yellowfin tuna from the eastern Pacific Ocean (east of long. 130°W) in hundreds of fish by size and gear (Kume and Joseph 1969).

Size interval (cm)	1963		1964		1965		1966	
	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear
101-110	653	336	4,082	173	3,386	30	2,926	54
111-120	473	455	2,245	465	2,211	93	2,044	116
121-130	508	390	720	1,078	1,895	444	1,312	304
131-140	237	751	448	804	905	758	718	515
141-150	240	541	320	469	498	466	536	575
151-160	212	144	102	104	194	205	204	200

strata with low expected values. The probability under Equation (1) of a returned tag being from a surface-caught fish (P_{i1k}) is

$$P_{i1k} = N_{i1k}/N_{i\cdot k} \ . \qquad (2)$$

The exact probability of all returns during the 1963-66 period being from surface-caught fish, given the distribution of returns among year and size categories, is

$$P_{\cdot 1\cdot} = \prod_{i=1}^{6} \prod_{k=1}^{4} (P_{i1k})^{R_{i\cdot k}} \ . \qquad (3)$$

Our estimate of $P_{\cdot 1\cdot}$ is 0.00152, which is very low and indicates that Equation (1) does not hold. Thus we may conclude that 1) tag returns are not independent (e.g., fish that were captured from a school and tagged may remain in the same school until recaptured), and/or 2) longline recoveries are reported at lower rates than surface recoveries, and/or 3) the fish were not equally available to both gears. Since all fish were at liberty for more than 10 mo before being recovered, the assumption of tag returns being independent seems likely to be valid. The independence of tag returns would seem to be a desirable subject for further research since the assumption is so often made in analyses of tag returns. A considerable number of southern bluefin tuna have been recovered and returned by longliners (Shingu 1970), indicating longline fishermen do cooperate in tagging programs. During the period of the study, the surface fishery was only beginning to move offshore (Calkins and Chatwin 1971), while the longline fishery was distributed throughout the area (Kume and Joseph 1969). Also, the fish that were released were caught by surface gear, tagged, and released in nearshore areas. Thus, tagged fish were probably more representative of fish exploited by the surface fishery than those that were exploited by the longline fishery, if two groups of fish existed. Thus it seems plausible that the tagged fish were not equally available to longline and surface gears.

This is further evidence of unequal availability of yellowfin tuna to the two gears in the Pacific. Previously, Hisada (1973) showed that yellowfin tuna caught near the surface using handlines were of the same size as those caught by longliners at the same time and in the same area of the western Pacific. However, the surface-caught fish tended to be more sexually mature except in areas in which the 26°C isotherm occurred at depths fished by longliners. He attributed this phenomenon to a preference for warmer waters by sexually mature fish and noted that larvae of yellowfin tuna tend to be found at water temperatures exceeding 26°C. Thus, some yellowfin tuna evidently behave in a fashion that makes them available to surface fishing but not to longline fishing. Further evidence along these lines is provided by Shingu and Tomlinson (Patrick K. Tomlinson, Inter-American Tropical Tuna Commission, La Jolla, Calif. Pers. commun., 1974) who found that the length-weight relationship estimated by Lenarz (1974) for surface-caught yellowfin tuna in the Atlantic was more representative of the longline catch in the eastern Pacific than was the relationship estimated by Chatwin (1959) for surface-caught yellowfin tuna in the eastern Pacific.

With the above in mind, we considered three hypothetical stock structures for the Atlantic yellowfin tuna fishery: 1) the same stock(s) are equally available to both gears, 2) half of the catch of the longline fishery comes from stock(s) not available to the surface fishery, and 3) the entire catch of the longline fishery comes from stock(s) not available to the surface fishery. The effects of the three hypotheses on estimates of fishing mortality and yield per recruit to the gear were examined.

Using the data in Table 2, we estimated the vector F of size-specific instantaneous mortality rates F_t under the three hypotheses which are identified by the proportion ϕ of the longline catch which comes from the stocks exploited by the surface fishery as $\phi = 1.0$, 0.5, and 0.0 respectively. For $\phi = 1.0$, all of the data in Table 2 was used to estimate the F vector. For $\phi = 0.5$, the surface catch plus 50% of the longline catch was used and for $\phi = 0.0$ only the surface catch was used for estimating F. When $\phi = 0$, an additional F vector was estimated for a longline fishery operating without the presence of a surface fishery by using only the longline catch. The F vectors were then used to calculate yield per recruit to the two gears. Estimation of a vector of size-specific F requires an estimate of natural mortality and size-specific F for one size category. In all instances, we chose to use an estimate of size-specific F for the fish >177.5 cm. This estimate will be referred to as Input F. The final value of size-specific F was set at 0.2 following Lenarz et al. (1974). The estimates (Figure 1) indicate that values of F for large fish are directly related to the portion of the longline catch that comes from the stock(s) exploited by the

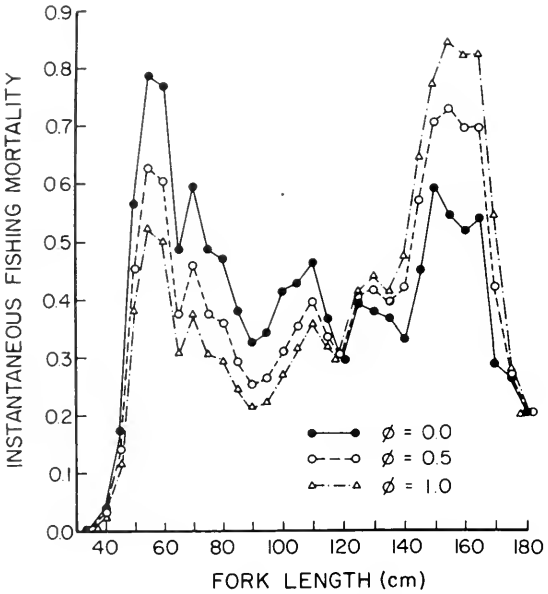


FIGURE 1.—Estimates of size-specific fishing mortality of Atlantic yellowfin tuna as a function of porportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery.

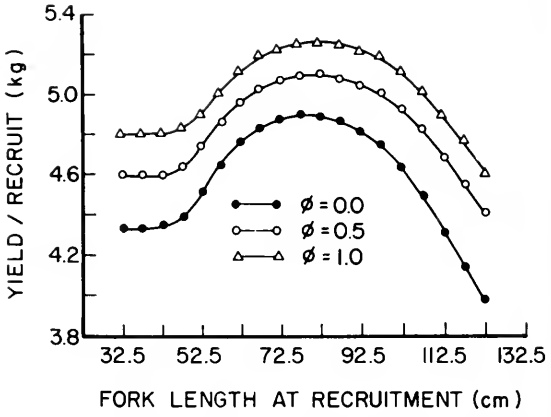


FIGURE 2.—Yield per recruit (kilograms) of Atlantic yellowfin to surface and longline gear as a function of size at recruitment and proportion of catch (ϕ) by the longline fishery that comes from stock(s) exploited by surface fishery. The vector of fishing mortality is equal to the value at the time of study.

surface fishery. The relative values of yield per recruit within a hypothesis are not significantly affected by the portion of the longline catch that comes from the stock(s) exploited by the surface fishery (Figure 2). Therefore, the three hypothetical stock structures do not seem to have much bearing on decisions concerning minimum size regulations.

Estimates of yield per recruit were also plotted as functions of fishing effort (mortality), size at recruitment, and portion of longline catch that comes from stock(s) exploited by the surface fishery. Again the relative values of the results are not significantly influenced by the stock structure (Figure 3a, b). We note that Figure 3 is in agreement with the conclusion of Fox and Lenarz (1974), "... that the Atlantic yellowfin fishery is approaching or has obtained a plateau where substantially increased sustainable average yield of yellowfin tuna will not be obtained by increasing fishing effort without some concomitant change in the constitution of the fishery. . . ." They used the production model approach under the alternative assumptions that either the longline or surface gear exploits the same or separate stock(s).

The effect of the surface fishery on the longline fishery was examined by estimating yield per recruit to the longline fishery in the presence and in the absence of a surface fishery (Figure 4). The results suggest that if the two gears exploit the same stock(s), the surface fishery reduces the potential yield per recruit to the longline fishery by about twofold at the position of the fishery during the study period (i.e., multiplier of effort = 1) and about fivefold for a threefold increase in effort. The same procedure was used to examine the effect of the longline fishery on the surface fishery (Figure 5). The results indicate that at the level of fishing effort at the time of study, the yield per recruit to the surface fishery would be increased by 25% if the longline fishery ceased.

Although the presence of each fishery reduces the yield per recruit of the other, the yield per

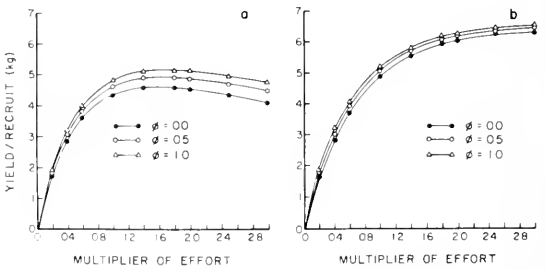


FIGURE 3.—Yield per recruit of Atlantic yellowfin tuna as a function of fishing effort and proportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery: (a) size at recruitment is 32.5 cm, (b) size at recruitment is 77 cm.

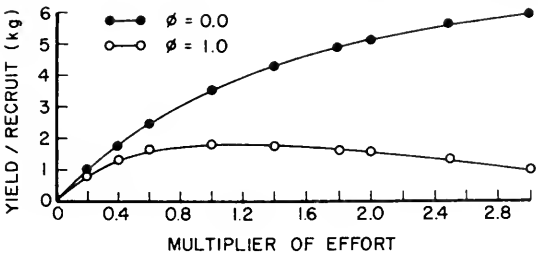


FIGURE 4.—Estimates of yield per recruit of Atlantic yellowfin tuna to the longline fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of a surface fishery.

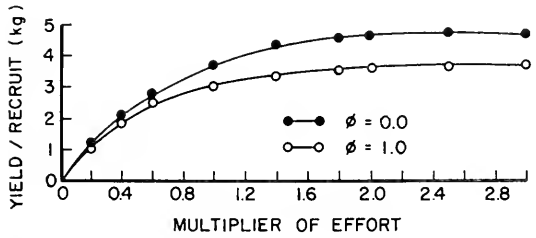


FIGURE 5.—Estimates of yield per recruit of Atlantic yellowfin tuna to the surface fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of longline fishery.

recruit of the combined fisheries is higher than the yield per recruit of either fishery alone. The results suggest that if a catch quota system is imposed on the Atlantic yellowfin tuna fishery, all components should be included unless it is shown that different stock(s) are being exploited by the gear.

The above results (Figures 4, 5) suggest that a stock of yellowfin tuna will produce a potentially higher yield per recruit to a longline fishery than to a surface fishery, if the fish are equally available to the two gears. However, until the question of availability is settled, it is not possible to predict the potential production to the two gears. We point out here that gear-specific availability is not well known for any tuna fishery and would be difficult to determine. Thus, we are faced with the prospect of probably being forced to determine empirically the production potential for each gear in each fishery. After a fishery is established, an analysis of the type conducted on the Atlantic yellowfin tuna fishery could be used to examine the effects of availability to the two gear types, and a tagging study could be designed to provide the required answers.

EFFECTS OF AGE-SPECIFIC SEX RATIOS OF ATLANTIC YELLOWFIN TUNA ON YIELD PER RECRUIT TO THE TWO TYPES OF GEAR AND STOCK FECUNDITY

While a number of authors have noted that the ratio of females to males appears to be less than 1:1 for catches of larger tunas, none to our knowledge has incorporated these observations into calculations of yield per recruit or stock fecundity. Beardsley (1971) reported that the ratio of female to male Atlantic longline-caught albacore was 233:365 during the December 1969-September 1970 period. Males increasingly dominated at sizes >100 cm. Females slightly outnumbered males between 92 and 100 cm. One explanation for the catch curves estimated by Beardsley is a 1:1 sex ratio at small sizes, a slightly slower growth for females for fish >90 cm, and beyond 100 cm, either a higher rate of natural mortality for females or a change in behavior that makes females less available than males to longline fishing. Other explanations exist, e.g., a combination of low sex ratio and slow growth of females throughout their life. Sakamoto (1969) noted for Atlantic bigeye tuna, ". . . males predominated in areas of higher water temperature. Proportion of females increase as the water temperature gets lower." His data indicate that as size increases the proportion of females decreases and females may grow slower than males in waters between lat. 30° to 50°N, but not in equatorial waters. Data presented by Kikawa (1964) indicate that southern bluefin tuna >150 cm are predominantly males, while females often outnumber males at smaller sizes. Thus, female southern bluefin tuna may grow more slowly than males.

Since there is considerable evidence for age-specific changes in the sex ratio of tunas, we believe that the effects of such changes on estimates of yield per recruit to each gear type and fecundity should be investigated. We have assumed sex ratios to be the same as with Pacific yellowfin tuna because no extensive studies of age-specific sex ratios for Atlantic yellowfin tuna have been published. We used results from a study by Murphy and Shomura (1972), who found that beyond 140 cm male yellowfin tuna greatly outnumbered females (Figure 6). The data in Figure 6 do not show a large excess of females in any size interval and thus no evidence of sex-specific growth is exhibited. Using their data and the age-length

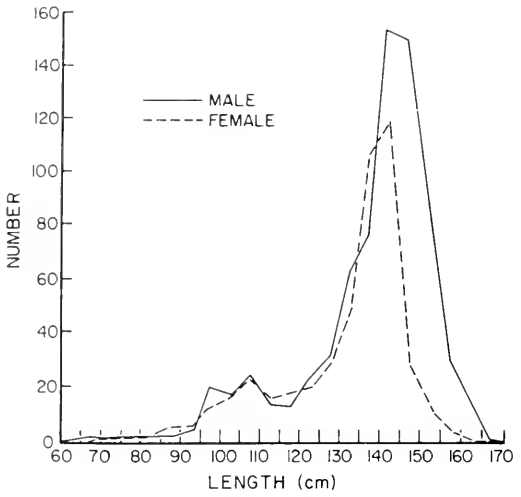


FIGURE 6.—Length distribution by sex of longline-caught yellowfin tuna in the central Pacific Ocean (Murphy and Shomura 1972).

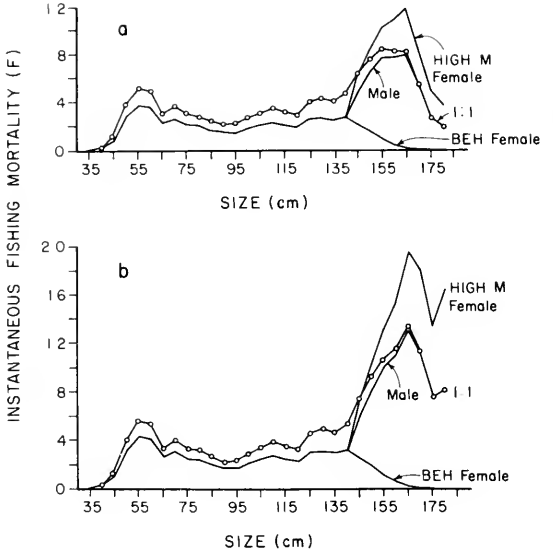


FIGURE 7.—Estimates of size and sex specific coefficient of instantaneous fishing mortality on annual basis (F) for Atlantic yellowfin tuna for 1:1, BEH and HIGH M hypotheses (see text): (a) low Input F, B) high Input F.

relationship of LeGuen and Sakagawa (1973), we estimated that beyond 140 cm

$$\ln R = 6.74 - 1.96t \qquad (4)$$

where R = ratio of females to males
t = age in years.

One interpretation of the above result (assuming that males have a coefficient of instantaneous natural mortality of 0.8 on an annual basis as do all fish <145 cm) is that female yellowfin tuna >140 cm have a coefficient of apparent natural mortality of 2.76. Assuming that the results of Murphy and Shomura apply to the Atlantic and that all yellowfin tuna are equally available to both gears, we separated the catch of yellowfin tuna into males and females using Equation (4) and Table 2, and estimated F for the males using Input F values of 0.2 and 0.8 for fish >177.5 cm (Lenarz et al. 1974). An alternative method would be to use the same Input F for the three hypotheses at the smallest size interval. This was attempted and resulted in either estimates of F_t which, based on the results of other studies, appeared to be too low under the 1:1 hypothesis or too high under the other hypotheses. The estimates of size-specific F are similar except for very large yellowfin tuna (Figure 7). Since the deviations in sex ratio from 1:1 occurs only at large sizes, we used both sets of estimates of F.

For females, three hypotheses were examined for estimating F: 1) the observed differences in sex ratios are artifacts, and consequently females have the same values of F and M as males (denoted 1:1); 2) females >140 cm have a higher natural mortality rate than males but are exploited at the same rate as males for all sizes (denoted as HIGH M); and 3) females have the same natural mortality rate as males but become less subject to fishing mortality beyond 140 cm (denoted as BEH for behavior changes). Under the BEH hypothesis, F_t for females >140 cm is equal to the ratio of the catch of females to the catch of males times F_t estimated for males. The alternative hypotheses considerably affected the estimates of size-specific F (Figure 7).

In the following analyses, we found that the BEH and HIGH M hypotheses produce similar results. To save space, we refer to only the one hypothesis that produced results which showed the greatest difference from the 1:1 hypothesis. Also, when not specifically indicated, size of recruitment and effort are assumed to be those at the time of the study, i.e., 1967-71 where the multiplier of effort is equal to unity.

Estimates of yield per recruit as a function of fishing effort are shown in Figure 8. The choice of Input F has little effect on the relative values of

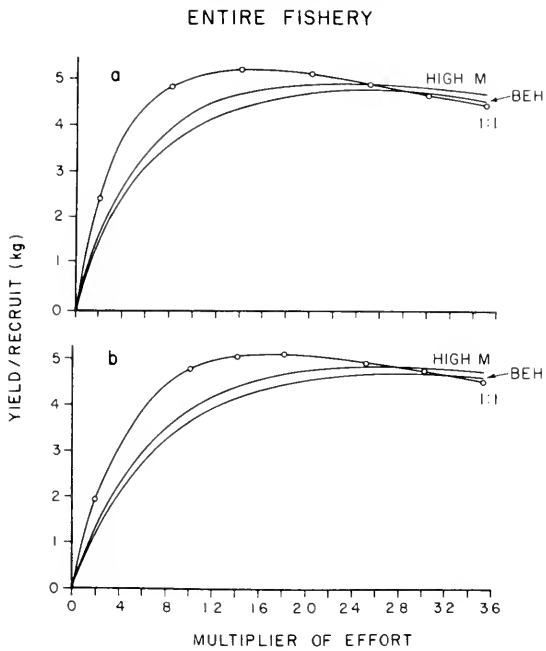


FIGURE 8.—Estimates of yield per recruit of Atlantic yellowfin tuna at size of recruitment at time of the study as a function of fishing effort and sex hypothesis: (a) high Input F, (b) low Input F.

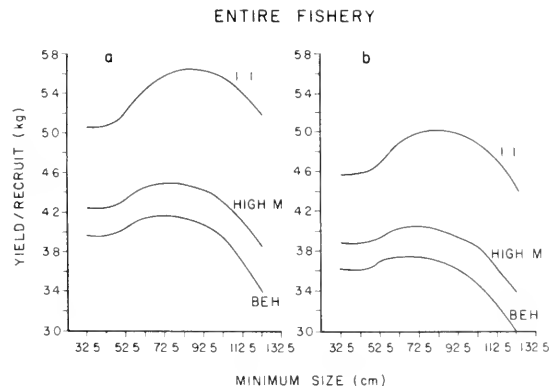


FIGURE 9.—Estimates of yield per recruit of Atlantic yellowfin tuna at level of fishing effort at the time of the study for 1:1, BEH and HIGH M hypotheses as a function of size at recruitment: (a) high Input F, (b) low Input F.

yield per recruit. Yield per recruit is closer to the maximum under high Input F than low Input F. The curves are considerably more dome-shaped when a 1:1 sex ratio is assumed than under the other two hypotheses. Under high Input F and the 1:1 hypothesis only a 3% increase in yield per recruit could be obtained by increasing fishing effort. Under the BEH hypothesis, a 20% increase in yield per recruit could be obtained by doubling the effort.

Estimates of yield per recruit as a function of size at recruitment are shown in Figure 9. Again the choice of Input F has little effect on the relative values of yield per recruit. A slightly greater dependence of yield per recruit on minimum size is obtained when the high Input F is used. Under high Input F, and the 1:1 hypothesis a 10% increase in yield per recruit could be achieved by increasing size at recruitment. Under the BEH hypothesis, only a 5% increase would occur. Eumetric fishing occurs when size at recruitment is raised from the current 32.5 to 82.5 cm under the 1:1 hypothesis and 72.5 cm under the BEH hypothesis.

Estimates of yield per recruit as a function of fishing effort were also calculated for each gear (Figure 10). The results show that the curves are more dome-shaped for the longline fishery than for the surface fishery under all three hypotheses. Furthermore, the longline fishery is more sensitive to fishing effort under the 1:1 hypothesis than under the other two. The curves for the surface fishery are dome shaped under the 1:1 hypothesis, but appear to approach an asymptote under the other two.

We also estimated yield per recruit for each gear when the other gear is not exploiting the stock (Figure 11). A comparison of Figures 10 and 11 reveals that yield per recruit to the longline fishery would increase by about 115% if surface fishing were eliminated under high Input F and the 1:1 hypothesis and 76% under high Input F and the BEH hypothesis. Yield per recruit to the surface fishery would increase by about 30% if the longline fishery were eliminated under high Input F and the 1:1 hypothesis and 22% under the BEH hypothesis. Thus, the nature of age-specific sex ratio has a greater effect on that of the longline fishery than on the relative success of the surface fishery. The curves for a longline fishery in the presence of a surface fishery are dome-shaped (Figure 10), while the curves in the absence of a surface fishery are not (Figure 11). This again points out the importance of not treating the two fisheries as separate entities unless it is shown that they exploit separate stocks.

Stock fecundity (egg production per recruit) relative to an unfished stock was estimated as a function of fishing effort. Stock fecundity was considerably affected by the choice of fecundity index

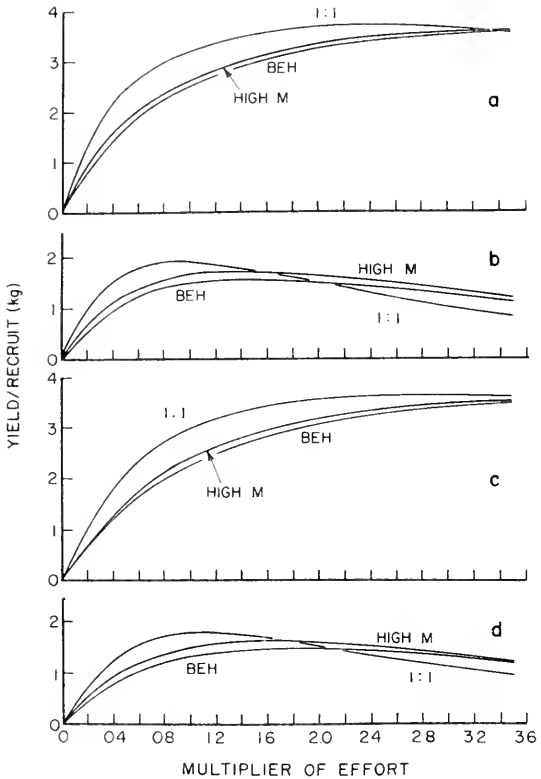


FIGURE 10.—Estimates of yield per recruit of Atlantic yellowfin tuna when both gear fish at size of recruitment at the time of the study as a function of sex ratio hypothesis, fishing effort, and gear: (a) surface gear with high Input F, (b) longline gear with high Input F, (c) surface gear with low Input F, and (d) longline gear with low Input F.

and sex ratio hypothesis but only slightly affected by the choice of Input F (Figure 12). At the level of fishing effort at the time of the study under high Input F and 1:1 hypotheses, the relative fecundity is 0.28 when the fecundity index I is used and 0.39 when fecundity index II is used. Under the HIGH M hypothesis, relative fecundity is 0.55 when fecundity index I is used and 0.61 when fecundity index II is used. Thus, at the level of fishing effort at the time of the study, the choice of fecundity has a 10 to 30% effect on estimates of relative fecundity, while the choice of sex ratio hypothesis has a 30 to 50% effect. The two choices, fecundity index and sex ratio hypothesis, also have considerable effect on relative fecundity when plotted as a function of size at recruitment (Figure 13).

The relationship between stock fecundity and recruitment has not been demonstrated for any tuna. As shown above, one of the difficulties in demonstrating such a relationship is obtaining a reasonably accurate estimate of stock fecundity. Even if stock fecundity could be accurately determined, the recruitment process is likely to be so complex that much more research would be required before a reliable predictor of recruitment could be developed.

It is interesting to note that similar estimates of yield per recruit and relative fecundity are obtained under the HIGH M and BEH hypotheses. Thus it appears that research should be directed toward determining whether or not the 1:1 hypothesis or one of the other two are valid rather than distinguishing between the HIGH M and BEH hypotheses. This research should be a fairly simple matter. The choice of fecundity index is also of significance for estimating relative fecundity. The difference between the two indices is caused mainly by different maturity schedules (Hayasi et al. 1972). The surface-caught fish appeared to mature at an earlier age than longline-caught fish, and could be an artifact related to the phenomenon noted by Hisada (1973); i.e., mature fish tend to prefer warm water. It should also be a fairly simple matter to determine the cause of the difference between the two indices.

SIMULATION MODEL OF PATTERNS OF DISPERSAL AND RECRUITMENT OF YELLOWFIN TUNA

Factors that could cause groups of tuna to not be available to all components of a fishery include nonrandom movements, random movements but nonrandom distribution of fishing gear or effort, and recruitment that is nonrandom in a geographical sense.

Extensive tagging experiments have not produced any clear-cut evidence of a definite migration pattern for yellowfin tuna in the eastern Pacific. Bayliff and Rothschild (1974) recently found evidence for both random dispersal and directed movements. They were not able to remove the effects on their data of lack of fishing effort in some time-area strata and of the coastal boundary. The evidence for directed movements indicated that such movements were generally parallel to the coast, suggesting that the presence of the coast influenced their results. Fink and Bayliff (1970), in a synthesis of extensive tagging data, proposed that recruitment to the nearshore surface fishery is not random in a geographical sense, but tends to take place off Mexico and in the Panama Bight.

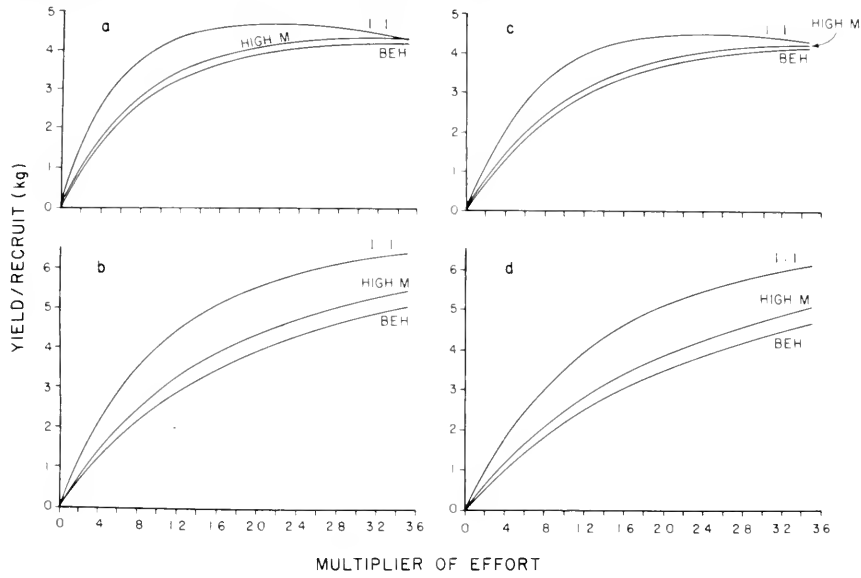


FIGURE 11.—Estimates of yield per recruit at size at recruitment at the time of the study as a function of fishing effort, sex ratio hypothesis, and fishing gear when only one gear is fishing: (a) high Input F and surface gear, (b) high Input F and longline gear, (c) low Input F and surface gear, and (d) low Input F and longline gear.

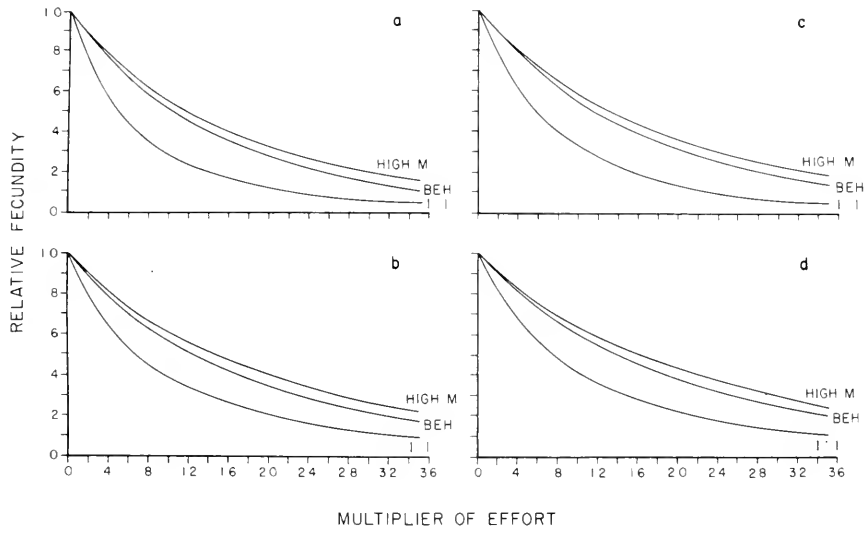


FIGURE 12.—Estimates of relative stock fecundity at size at recruitment at the time of the study as a function of fishing effort, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity Index II, (c) low Input F and fecundity index I, and (d) low input F and fecundity index II.

With the above results in mind, we developed a computer simulation model to examine the interrelationships of: 1) patterns of movement of fish; 2) patterns of recruitment (i.e. by area), and 3) fishing strategy for two gear types (surface and longline) fishing alone or together on the same population.

The model is general in that it allows the user to

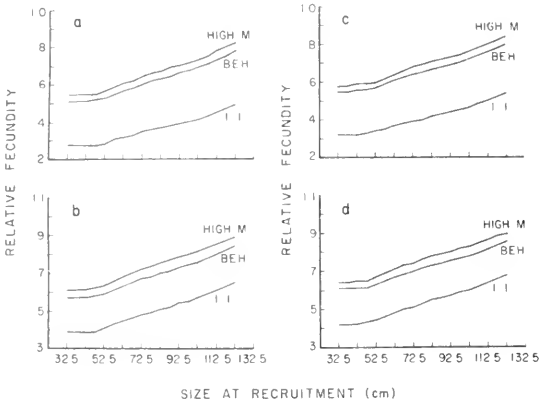


FIGURE 13.—Estimates of relative stock fecundity at level of fishing effort at the time of study as a function of size at recruitment, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity index II, (c) low Input F and fecundity index I, and (d) low Input F and fecundity index II.

specify the nature of movements, locations of recruitment, parameters of growth, and natural fishing mortality.

We crudely represented the eastern Pacific Ocean with the grid of 5° square areas shown in Figure 14. The number of fish of a specific age in each cell at time t is given by the vector

$$N_t = AS_tN_{t-1} \quad (5)$$

where N_t (112 × 1) has elements $(n_i)_t$ equal to the number of fish in cell i at time t, S_t (112 × 112) is a diagonal matrix with elements $(s_{ii})_t$ equal to the survival rate of fish in cell i from time $t-1$ to time t, A(112 × 112) is a probability transfer matrix with elements (a_{ij}) equal to the probability of a fish in cell j moving to cell i, and where N_0(112 × 1) has elements $(n_i)_0$ equal to the number of recruits in cell i. Five consecutive year classes are in the system at a time.

For our work we specified A, the transfer matrix, by the assumption that for any cell the probabilities of fish remaining stationary and moving to each of eight adjacent cells is the same, i.e., 1/9. Any other transfer has zero probability. This general rule is modified as follows:

1) Probabilities of remaining stationary in cells adjacent to the shore are augmented by the sum of probabilities of those movements which would otherwise put fish on land and the probability of occurrence on land is zero.

COLUMN

ROW	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2	15	16	17	18	19	20	21	22	23	24	25	26	27	28
3	29	30	31	32	33	34	35	36	37	38	39	40	41	42
4	43	44	45	46	47	48	49	50	51	52	53	54	55	56
5	57	58	59	60	61	62	63	64	65	66	67	68	69	70
6	71	72	73	74	75	76	77	78	79	80	81	82	83	84
7	85	86	87	88	89	90	91	92	93	94	95	96	97	98
8	99	100	101	102	103	104	105	106	107	108	109	110	111	112

FIGURE 14.—Representation of eastern Pacific Ocean. Each cell represents a 5° square area. Hatched cells represent land. Column 1 is western boundary and Column 14 is eastern boundary. Row 1 is northern boundary and row 8 is southern boundary.

2) Probabilities projecting beyond the northern and southern edges are similarly absorbed on the boundaries.

3) In cells of rows 2 and 7, probabilities of moving toward rows 1 and 8 are decreased by half with the probability of remaining stationary increased by a like amount. This is an attempt to simulate a stock encountering increasingly marginal conditions as the northern and southern boundaries are approached.

4) Probabilities of remaining stationary on the western edge are augmented by the probability of returning from beyond the boundary in a single time interval. The remainder of the fish that move beyond the western boundary are lost to the system.

The speed of dispersion is controlled both by A and the time interval. The time interval was 3 mo for this study. The combination of A as defined and time interval of 3 mo allows a fish to travel a maximum of 1,200 mi in a year. Only 1 out of 820 surviving fish that begin the year in the center of the grid travel 1,200 mi in a year. These relatively slow random movements seemed reasonable, based on the results shown in Bayliff and Rothschild (1974) and recent results of IATTC tagging studies (Inter-American Tropical Tuna Commission[3]).

Two alternative recruitment models were examined. For the first, denoted as inshore re-

[3]Cited with permission of M. Clifford Peterson, Acting Director of the Inter-American Tropical Tuna Commission. From the Inter-American Tropical Tuna Commission Bi-monthly Report, March-April 1976:8-13.

cruitment, recruits are divided equally among the five cells 51, 52, 69, 83, and 84, which resemble the recruitment areas proposed by Fink and Bayliff (1970). For the other alternative, denoted as uniform recruitment, recruits are divided equally among all cells except those on the boundaries or on land. Total annual recruitment is 100 fish. We assumed 1) that fish are 1 yr old when recruited, 2) growth proceeds according to the von Bertalanffy curve of LeGuen and Sakagawa (1973), and 3) the coefficient of instantaneous natural mortality is 0.8 on annual basis and is independent of time and location. Fish >6 yr old (175 cm) were removed from the system. Consequently, under constant conditions the fishery reaches equilibrium in 5 yr. The system was always run for 5 yr before an experiment was begun.

We first examined the effects of sampling location, dispersal, and location of recruitment on age distribution and the resulting apparent rate of natural mortality obtained from unbiased samples from an unfished population. Mortality was estimated with the standard linear regression model ($\ln N_t = \ln N_0 - Mt$) from the age distribution of fish in each cell. It is assumed that mortality is constant after full recruitment, and that the modal age represents first age of full recruitment. The results reveal that M is usually overestimated as would be expected when fish emmigrate from a sampled area (Figure 15). Estimates of M tend to be relatively high near areas of spawning with inshore recruitment. In the case of uniform recruitment, estimates of M tend to be highest on the western boundary where fish are lost to the system. Modal age tends to increase in a westerly direction for inshore recruitment and stay relatively constant for uniform recruitment (Figure 15). The modal size of actual catches of surface-caught yellowfin tuna in the eastern Pacific increases in a westerly direction (Figure 16). Although the surface fishery probably does not take an unbiased sample of the size distribution of the population, the data are suggestive of reduced recruitment in the western areas.

We simulated a 20-yr hypothetical yellowfin tuna fishery to examine interactions among a longline fishery, inshore surface fishery, ocean-wide surface fishery, and ocean-wide surface fishery that does not heavily exploit young fish as follows:

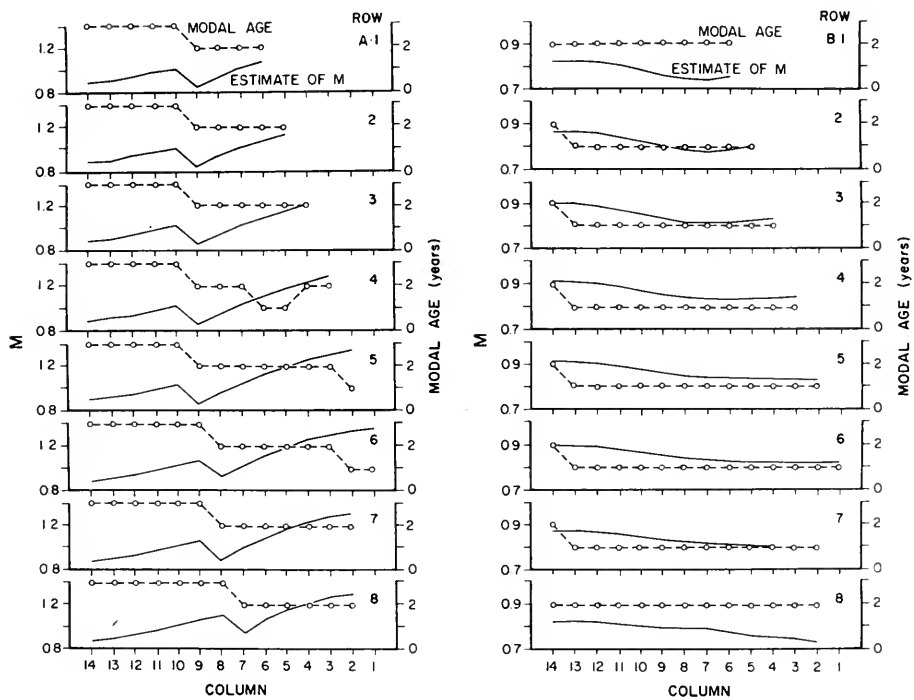
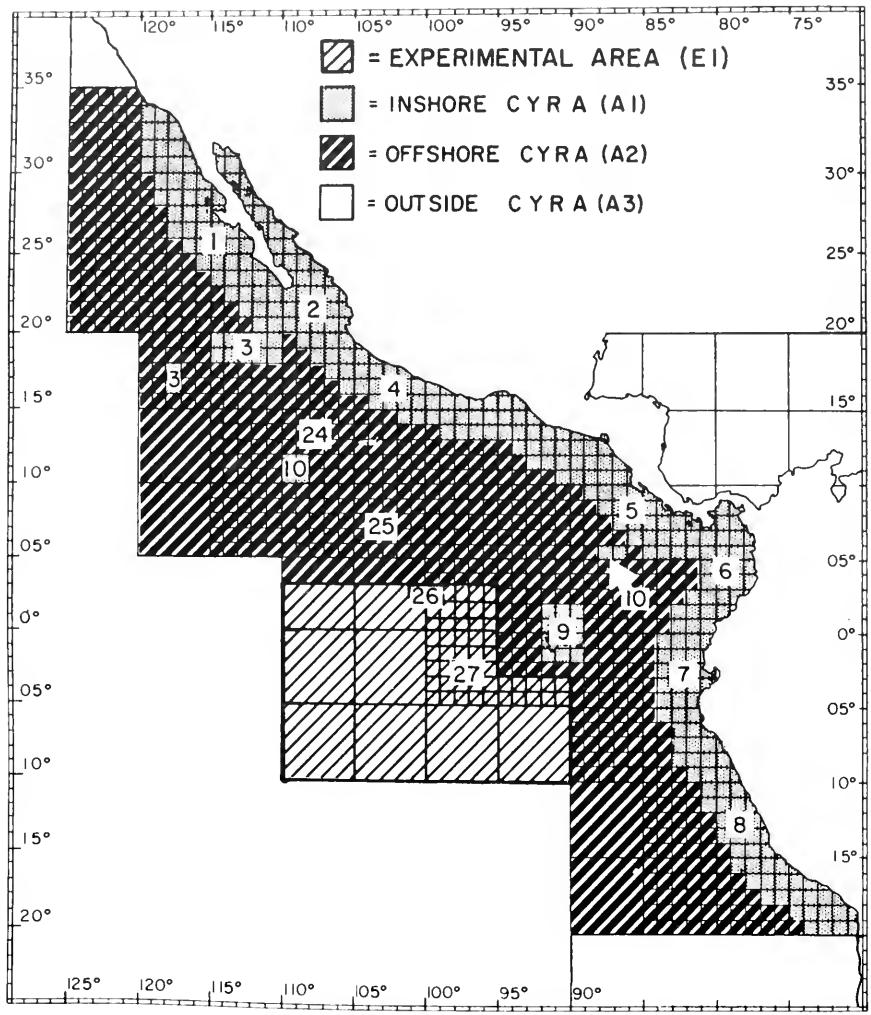


FIGURE 15.—Estimates of coefficient of instantaneous natural mortality on annual basis (M) and modal age of yellowfin tuna by row and column: (A) inshore recruitment, and (B) uniform recruitment.



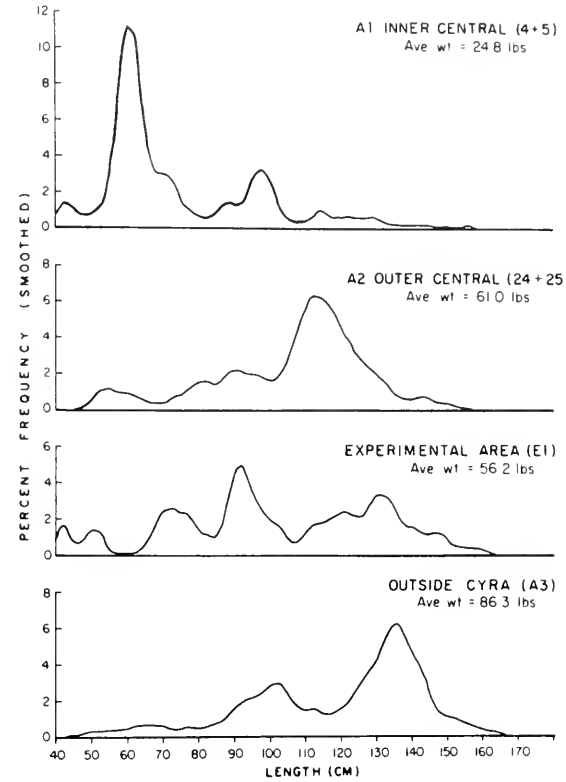


FIGURE 16.—Taken from the Inter-American Tropical Tuna Commission (1974): (a) the eastern Pacific Ocean showing areas A1, A2, and A3. The numbers within the areas designate subareas used for size composition studies, and (b) length-frequency distribution of yellowfin tuna in the inner area (areas 4 and 5), the outer area (areas 24 and 25) of the central region of the CYRA (Commission Yellowfin Regulatory Area), in the experimental area (E1), and in the area to the west of the CYRA (A3).

1) For the first 5 yr only longliners fished and only in rows 5 to 8.

2) For the next 5 yr, this longline fishery was augmented with surface gear in all cells adjacent to the coast.

3) Next, exploitation by the surface gear was expanded to include all cells for 5 yr.

4) Finally, for the last 5 yr, age specific surface fishing mortality was reduced by 75% for fish <2.5 yr of age because much of the surface catch of yellowfin tuna in offshore areas of the eastern Pacific comes from schools associated with porpoise. Typically, porpoise schools contain few yellowfin tuna <2.5 yr of age (Calkins 1965).

Steps 1, 2, and 3 resemble the sequence of events in the eastern Atlantic fishery for yellowfin tuna. Yellowfin tuna first were exploited in a significant fashion by longliners in a 10° band along the equator, then a nearshore surface fishery became significant, and in recent years some exploitation by surface gear in offshore areas has occurred. To our knowledge, step 4 has not occurred in the Atlantic. Age-specific fishing mortality rates similar to those by surface gears estimated by Lenarz et al. (1974) for the Atlantic yellowfin tuna fishery were used (Table 5). The Ricker yield equation was used to calculate yield for each time-area stratum.

Total yields per recruit were calculated and are shown in Figure 17. Yields per recruit are quite similar for both recruitment models except near shore, where yield per recruit was considerably higher for the inshore recruitment model than for the uniform recruitment model. The difference in yield per recruit between the two models decreases slightly as time increases. Yield per recruit closely approached equilibrium yield within 3 yr after a change was made in the fishery. Total equilibrium yield per recruit with an inshore surface fishery

TABLE 5.—Estimates of age-specific F on an annual basis used as baseline for simulation. See text for modifications of mortality rates during simulation.

Age (yr)	Longline gear	Surface gear	Surface gear with reduced F
1.0	0.00	0.30	0.08
1.5	0.00	0.30	0.08
2.0	0.05	0.22	0.06
2.5	0.15	0.20	0.20
3.0	0.25	0.18	0.18
3.5	0.35	0.30	0.30
4.0	0.45	0.35	0.35
4.5	0.40	0.42	0.42
5.0	0.40	0.27	0.27
5.5	0.20	0.20	0.20
6.0	0.05	0.15	0.15

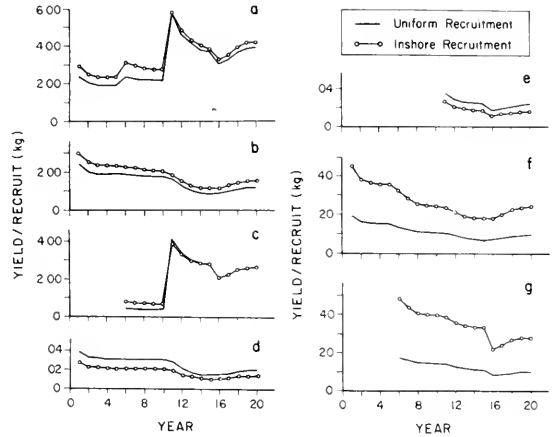


FIGURE 17.—Yield per recruit of hypothetical yellowfin tuna fishery: (a) total, (b) longliners in all areas, (c) surface gear in all areas, (d) longliners in cells 71 and 85, (e) surface gear in cells 71 and 85, (f) longliners in cells 69, 84, and 97, and (g) surface gear in cells 69, 84, and 97.

and longline fishery was about 17% higher than with a longline fishery alone, 54% higher with a uniform surface fishery than with only a longline and inshore surface fishery, and increased by 9% when F for small fish was reduced by 75%. Under the assumption that the catchability coefficient is independent of area, the surface fishery increased its equilibrium yield per recruit about fourfold by increasing its effort about 12-fold when it expanded into offshore waters. The same action decreased yield per recruit to the longliners by about 55%.

We next examined the potential yield per recruit to longliners in rows 5, 6, 7, and 8 by starting a longline fishery with the age-specific F vector multiplied by the scalar 0.3 and then multiplying by 1.3 each year afterward. Yield per recruit appears to approach an asymptote of about 6 kg for inshore recruitment and 5 kg for uniform recruitment (Figure 18). The reduction in catch per recruit per effort by fishing is not significantly affected by choice of recruitment model. Even though catch per recruit per effort at high levels of effort was only about 20% of that at the beginning of exploitation, overfishing in a yield-per-recruit sense did not occur. Average size of fish in the catch was not significantly affected by the recruitment model, and decreased from about 50 to 30 kg with increased fishing effort (Figure 18).

A simulation for an inshore surface fishery indicated an asymptotic production curve with a

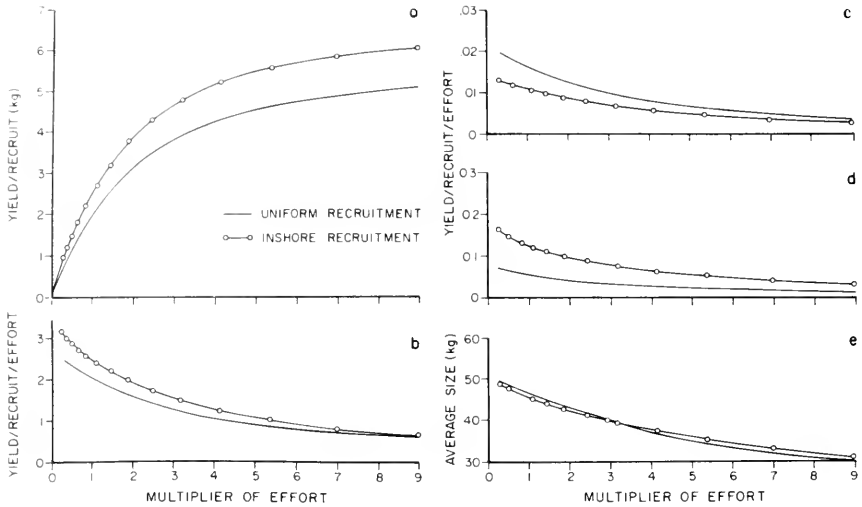


FIGURE 18.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical longline fishery: (a) total yield per recruit, (b) total yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size in all squares.

maximum yield per recruit of about 1.4 kg for uniform recruitment and 2.2 kg for inshore recruitment (Figure 19). Catch per recruit per effort was reduced by about 75% under both alternatives. The ratio of maximum yield per recruit for a longline fishery to an inshore surface fishery was about 2.7 for inshore recruitment and 3.4 for uniform recruitment. Average size of fish in the catch was about 2 kg higher for uniform recruitment than for inshore recruitment and decreased from 16 or 18 kg to 8 or 11 kg with increased fishing effort (Figure 19).

Simulation of a uniform surface fishery revealed that choice of recruitment model had an insignificant effect on yield per recruit, catch per recruit per effort, and average size of catch, except that catch per recruit per effort in the nearshore area was relatively high for inshore recruitment (Figure 20). A 75% reduction in F for fish <2.5 yr old had considerable effect on the results. Maximum yield increased from about 5.1 to 6.9 kg when F was reduced. Both yield curves are dome-shaped. Catch per recruit per effort became relatively higher at high levels of effort when F was reduced. As expected, average size was considerably higher for reduced F.

With inshore recruitment, maximum yield per recruit changes from about 2.2 kg for an inshore fishery (Figure 19) to about 5.1 kg for a uniform

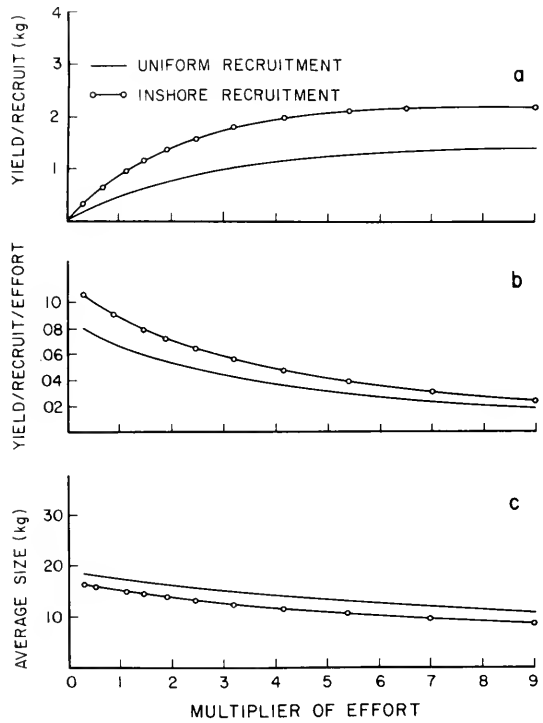


FIGURE 19.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical inshore surface fishery: (a) yield per recruit, (b) yield per recruit per effort, and (c) average size of fish in catch.

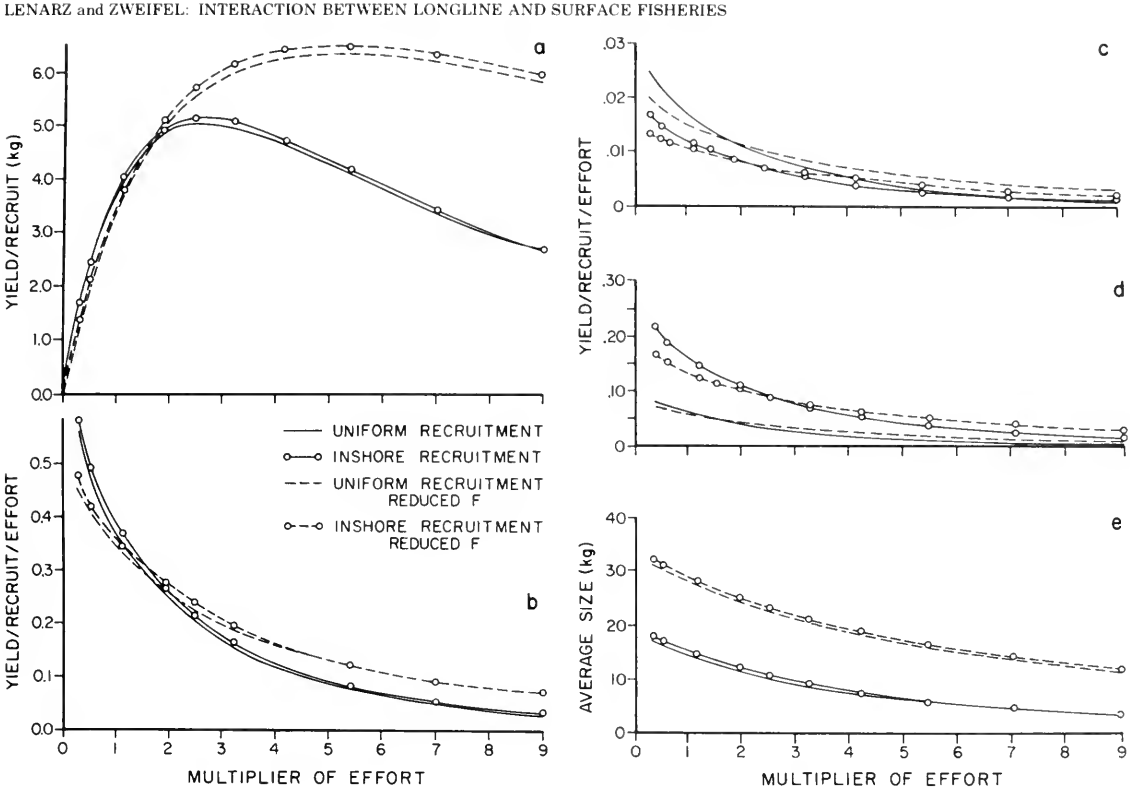


FIGURE 20.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical uniform surface fishery: (a) yield per recruit, (b) yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size of fish in catch.

fishery (Figure 20). With uniform recruitment, maximum yield per recruit changes from about 1.4 kg for an inshore fishery to about 5.0 kg for a uniform fishery.

The results of this section indicate that the pattern of recruitment is primarily of interest for examining the potential of a nearshore surface fishery to a surface fishery that exploits the entire area or a longline fishery. The presence of some small yellowfin tuna in length-frequency data for offshore areas from the eastern Pacific fishery (Figure 17) reveals that some recruitment occurs offshore. Recruits apparently are not highly available to surface fishing offshore because most yellowfin tuna are caught in schools associated with porpoise. Such schools normally contain only low percentages of small yellowfin tuna. A well-designed tagging study could provide estimates of the exploitation rate by size for yellowfin tuna in the offshore areas. Until the pattern of recruitment is determined, it will be necessary to continue estimations of relative production to longliners, inshore surface gear, and offshore surface gear in an empirical fashion.

We examined only one reasonable example of an infinite number of possible configurations of the transfer matrix A and time interval. Further use of the model should include a sensitivity analysis of the results to choice of A and number of cycles per year.

SUMMARY AND CONCLUSIONS

This paper examines three aspects of dual fisheries (surface and longline) on yellowfin tuna. Models of yellowfin tuna fisheries are developed to evaluate possible effects of unknown components of the biology and behavior on the fisheries. The results, while not conclusive because of insufficient knowledge, indicate the magnitude of the effects of those factors which were examined.

We present evidence that not all yellowfin tuna are equally available to longline and surface fisheries in the Pacific Ocean. We show that three

models of availability of yellowfin tuna to the two types of gear in the Atlatnic Ocean do not have much effect on decisions concerning minimum size regulations. If fish are equally available to both gear types, yield per recruit is higher to a longline fishery than to a surface fishery, but is higher for the combined gears than to either gear fishing alone.

We also note that there is considerable evidence that large females of all commercially important *Thunnus* are caught in fewer numbers than large males. The effect of this phenomenon on yield per recruit and relative stock fecundity was examined for Atlantic yellowfin tuna. When plotted against fishing effort, yield per recruit is more dome-shaped when the sex ratio is 1:1, as is usually assumed, than when the sex ratio is as observed. Changes in size at recruitment also have a greater effect on yield per recruit when the sex ratio is 1:1 than when the sex ratio is as observed. Competition between longline and surface fishing is more intense when the sex ratio is 1:1 than otherwise. The fishery has a greater effect on stock fecundity if the sex ratio is 1:1 instead of that observed.

Tagging studies of yellowfin tuna in the eastern Pacific indicate that movements are fairly slow compared with more highly migratory species such as albacore and bluefin tuna and have not produced any clear-cut evidence of a definite migration pattern. Size composition of the catch suggests that recruitment to the fishery occurs mainly along the coast of Central America. A simulation model was developed for the eastern Pacific to examine the interrelationships of patterns of movements of fish, patterns of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either along the coast or throughout the eastern Pacific. The results indicate that either pattern of recruitment could allow the increased catch observed in the Pacific as the surface fleet moved offshore. However, the pattern of recruitment does affect the potential yield per recruit of a nearshore surface fishery relative to a surface or longline fishery that exploits the entire area. Both choices of recruitment models resulted in an asymptotic relationship between yield per recruit and effort for a longline fishery over the range of effort examined. Overfishing in a yield per recruit sense did not occur, even though catch per effort decreased by 80%. Approximately the same results were obtained for an inshore surface fishery. However, curves of yield per recruit plotted against effort for a surface fishery that exploits the entire area are dome-shaped.

The study reveals several biological and behavioral parameters which, because of lack of knowledge or information, are rarely considered but do appear to have a significant effect on some aspects of the dynamics of yellowfin tuna fisheries. Tagging and fecundity studies are suggested in order to fill these gaps. Perhaps as important, other aspects of the dynamics of yellowfin tuna fishing appear to be insignificantly affected by the examined parameters.

ACKNOWLEDGMENTS

This study was stimulated by Brian J. Rothschild, who has had a long interest in the interactions between longline and surface fisheries for tunas. The work benefited from discussions with Rothschild and William W. Fox, Jr. of the Southwest Fisheries Center La Jolla Laboratory; William H. Bayliff and Patrick K. Tomlinson of the Inter-American Tropical Tuna Commission, La Jolla, Calif.; Allan Fonteneau of the Centre de Recherches Oceanographiques, Abidjan, Ivory Coast; and Frank Mather III of the Woods Hole Oceanographic Institution. Many of the computer runs were made by Atilio Coan and Kenneth Brenneke of the Southwest Fisheries Center La Jolla Laboratory. We thank William H. Bayliff, Jerry Wetherall of the Southwest Fisheries Center Honolulu Laboratory and John P. Wise, National Marine Fisheries Service, Washington, D.C., for reviewing the paper. We owe considerable thanks to an unnamed referee who made many useful suggestions and to Lorraine Prescott for her patient and excellent typings of several versions of this paper.

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ASPECTS OF BROWN SHRIMP, *PENAEUS AZTECUS*, GROWTH IN THE NORTHERN GULF OF MEXICO

MICHAEL L. PARRACK[1]

ABSTRACT

The growth of brown shrimp, *Penaeus aztecus*, was studied by utilizing forms of growth models compatible with mark-recapture data. The analysis of 5,100 individuals marked and later recaptured in the northern Gulf of Mexico indicates that the von Bertalanffy model is slightly superior to the logistic in reflecting growth in length and the monomolecular model is superior to the Gompertz in expressing growth in weight. Linear functions are apparently inadequate growth models for brown shrimp. Estimated size-age relationships are appreciably different for each sex in that females are much larger than males of the same age. The pattern of growth shown in this analysis for populations in the northern Gulf is different from that reported in the southern Gulf off the Mexican coast and that reported in U.S. Atlantic coastal waters.

The commercial importance of brown shrimp, *Penaeus aztecus* (Ives 1891), has precipitated several studies of the growth rate for individuals of that species. Definition of the growth rate is necessary in order to develop an understanding of the population dynamics of the resource. Growth models have been reported for wild populations in the northwest Atlantic off North Carolina (McCoy 1972) and in the southern Gulf of Mexico off Tampico, Mexico (Chávez 1973). Several workers have described the growth rate of small brown shrimp in the northern gulf (George 1962; St. Amant et al. 1963, 1966; Loesch 1965; Ringo 1965; Jacob 1971; Wengert 1972; Gaidry and White 1973; Rose et al. 1975; Welker et al. 1975; Knudsen et al. 1977). The growth rate of larger brown shrimp, however, has not been documented for populations in the northern gulf.

Generally, growth equations define the relation between the size and age of individual animals. Three such equations descriptive of growth are the logistic (Pearl and Reed 1920), von Bertalanffy (Bertalanffy 1938), and Gompertz (Gompertz 1825; Silliman 1967) functions. The logistic and von Bertalanffy models are employed to reflect growth in length whereas the Gompertz is usually used to model growth in weight. The von Bertalanffy function may be directly fit to weight data to model growth in weight. If it is so used, it is then correctly referred to as the monomolecular growth model (Medawar 1945; Fabens 1965). This study appraised the abilities of these functions to model brown shrimp growth. Additionally the linear relation between size and age was also considered.

The absolute age of shrimp cannot be determined directly by counting annuli on hard parts. Shrimp molt many times during their life cycle; all hard parts are lost, then reformed with each molt. Therefore, age-size data of individuals cannot be obtained for growth modeling; another technique must be employed. Although the age of brown shrimp at mean size has been discerned from large volume size-frequency samples (Chávez 1973), age was not directly observable and therefore was inferred. Mark-recapture data affords a direct measure of the changes in size per change in time. Forms of the growth functions were employed to utilize mark-recapture data so that error resulting from incorrect age determination was avoided.

METHODS

Brown shrimp spawn in offshore Gulf of Mexico waters (14-100 m deep) throughout the year (Cook and Lindner 1970). Eggs hatch within 14-18 h (Cook and Murphy 1966) and larvae undergo metamorphosis within 12-15 days (Cook and Lindner 1970). Shrimp then migrate into estuaries to undergo their juvenile period. Large juvenile shrimp, usually 75-90 mm total length, migrate to offshore waters as they become sexually mature, thus completing the life cycle. Ap-

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proximately 80% of the recaptured individuals utilized in this analysis were large juveniles when marked. These shrimp were marked and released in estuarine waters before migrating to offshore waters (Table 1). The remaining 20% were large adults marked and released in offshore gulf waters along the Texas coast. These marking experiments were carried out during 1967, 1968, and 1969. A full explanation of the data is given by Clark et al. (1974). These data include total length (i.e., the distance from the anterior end of the rostrum to the posterior end of the telson) when released and when recaptured, the dates of release and recapture, and the sex of each individual. Data entries with the same release and recapture dates do not reflect growth and therefore were not used to estimate growth rates.

In order to analyze growth in weight, release and recapture length were converted to weights according to weight-length relations. These relations were estimated from data collected from the commercial landings at Galveston, Tex., during June, September, and December of 1965 and March of 1966 (Fontaine and Neal 1971). Parameters of the model weight $= a$ (length)^b were estimated for males and for females separately by minimizing the expression $\sum^{n} (W - W_o)^2$ where W is weight defined by the model, W_o is observed weight, and n is the number of observations. The Marquardt algorithm (Marquardt 1963) was employed to find the minimum. Plots of the estimated relations through the scatter of the observations were observed to discern male/female differences and the predictive usefulness of the models.

Since mark-recapture data were employed, growth functions of interest were expressed in terms of the change in age rather than absolute age (see Appendix for derivation of equations). Each recaptured individual was of some unknown age on the date marked and on the date recaptured so that the change in age is equivalent to the time at large. Expressed in these terms the logistic function changes from

$$S_a = S_\infty/(1 + be^{-ka}) \quad (1a)$$

to

$$S_r = S_\infty/(1 + [(e^{-k(\triangle a)})\ (S_\infty - S_m)/S_m]) \quad (1b)$$

by substitution and rearrangement of terms. Likewise, the von Bertalanffy equation

$$S_a = S_\infty(1 - be^{-ka}) \quad (2a)$$

is expressed as

$$S_r = S_\infty - (S_\infty - S_m)e^{-k(\triangle a)}. \quad (2b)$$

The Gompertz function

$$S_a = S_i \exp[G(1 - \exp[-g(a - a_i)])] \quad (3a)$$

becomes

$$S_r = S_i[\exp G][S_m/(S_i \exp G)]^{\exp[-g(\triangle a)]}. \quad (3b)$$

A linear function of size upon age

$$S_a = b + ka \quad (4a)$$

is written

$$S_r = S_m + k(\triangle a). \quad (4b)$$

Definitions of symbols employed above are:

S_a = size at age a,
S_r = size at recapture,
S_m = size when marked,
S_i = size of the smallest animal in the data,
a_i = age of the smallest animal in the data,

TABLE 1.—Brown shrimp mark-recapture experiments, northern Gulf of Mexico.

Release area	Release date	Length range (mm) of released shrimp	Length range (mm) of recovered shrimp	Number recovered
Galveston Estuary	May 1967	66-175	71-124	13
50 mi east of Galveston, Tex.	June 1967	83-147	86-178	301
60 mi southeast of Freeport, Tex	Sept. 1967	122-181	124-196	40
Biloxi Bay, Miss.	May 1968	90-122	90-181	4,218
40 mi southeast of Freeport, Tex	Feb.-Mar. 1969	109-168	136-185	69
Galveston Estuary	June-July 1969	90-128	91-182	257
50 mi southeast of Freeport, Tex.	Nov 1969	145-203	141-213	593

S_∞ = an equation parameter, the asymptotic size,
b = an equation constant related to the size at birth,
$\Delta a = a_r - a_m$ = time at large,
a_r = age of an individual on the date recaptured,
a_m = age on the date marked and released,

and G, g, and k are equation parameters.

Equation parameters S_∞, k, G, and g were estimated by utilizing the Marquardt algorithm to minimize the residual sum of squares:

$$\sum^{n} (S_r' - S_r)^2$$

where n = the number of individuals marked and recaptured,
S_r' = the observed size at recapture, and
S_r = the size at recapture as estimated by the growth equation.

The remaining equation constants, b in Equations (1a) and (2a) and a_i in Equation (3a), are respectively computed:

$$b = (S_\infty / S_b) - 1 \quad (5a)$$

$$b = (S_\infty - S_b)/S \quad (5b)$$

$$a_i = \ln\left[1 - \frac{\ln(S_b/S_i)}{G}\right]g \quad (5c)$$

where S_b is the size at birth and other symbols are as before. The parameter b in Equation (4a) is simply the size at birth.

Studies of the early development of brown shrimp indicate that newly hatched larvae are 0.35 mm total length (Cook and Murphy 1971). Estimates of the equation constant b in the logistic and von Bertalanffy models were based on that length at birth.

Shrimp eggs are 0.26 mm in diameter (Cook and Murphy 1971) and about the density of water (Cook and Lindner 1970) so that the weight at hatching is about 0.000009 g. Brown shrimp undergo metamorphosis 11 to 15 days after hatching (Cook and Lindner 1970) and are 0.0008 g at that time (Wheeler 1969). The weight at birth was calculated as the midpoint between that weight and the egg weight. Calculations of b and a_i in the various models were based on that weight at birth.

RESULTS

Growth in Length

In anticipation that differences in growth between sexes may exist, equations were fit for males and females separately. Estimated equation parameters (Table 2) are quite different between sexes. The fitted models indicate that females are much larger than males of the same age. The estimates of the growth coefficient k do not differ greatly between sexes for both the logistic and the von Bertalanffy models; the 90% probability support plane confidence intervals (Conway et al. 1970) extensively overlap for both models. The estimates of asymptotic length are, however, greatly different and such confidence intervals on those estimates are very disjoint. Pooling all data together to estimate overall growth functions for both sexes combined was therefore judged unrealistic.

The relative abilities of the von Bertalanffy, logistic, and linear models to correctly reflect growth was judged by comparing residual sums of squares (Table 3). The von Bertalanffy function produced the smallest residual and the linear model the largest. The residual sum of squares for the linear model was well over three times that of the von Bertalanffy and logistic models for both males and females. The difference between the two nonlinear models was much smaller; the residual of the logistic was but 8% larger than that of

TABLE 2.—Growth models for brown shrimp. Lengths (L) in millimeters, weights (W) in grams, and ages (a) in months.

Model	Males	Females
Logistic	$L = 162.8/(1 + 464.1429e^{-0.5664a})$	$L = 187.5/(1 + 534.7143e^{-0.6116a})$
von Bertalanffy	$L = 168.7(1 - 0.9979e^{-0.3357a})$	$L = 193.6(1 - 0.9982e^{-0.3363a})$
Linear	$L = 0.35 + 4.2181a$	$L = 0.35 + 7.8209a$
Gompertz	$W = 5.07(\exp[1.9996(1 - \exp[-0.3735(a - 4.6688)])])$	$W = 3.55(\exp[2.8359(2 - \exp[-0.4410(a - 3.2549)])])$
Monomolecular	$W = 43.51(1 - 0.9999e^{-0.1546a})$	$W = 74.32(1 - 0.9999e^{-0.1416a})$
Linear	$W = 0.0004045 + 1.8018a$	$W = 0.0004054 + 3.901a$

the von Bertalanffy in the case of males and 5% larger for females.

TABLE 3.—Residual sums of squares for six brown shrimp growth models.

Model	Males	Females
Length		
Von Bertalanffy	44,161.65	155,797.40
Logistic	47,661.96	163,278.00
Linear	162,661.15	599,677.13
Weight		
Monomolecular	5,548.57	33,930.69
Gompertz	7,027.72	38,751.26
Linear	12,335.42	67,526.07
Number of observations	1,536	3,588

The difference in growth between sexes and the ability of the von Bertalanffy model to fit the observations is visible from plots of the observed lengths about the growth models. Data points were plotted by first calculating the age at release from the fitted model, adding time at large to compute the age at recapture, then plotting that age and the recapture size. The plots (Figure 1A, B) show that sex specific growth does exist and that the differences are of significant magnitude. Further, the von Bertalanffy model does visibly fit the observed data. Although the observed data do

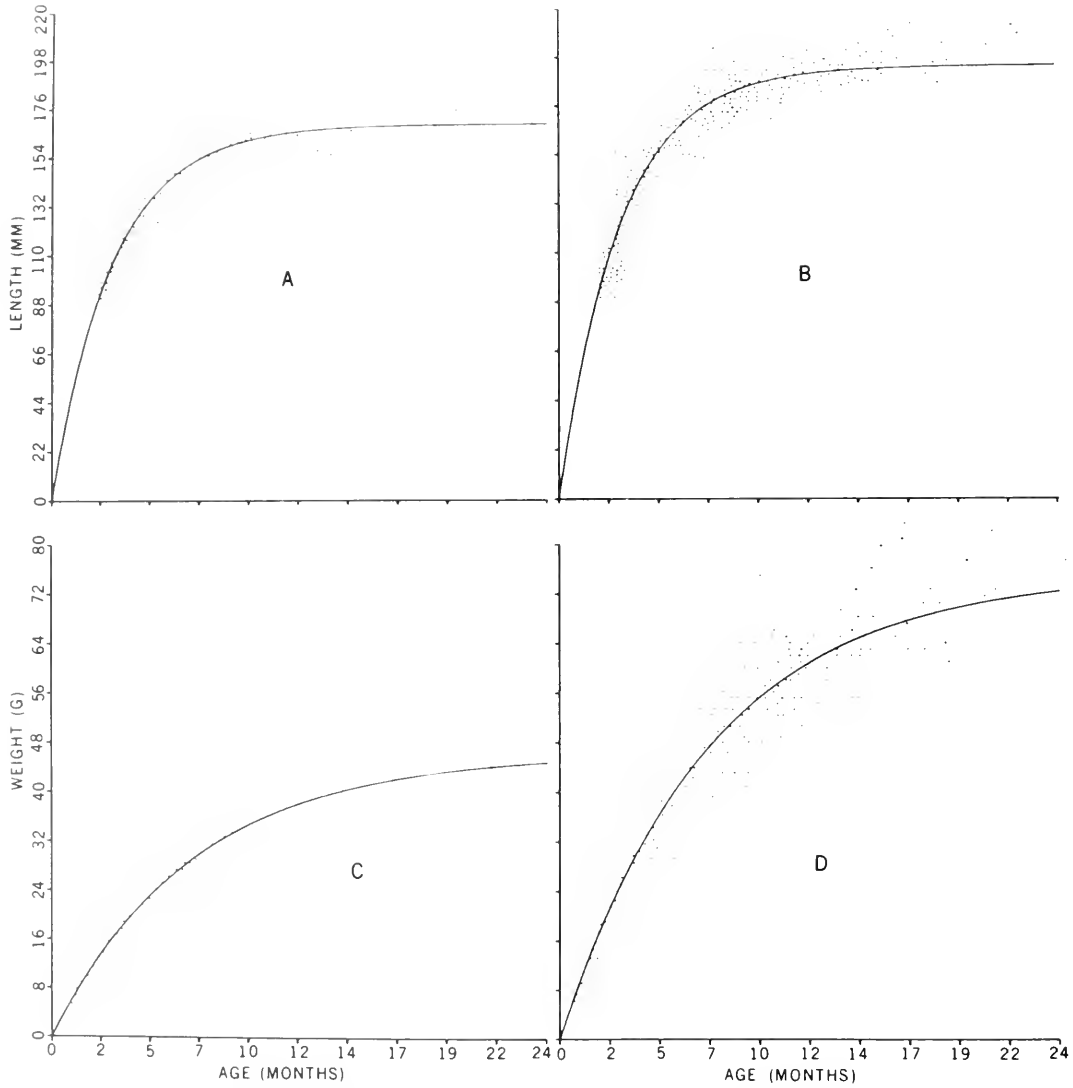

FIGURE 1.—Brown shrimp growth models. A) von Bertalanffy growth model, males; B) von Bertalanffy growth model, females; C) monomolecular model, males; D) monomolecular model, females.

not in general fall close to the modeled line, the scatter is not severe.

Growth in Weight

The Marquardt algorithm (Marquardt 1963) was employed to estimate parameters of weight-length relations used to transform individual release and recapture lengths into weights so that growth in weight could be modeled. Plots of the estimated relations (Figure 2) indicate them to be sex specific. Support plane confidence intervals (Conway et al. 1970) on equation parameters (90% probability) for males did not overlap those for females further indicating that the functions differ between sexes. In addition the data were logged to linearize the relation and covariance analysis techniques applied to test for differences between sexes. The probability that the linearized functions are the same is small ($P_r < 0.001$) further indicating the sex specificity of these relations. Further inspection of the plots shows the scatter of observations to be restricted and that the models effectively fit. These sex specific models were therefore employed to transform the data.

The magnitude of residual sums of squares (Table 3) indicates the monomolecular model is the best predictor of weight at age and the linear model the poorest. The residual term for the linear fit is about twice as large as that for the monomolecular model and about 1.8 times that of the Gompertz for both sexes. The reduction in residuals of the monomolecular model as compared with the Gompertz was much smaller, 25% in the case of males and 14% in the case of females.

As in the case of growth in length, estimated growth parameters indicate that growth in weight is sex dependent. Both the Gompertz and the monomolecular model estimate females to be much larger than males of the same age. Asymptotic weight (monomolecular model) is estimated to be 75 g for females and 46 g for males; support plane confidence intervals (90% probability) on these estimates do not overlap. Estimates of the parameter k in the monomolecular model appear to be about the same for both sexes and in fact the support plane confidence interval for males completely includes that interval for females.

The differences in growth between sexes and the degree of fit of the monomolecular model is shown in Figure 1. Although appreciable scatter is ap-

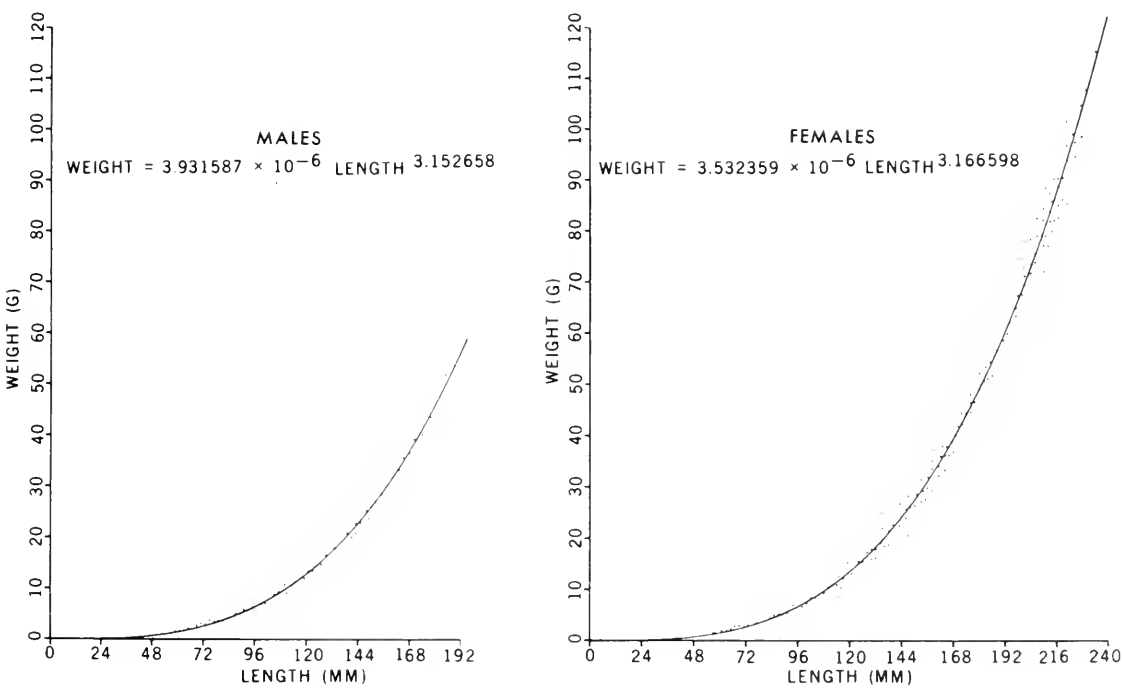

FIGURE 2.—Weight-length relationships for brown shrimp.

parent, systematic departure of the observed points from the model is not evident so that the model does reflect the data.

CONCLUSIONS

The relative abilities of prediction of the different models can be judged by comparison of their residual sum of squares. The comparison strongly suggests that the linear function was by far the poorest model of brown shrimp growth both in length and weight. Although the size-age relation does appear linear for small young individuals, the rate of increase in size decreases with age, a phenomenon documented for many organisms both terrestrial and aquatic. A nonlinear function is therefore required to model brown shrimp growth throughout their entire life span.

The residual sum of squares for the von Bertalanffy equation was smaller than the logistic equation when modeling weight; however, these differences were not large. It is therefore not completely evident that the von Bertalanffy equation is vastly superior to the logistic and Gompertz in the modeling of brown shrimp growth. The von Bertalanffy equation did, however, constantly fit these data best for both sexes in the modeling of both length and weight. This study does therefore show the von Bertalanffy model to be slightly superior to the logistic and the monomolecular model superior to the Gompertz for both sexes.

The difference in the size-age function between sexes was found to be large. This phenomenon was previously reported for brown shrimp in the southern Gulf of Mexico (Chávez 1973) and northwest Atlantic (McCoy 1972) and for many other marine organisms. This study indicates that male brown shrimp apparently grow to approximately only three-fifths the weight and five-sixths the length of females; however, the coefficients of growth, as indexed by k in the monomolecular and von Bertalanffy models, are roughly equivalent. It is interesting to note that the rate of increase in size tends to fall off at an earlier age for males than for females (see Figure 1). Since, in general, a decrease in that rate roughly conforms to the age of maturity and sexual activity, it is not unreasonable to assume that males mature at a younger age than do females.

Comparison of growth functions derived herein with those generated by other workers indicate that brown shrimp growth in the northern Gulf of Mexico is very different than that in the southern gulf and in U.S. Atlantic coastal waters. Growth functions derived from populations off Mexico (Chávez 1973) demonstrated a faster and prolonged growth compared with growth observed in this study. That trend was consistent for both males and females. Studies off North Carolina (McCoy 1972) showed growth in Atlantic waters to be very rapid although a smaller asymptotic size was realized. As before, that trend was the same for both sexes. The kinds of data used and the methods employed to fit the growth models differed in all three studies; therefore, some disagreement in results may be expected. The magnitude of the differences observed, however, indicated truly different rates of growth may well exist in the three geographical locations. The growth of wild populations of white shrimp, *Penaeus setiferus*, a similar species, is correlated with water temperature (Gaidry and White 1973) in the shallow estuarine and nearshore areas they inhabit throughout their entire life span. Since the temperature of seasonally homothermic deep offshore waters where brown shrimp spend their adult life may be assumed to increase with decreasing latitude, the differences in growth between northwest Atlantic, northern gulf, and southern gulf brown shrimp populations are likely positively correlated with gross water temperature.

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APPENDIX

The linear, logistic, and Gompertz functions were expressed in terms of size at release age, size at recapture age, and change in age (time at large) following the rationale presented by Fabens (1965) for the von Bertalanffy function (as follows).

Each individual was of some unknown age (a_m) upon the date marked (t_m) and released. Upon the recapture date (t_r) the individual was of an unknown older age (a_r) so that the difference between the release and recapture date (Δt) is equivalent to the increase in age (Δa) of that individual:

$$\triangle a = \triangle t = t_r - t_m = a_r - a_m . \tag{A1}$$

That equality can be substituted into the von Bertalanffy function when expressed in terms of the size at recapture (S_r) and the age at recapture. Therefore the von Bertalanffy equation

$$S_r = S_\infty [1 - b \exp(-ka_r)] \tag{A2}$$

becomes $S_r = S_\infty (1 - b \exp(-ka_m) \exp[-k(\triangle a)])$. (A3)

The equation, when expressed in terms of the size when marked (S_m) with rearrangement, is:

$$b \exp(-ka_m) = 1 - (S_m / S_\infty). \tag{A4}$$

That expression is substituted into Equation (A3) to yield the required function:

$$S_r = S_\infty - (S_\infty - S_m) e^{-k(\triangle a)}. \tag{A5}$$

That form can then be employed to estimate the equation parameters k and S from mark-recapture data. The final parameter (b) can be calculated directly by first rearranging terms of the original function:

$$S_a = S_\infty (1 - be^{-ka}) \tag{A6}$$

so that $b = [1 - (S_a / S_\infty)] / e^{-ka}$ (A7)

where S_a is the size at age a. If the size at birth, i.e., at age 0, is known, then:

$$b = 1 - (S_b / S_\infty) \tag{A8}$$

where S_∞ is estimated from Equation (A5) and the size at birth (S_b) is derived from life history studies.

That same rationale was applied to the logistic function. The size of a recaptured individual is expressed:

$$S_r = S_\infty / [1 + b \exp(-ka_r)] . \tag{A9}$$

Since $a_r = a + a_m$ substitution gives:

$$S_r = S_\infty / (1 + b \exp[-k(\triangle a)] b \exp(-ka_m)] . \tag{A10}$$

Expressing the logistic equation in terms of the size marked and rearrangement of terms gives:

$$b \exp(-ka_m) + [(S_\infty - S_m) / S_m] . \tag{A11}$$

Substitution yields:

$$S_r = S_\infty / [1 + ((e^{-k(\triangle a)}) (S_\infty - S_m) / S_m)] . \quad \text{(A12)}$$

Since S_r, S_m, and Δa were all directly observable from mark-recapture data, the logistic equation parameters S_∞ and k may be estimated from the data set. The remaining equation constant was calculated by rearrangement of terms:

$$b = ((S_\infty / S_a) - 1) / e^{-k(a)} . \quad \text{(A13)}$$

From life history studies the size at birth, S_b, was determined. Since at birth age is zero ($a = 0$) the expression can be written:

$$b = (S_\infty / S_b) - 1. \quad \text{(A14)}$$

The Gompertz function was likewise expressed in terms of the mark-recapture data. From Equation (3a), the size at the time of marking is:

$$S_r = S_i \exp[G(1 - \exp[-g(a_r - a_i)])] \quad \text{(A15)}$$

and by substitution becomes

$$S_r = S_i \exp[G - G (\exp[-g(a_m - a_i)]) (\exp[-g(\triangle a)])] . \quad \text{(A16)}$$

Writing in terms of the size at recapture and rearrangement of terms gives:

$$\exp(-G \exp[-g(a_m - a_i)]) = S_m / (S_i \exp G). \quad \text{(A17)}$$

Substitution yields the expression required to estimate the constants G and g from the mark-recapture data:

$$S_r = [S_i \exp(G)] [S_m / (S_i \exp(G))]^{\exp[-g(\triangle a)]} \quad \text{(A18)}$$

where S_i was the smallest size observed in those data. The remaining equation constant, a_i, was then calculated by writing Equation (3a) in terms of the size at birth:

$$S_b = S_i \exp[G(1 - \exp[-g(a - a_i)])] . \quad \text{(A19)}$$

Since at birth age is zero ($a = 0$) the expression can be written as:

$$a_i = \ln(1 - [\ln(S_b / S_i) / G] / g) \quad \text{(A20)}$$

where S_b, the size at birth, was determined from natural history studies. The linear function:

$$S_a = b + ka \quad \text{(A21)}$$

requires a much simpler derivation. Expressed in terms of the size at recapture:

$$S_r = b + ka_r . \quad \text{(A22)}$$

Substitution gives:

$$S_r = b + k (\triangle a + a_m) . \quad \text{(A23)}$$

The function expressed in terms of the size at release

$$S_m = b + ka_m \tag{A24}$$

can be rearranged to

$$a_m = (S_m - b)/k \tag{A25}$$

which can be substituted into Equation (A23) to give

$$S_r = k \cdot a + S_m . \tag{A26}$$

The remaining parameter b is simply the ordinate intercept or the size at birth.

THERMAL BEHAVIORAL RESPONSES OF SELECTED CALIFORNIA LITTORAL FISHES

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ABSTRACT

Two horizontal temperature gradients were used to measure behavioral responses to temperature of various life stages of 16 species of temperate marine fishes from southern California, and we offer guidelines for standardization of collection, acclimation, preexperimental holding, and testing conditions. We classified behavioral responses to thermal gradients using eight experimental parameters: initial, mean, modal, and final selected temperatures; range of selected temperatures; skewness; kurtosis; and the degree of dispersion between individuals. We found four behavioral responses to changes in temperatures with time: 1) immediate—no general shift in selected temperature with time, 2) fast—a shift in selected temperature over the first 2 h of the experiment only, 3) slow—a shift in selected temperature over more than 2 h in the experiments, and 4) positioned—a wide range of selected temperatures and a tendency to remain in a given position in the gradient until conditions become extreme. Effects of preexperimental acclimation temperatures on thermal selection did not last longer than 4h. One day of food deprivation resulted in lower selected temperatures and changed the precision of selection and aggregating tendencies, although the direction of the change varied between species.

Over the last several decades, the behavior of fishes with respect to thermal gradients has been investigated by many workers (see review by Coutant 1977). Most studies in the literature, however, have dealt with freshwater or estuarine species that occur in large part in eastern North America. Little work has been carried out on temperate marine species, which, except for intertidal inhabitants, generally experience smaller natural diurnal and seasonal temperature fluctuations.

Our two horizontal gradients and experimental procedures were built on many of what appear to be the best attributes of previous studies. Variation in reported experimental techniques makes comparisons between studies difficult. We suggest guidelines for method standardization in this paper.

Horizontal gradients were chosen because they allowed experimentation with groups, permitted demersal fish to be in contact with a bottom and pelagic species to swim freely. This type of gradient also allowed us to combine some of the best attributes of spatial gradients (e.g., Norris 1963) and temporal ones (e.g., Beitinger 1976). Further, our study, in conjunction with a field survey, was designed to assess the effects of temperature on the distribution, behavior, and physiology of fishes found in King Harbor, Redondo Beach, Calif. This harbor, which receives the thermal discharge from an electricity generating station, as well as cold, upwelled water from the adjacent Redondo Submarine Canyon, contains a highly diversified thermal environment (Stephens 1972), including many horizontal gradients.

Our intent is to introduce a comprehensive approach to thermal response testing, including equipment design, preexperimental and experimental methodology and protocol, and to show representative examples of behavioral responses. We have examined to date the behavior of various life stages from larvae to adults of 16 fish species from 10 families. Comparative studies of laboratory and field results are in preparation.

EXPERIMENTAL CRITERIA

A wide range of experimental methodology exists in the literature (see review by McCauley 1977). McCauley and Tait (1970) stated, "Comparison of preference temperatures in the literature is

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questionable, because of differences in experimental techniques." Preexperimental feeding regimes differ significantly between studies. Cherry et al. (1975) discontinued feeding 2.5 to 3 days before testing; in contrast, Reynolds and Thomson (1974) fed fish approximately 2 h prior to experimentation. The time that the fish were allowed to adjust to the experimental chamber before initiation of data collection was also variable. Tat'yankin (1972) used a habituation period of only 0.5 h, while McCauley and Read (1973) used a period of 2 days. Length of time between observations was not consistent between studies. Ferguson (1958) observed fish hourly, but Norris (1963) recorded fish position every 6 s. Although most investigations used organisms once, Javaid and Anderson (1967) reused fish between successive experiments. Some of the differences in experimental techniques may have been due to species-specific problems; however, in many studies the primary concern was simply to provide a thermal gradient, to place test organisms in it, and to measure their response. Often, little attention was paid to factors relevant to the well-being of the fish (e.g., shock from capture and handling, nutritive condition) and to simulating natural intensities and quality of light.

General procedural recommendations have been made by Richards et al. (1977). Our methods build on techniques from past studies, including their best attributes. Some of the differences in experimental techniques are subtle, but important, especially since this investigation concerns marine species, on which little work has been done. The methods, procedures, and physical conditions of collection, handling, and experimentation in this study were chosen to minimize trauma to test organisms. The following methods and rationales that we employed are provided as suggestions toward standardization:

1) Our preferred methods of obtaining test organisms involved collecting by means of lift nets or traps or to rear them from eggs. These minimized damage to the fishes.
2) Fish feeding was established in the laboratory. We tested only fish that fed, as this indicated that they were most likely not in shock from collection.
3) We brought fish to desired acclimation temperatures, from that at which they were collected, at a rate of 1°C/day. The test specimens were held for at least 2 wk prior to testing. The length of the holding period was particularly important to assure acclimation to cold temperatures (Brett 1970).
4) We did not use anaesthetics in collections or preexperimental handling; Goddard et al. (1974) have shown that MS-222[4] can influence thermal behavioral responses for several weeks after treatment.
5) We fed the fish ad libitum just prior to their placement in the gradient. This standardized the feeding history, which has been shown to alter temperature selection (Ivlev and Leizerovich 1960; Javaid and Anderson 1967).
6) We placed the fish in the experimental chamber, adjusted to their acclimation temperature, on the evening preceding testing. This allowed adjustment to the new surroundings prior to experimentation. No fish were reused.
7) Testing fish in groups allowed us to assess the effects of temperature on populations, but we could only use this methodology to study gregarious species that did not display agonistic behavior.
8) We established the temperature gradient about the fish. Introduction of test organisms to an established gradient, even at the location of their acclimation temperature, can result in the fish darting to another part of the tank and experiencing a temperature shock.
9) We shifted isotherms during an experiment, and the hot and cold ends were reversed between experiments. This allowed us to attempt to partition any tendencies of the fish to select a particular compartment independent of temperature.
10) We shielded the test chamber from external light and observed the fish from above downward-directed experimental lights to insure that the fish would not respond to presence of the experimenter.
11) We used low levels of lighting, during the experiment, based on minimum intensities for schooling and larval feeding (Blaxter 1970). These levels of illumination did not appear to disturb the fish as was sometimes the case with brighter light. Additionally, Sullivan and Fisher (1954) reported increased precision of temperature selection at low light

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or by Occidental College.

intensities. We employed natural day lengths during preexperimental holding as well as during testing.

DESIGN OF GRADIENTS

We built two horizontal gradients: one for juveniles and adults and another, smaller one, for larvae and placed them in a sound-insulated and lightproof room. A differential of at least 10°C between the hot and cold ends of the gradient was established prior to collection of data used for behavioral analyses. We adjusted the size and position of the temperature gradient to keep the experimental fishes from the extreme end compartments; differentials of up to 25°C were employed for species with wide preferred temperature ranges.

Gradient for Juvenile and Adult Fishes

We divided this gradient (360 cm long × 60 cm wide × 60 cm deep, Figure 1) along its longitudinal axis to produce two experimental chambers (15 and 44 cm wide). The size of the test organisms determined which side of the gradient was used. Heating and cooling were controlled, primarily at the ends of the gradient. A rheostat connected to an immersion heater allowed us to minimize the frequency of the heater turning on and off, reducing fluctuations in heat production. A stainless steel (type 316) coil heat exchanger with cold freshwater coolant (1°C) chilled the seawater in the gradient. Two additional heat exchangers constructed of polyvinyl chloride and run along the bottom from the ends to the center of the experimental chamber served to produce a more even temperature gradient.

Formation of thermal currents can limit the temperature range and controllability of a horizontal gradient. Twelve pairs of surface and bottom baffles impeded thermal currents and divided the gradient into 11 experimental compartments.

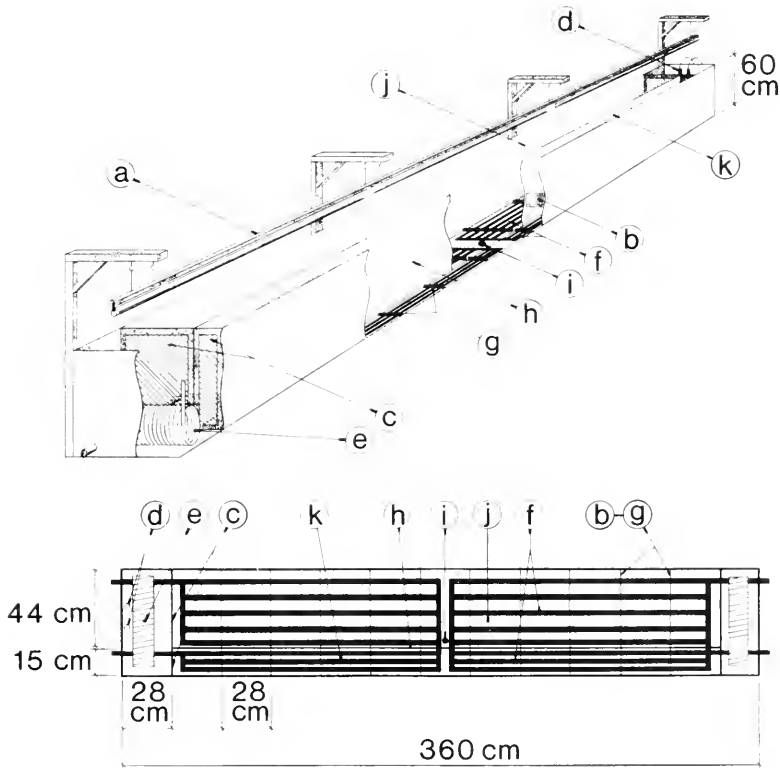

FIGURE 1.—Large experimental chamber for temperature selection measurement in fishes: a) daylight-simulating fluorescent light, b) surface baffle, c) screens separating experimental chambers (j and k) from the end heating and cooling compartments, d) 500-W heaters, e) stainless steel heat exchangers, f) polyvinyl chloride heat exchanger, g) bottom baffles, h) wall separating the large and small experimental chambers, i) drain, j) large experimental chamber, k) small experimental chamber.

The baffles could be lowered or raised with the water level so that they entered the water to a depth of 2 cm. Gentle aeration, from the bottom of each compartment, further eliminated vertical stratification. This also aided removal of any supersaturated gases that Gift (1977) reported to be potential problems in thermal gradients. A nylon screen prevented the test organisms from entering the area where the heating and cooling took place and also provided a flat surface over the bottom baffles. We subdivided the experimental gradient that consisted of 11 compartments each containing a centrally located thermistor probe into 21 visual units that were not visible to the test organisms, by forming an additional compartment centered midway between two thermistors. The mean temperature of two adjacent probes was used for these additional compartments. Daylight-simulating fluorescent fixtures (Duro-test Vitalities), with the use of diffusers, provided a light intensity of 60-70 fc at the water surface.

Gradient for Larval Fishes

The temperature gradient for larval fishes (Figure 2) operated on a counter-current principle. Alternation of hot and cold water entering the experimental chamber between replicate runs eliminated any potential rheotactic interference. The inner experimental trough (1.75 m long × 5 cm diameter; 0.6 mm wall thickness) contained two nylon screens 1.5 m apart that defined the experimental chamber. Seawater velocities of 0.1 to 0.9 mm/s were selected based on known larval swimming speeds (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972), because velocities in this range would not present the larvae with any significant difficulty in maintaining a chosen position. Wilson (1974) successfully employed velocities of up to 10.8 mm/s with pelagic marine fish larvae in studying behavioral responses of pollutants.

Hunter and Thomas (1974) showed that larval anchovies aggregated at patches of food (*Gymnodinium splendens*). All entering seawater was filtered to 5 μm to rule out possible position selection by larvae based on presence of prey organisms. Eleven evenly spaced thermistor probes coupled to a telethermometer were used to monitor temperature. We subdivided the experimental chamber into 21 visual compartments and enclosed the trough in a lightproof box. A daylight-simulating fluorescent lamp, with the use of a diffuser, produced 10-15 fc at the water surface.

DEFINITIONS

The term "preferred temperature" has been used in various contexts in the literature (e.g., Brett 1952; Javaid and Anderson 1967; McCauley and Tait 1970; Tat'yankin 1972; McCauley and Read 1973). Much of the variation in the use of this

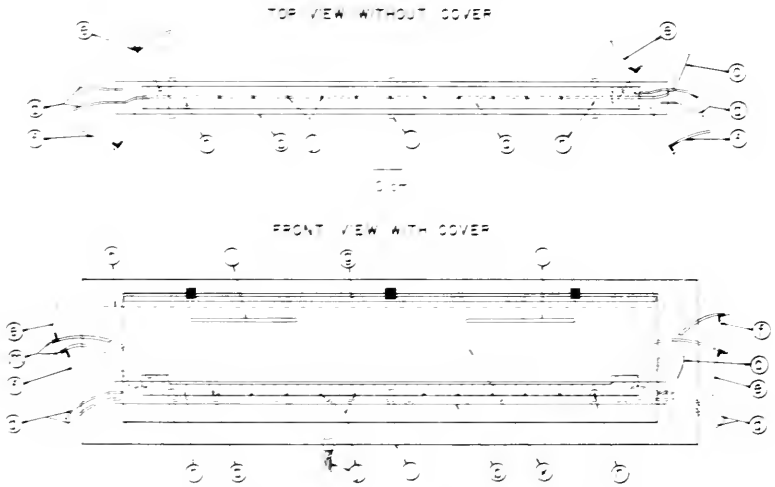

FIGURE 2.—Small experimental chamber for temperature selection measurements in larval fishes: a) experimental chamber, b) water jacket, c) air line, d) drains, e) seawater input line, f) freshwater input line, g) daylight-simulating fluorescent light, h) light diffuser, i) viewing slits, j) thermistor probes, k) door on lightproof cabinet, l) supports for water jacket, m) water flow control valves, n) nylon screen on ends of experimental chamber.

term can be attributed to different species exhibiting various behavioral patterns in a gradient tank, just as they do in their natural habitats. This makes it impossible to use only one procedure to determine the preferred range for all species under all conditions. We determined the preferred range and final perferendum by evaluating, on a case-by-case basis, the behavioral responses of a species subjected to known conditions such as acclimation temperature, feeding patterns, and captivity environment.

Experiments with larvae lasted 5-6 h, but juveniles and adults were tested for approximately 7-8 h. An "experiment," in this study, consisted of a set of individual runs, with each "run" being the observation of the position and water temperature selected by each fish in the gradient at a fixed point in time. We employed constant time intervals between runs for any experiment: 5 min for larvae and 15 min for juveniles and adults. Run selected temperatures were the primary data source, and we calculated their mean, mode, and variance prior to combining them with data from other runs to determine the preferred temperature.

DATA ANALYSES

Reynolds (1977) reported that skewness of temperature preference frequency distributions required a complete description of the distribution. We examined the following parameters to delineate thermal behavioral responses, the initial, mean, modal, and final selected temperatures, standard deviation about the mean, coefficients of skewness and kurtosis, and coefficient of dispersion. The first four parameters defined the preferred temperature range. The standard deviation about the mean selected temperature quantified movement through a range of temperatures and gave a measure of the degree of eury- or stenothermal preference. We used coefficients of skewness and kurtosis (Sokal and Rohlf 1969) in testing for normality and then to help define the shape of the temperature-specific fish frequency of occurrence distribution and to refine interpretation of behavioral types. The coefficient of dispersion quantified the tendency of a species to aggregate or school and gave the percentage of use of the experimental chamber by all fish within one standard deviation of the run selected temperature.

The frequency of occurrence of all experimental temperatures was not uniform due to the shifting of the gradient as well as having a variable number of degree intervals per run and generally fewer than the 21 compartments. This caused a bias in the number of fish observed at a particular temperature when summed over an entire experiment. To compensate for this, prior to calculation of the mean and modal selected temperatures, we adjusted the data by using the number of fish per total occurrence of a particular temperature in all experimental compartments rather than the actual number of fish at each temperature.

We defined the "initial selected temperature" as that chosen by the fish immediately following establishment of a gradient of 10°C. The modal selected temperature was determined from the percent occurrence frequency distribution derived from adjusted data. After an initial time of apparent searching and testing of water conditions the experimental animals selected a temperature or range of temperatures at which they remained for the duration of the experiment. We called this the final selected temperature (or temperature range) and determined it from plots of selected temperature against time. The mean selected temperature was derived by methods presented in Appendix Table 1.

EXPERIMENTAL TECHNIQUES AND BEHAVIORAL RESPONSES

Our experimental techniques and data interpretation methods are useful for a wide variety of behavioral types. There are three salient features of this methodology: 1) the shifting and reversal of the temperature gradient to partition position preference from thermal preference, 2) the extended duration of the experimental period and its relationship to the thermal history of the test organisms, and 3) the criteria for behavior evaluation.

Shifting and Reversal of Temperature Gradient

Hasler (1956) pointed out that fishes in experimental gradients can position themselves according to small deformities in the tank structure. We employed two methods to eliminate this factor: shifting the position of a given isotherm in the gradient during an experiment, and reversing the hot and cold ends between replicate experiments.

Shifting the isotherm position during an experiment required the fish to thermoregulate actively, similar to those studied by Beitinger (1976, 1977) in his temporal gradient. This technique demonstrated that the fish could follow an isotherm and did not necessarily arbitrarily select a position in the experimental tank. The precision with which a group of fish followed an isotherm varied between species and was related to the size of their preferred temperature range. Juvenile surfperch, *Damalichthys vacca*, for example, which preferred a narrow range of temperatures, closely followed an isotherm (approximately 11°C) (Figure 3). In contrast, juvenile topsmelt, *Atherinops affinis*, after initially selecting approximately 22°C, remained within that compartment, and shifting the gradient did not cause them to move until the temperature reached 26°-27°C. This isotherm was then tracked (Figure 3). Topsmelt are physiologically eurythermal, at least during embryonic stages, and the upper limit for hatching of topsmelt eggs is 26.8°C (Hubbs 1965). Brett (1956) suggested that the preferred temperature may not be a strong enough directing force to move

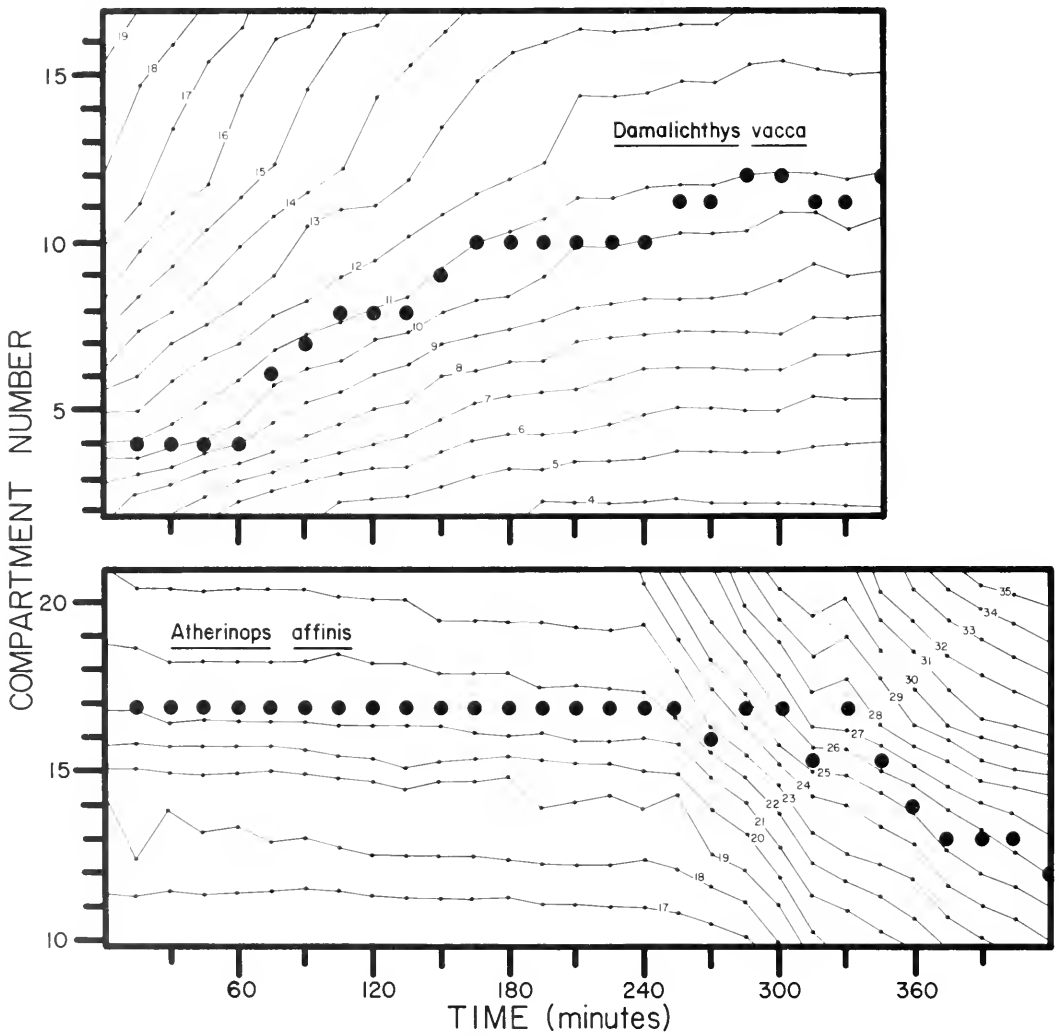

FIGURE 3.—Changes in fish and isotherm position in the experimental gradient. Juvenile *Damalichthys vacca* followed the 10°-11°C isotherms. Juvenile *Atherinops affinis* remained in the position they initially selected and moved very little until the temperature reached 26°-27°C. They then followed the temperature range of 25°-27°C. The small numbers indicate isotherms. Large dots indicate the mean temperature selected by nine individuals.

fish with wide temperature tolerances from a particular area until stress-inducing conditions are reached.

Temperatures Selected and Their Relationship to Thermal History

We classified the behavioral responses of the 16 species surveyed into four groups based on changes in temperatures selected throughout an experiment: 1) immediate response—no general shift in selected temperature over time, 2) fast response—a shift in selected temperature not exceeding the first 2 h of the run, 3) slow response—a shift in selected temperature over more than 2 h, and 4) positioned response—a broad preference and a tendency to remain in a given position in the gradient until conditions become extreme.

Shiner surfperch, *Cymatogaster aggregata*; pile surfperch, *Damalichthys vacca*; black surfperch, *Embiotoca jacksoni*; and black croaker, *Cheilotrema saturnum*, showed the first behavioral pattern of immediate response (Figure 4). These fishes moved most quickly from their preexperimental acclimation temperature to their final selected one or range, remaining there for the duration of the experiment. These fishes generally had the narrowest selected temperature ranges and also aggregated tightly (Table 1).

Fishes with a fast response to the temperature gradients included speckled sanddab, *Citharichthys stigmaeus*; señorita, *Oxyjulis californica*; spotted sand bass, *Paralabrax maculatofasciatus*; and sculpin *Scorpaena guttata* (Figure 5). These species required up to 2 h to home in on a selected temperature and also generally did not aggregate as tightly, nor select as narrow a temperature range as those fishes that showed an immediate response to the temperature gradients (Table 1).

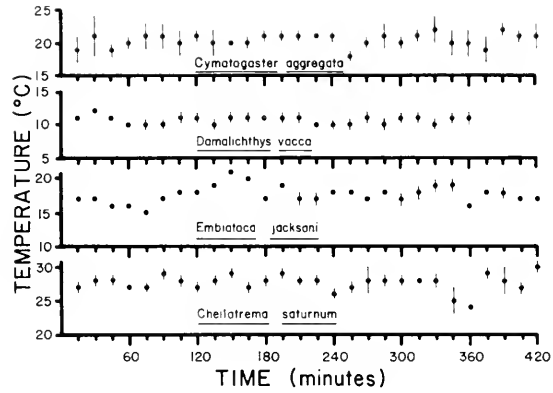

FIGURE 4.—Immediate response to temperature change. These species showed no trend in selected temperature with time. Dots are mean selected temperatures and vertical lines are 1 SD about the means. Results are for duration of one experiment.

All larvae studied responded slowly under experimental conditions. These included topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*; rockpool blenny, *Hypsoblennius gilberti*; and painted greenling, *Oxylebius pictus* (Figure 6). Four older fishes also showed this behavior: kelp bass, *Paralabrax clathratus*; olive rockfish, *Sebastes serranoides*; California halibut, *Para-*

TABLE 1.—Behavioral responses of larval and juvenile fishes in temperature selection experiments. Initial and final selected temperatures are taken from Figures 4-6 and other similar experimental data.

Species	Experimental date	No. of fish	Mean Standard length (mm)	Mean Acclimation temperature (°C)	Selected temperatures (°C)					Coefficient of skewness (g_1)	Coefficient of kurtosis (g_2)	Coefficient of dispersion (%)
					Mean	SD	Mode	Initial	Final			
Immediate response:												
Cymatogaster aggregata	12 June 1975	8	109	18.2	19.9	2.1	19	18.7	21	0.22	2.87	24
Damalichthys vacca	6 June 1975	9	69	18.1	10.5	0.9	10	11.4	11	0.41	4.61*	12
Embiotoca jacksoni	13 Dec. 1974	7	118	16.7	18.0	1.6	18	17.0	18	−0.61*	4.54*	5
Cheilotrema saturnum	6 Oct. 1975	7	42	17.0	27.6	2.0	28	26.6	28	−0.79*	3.12	13
Fast response:												
Citharichthys stigmaeus	22 Dec. 1975	9	90	18.9	10.1	2.6	10	14.8	10	0.43	3.44	33
Oxyjulis californica	28 May 1975	6	120	17.2	15.5	1.9	15	15.0	16	−0.69*	5.44*	11
Paralabrax maculatofasciatus	31 July 1975	6	179	20.6	24.2	3.1	27	21.2	25	−0.83*	2.70	29
Scorpaena guttata	24 Nov. 1975	6	64	17.6	17.5	4.2	19	17.2	17	−0.63*	4.01*	35
Slow response:												
Atherinops affinis (larvae)	31 July 1975	6	14.5	21.5	25.2	2.9	27	21.9	27	−1.07*	4.12*	26
Leuresthes tenuis (larvae)	9 May 1975	6	8.1	16.5	25.2	4.1	26	19.2	27	−0.12	2.86	37
Hypsoblennius gilberti (larvae)	2 July 1975	6	4.4	19.4	22.2	3.1	19	19.7	26	0.39	2.10	36
Oxylebius pictus (larvae)	14 May 1975	6	3.4	16.0	26.8	3.3	27	19.7	29	0.82*	3.24	30
Paralabrax clathratus	28 July 1975	6	196	21.0	13.5	3.1	14	17.2	15	0.13	2.70	47
Sebastes serranoides	11 Dec. 1974	8	82	17.0	18.0	1.3	18	16.2	17	−0.21	2.44	4
Paralichthys californicus	15 Oct. 1975	5	94	20.5	20.8	6.6	24	20.3	22	−0.10	1.91*	65
Pleuronichthys coenosus	3 Dec. 1975	4	134	10.0	7.5	2.5	7	10.8	7	1.40*	5.15*	23
Positioned response:												
Atherinops affinis	14 Jan. 1976	9	60	15.0	23.3	3.2	26	16.4	26	−0.71*	2.41	4

*$P < 0.05$.

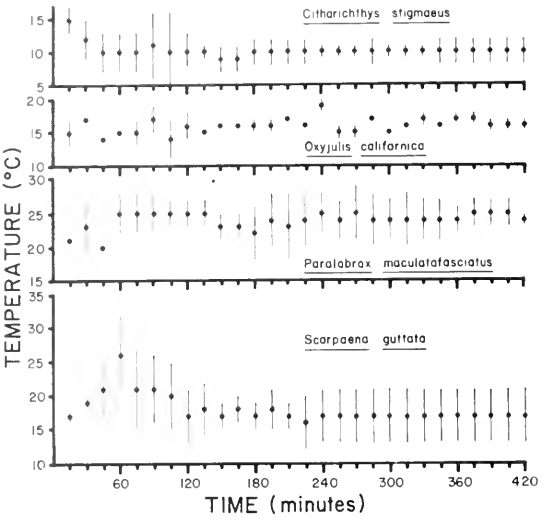

FIGURE 5.—Fast response to temperature change. These species changed their selected temperatures over the first 2 h of the experiment only. Symbols as in Figure 4.

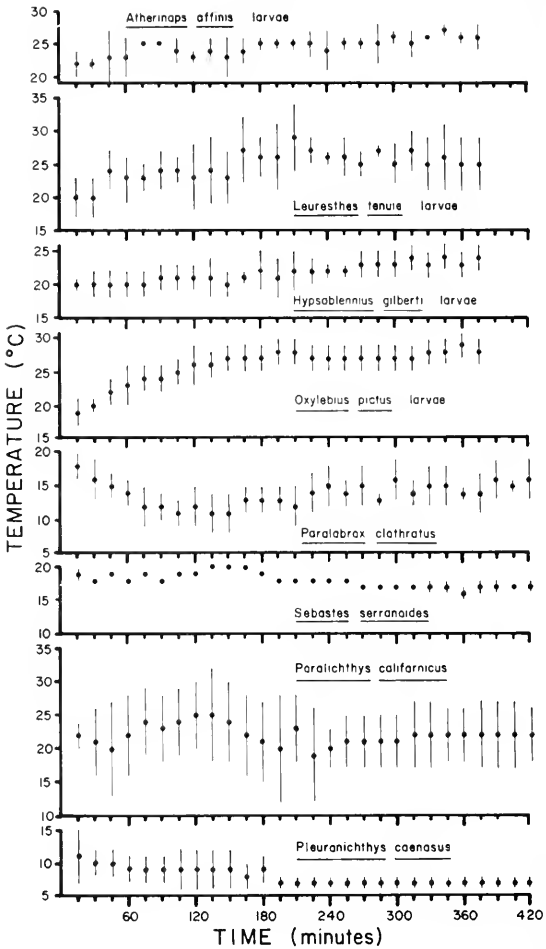

FIGURE 6.—Slow response to temperature change. These fishes changed their selected temperature over more than 2 h in the experiments. Symbols as in Figure 4.

lichthys californicus; and C-O turbot, *Pleuronichthys coenosus* (Figure 6). Members of this group required more time to stabilize their response than either the immediate or fast responders. The temperature selection acuity and aggregating tendencies of these fishes were similar to those of the second group (Table 1).

Juvenile topsmelt were the only species observed that showed a positioned response (Figure 3). Ehrlich et al. (in press) discussed this behavior in detail. California grunion are closely related to topsmelt, and we have observed them together, in the field, throughout larval, juvenile, and adult stages. Possibly juvenile California grunion, which were not tested, may show similar responses.

Preexperimental acclimation temperatures showed the greatest effect on thermal selection of the fishes during the first 2 h after establishment of the gradient (Figures 4-6). The short duration of the influence of thermal history on temperature selection has also been reported by Doudoroff (1938). Clearly, trying to determine a preferred temperature for these species or others with similar responses, during the transition period, would make data interpretation difficult. After this initial period, the fishes, in most cases, chose a final selected temperature, which may be synonymous with what Fry (1947) termed the "final preferendum." He defined this as the temperature range that the fish would eventually select, independent of their acclimation temperatures. Topsmelt, however, did not show this pattern, for their initial selected temperature gave a good indication of their preference and was independent of their acclimation temperature (Ehrlich et al. in press). Doudoroff (1938) also found that fishes did not select the temperatures to which they had been acclimated but rather selected a common range of temperatures, which he suggested must have some physiological significance.

Figures 4-6 show that the final preferendum was reached within several hours after the establishment of the gradient. This is considerably less time than the approximately 24 h reported by

Reynolds and Thomson (1974) or Reynolds and Casterlin (1976). The differential, however, between the acclimation and the final preferendum must be considered. Reynolds and Thomson (1974) tested fish acclimated 17°C below their final preferendum. Crawshaw (1975) used a range of acclimation temperatures from 22°C below to 3°C above the final preferendum and found that as the temperature differential diminished so did the time required to reach the final preferendum. Differentials of 5°C required as little as 1 h and 3°C only 0.5 h (Crawshaw 1975). Based on the temperature differences between acclimation and the final preferendum (Table 1), Reynolds' and our results generally fit the pattern described by Crawshaw.

Behavioral Criteria

Most studies pertaining to behavioral responses of fishes to thermal gradients have been concerned with only one factor: the final preferendum. Additional information, however, can be obtained from examination of parameters associated with the frequency distribution of the selected temperatures, particularly: skewness (degree of distortion from symmetry) and kurtosis (peakedness). Ivlev and Leizerovich (1960) compared the percent of the area under the curve of number of fish per temperature against the mode of the distribution as well as the percentage of the curve on either side of the mode. Reynolds and Casterlin (1976) and Reynolds (1977) discussed the relationship between various measures of central tendency (mean, mode, and median) and skewness. They also improved descriptions of thermal behavioral responses by quantifying skewness but did not state the statistical significance of the skewness. Sokal and Rohlf (1969) stated that the absolute value of coefficients of skewness and kurtosis have little meaning and that they must be tested for statistical significance. We identified distinct behavioral types with respect to the frequency distribution of selected temperatures by examining skewness and kurtosis. The responses were, in part, species-specific but also varied with ontogenetic stage and nutritive condition. Reynolds and Casterlin (1976) showed that skewness also varied diurnally. Kurtosis can be used to assess whether the test organisms display eury- or stenothermal behavioral responses (Ivlev and Leizerovich 1960). A narrow preferred temperature range will be overly peaked about the mean (leptokurtic), and a broad range of preferred temperatures will show no obvious mode or only a very slight one (platykurtic). The coefficient of kurtosis is particularly useful for quantifying the strength of the temperature selection response in populations that are not normally distributed where normal parameters such as mean and standard deviations are inappropriate.

A normal bell-shaped frequency distribution is representative of species with a wide preferred temperature range that is not close to lethal or avoided temperatures. Speckled sanddabs displayed this type of behavior (Table 1, Figure 7). Newly hatched larvae, however, of species such as California grunion showed little temperature selection acuity and preferred an even wider range of temperatures ($g_1 = 0.003$, $0.5<P$), ($g_2 = 1.75$, $0.01<P<0.025$). This behavior resulted in a platykurtic distribution (Figure 7). Reynolds and Thomson (1974) reported that newly hatched Gulf grunion, *Leuresthes sardina*, also showed no acute temperature preference. The precision with which larval California grunion selected temperatures increased by 2 days posthatching, producing a

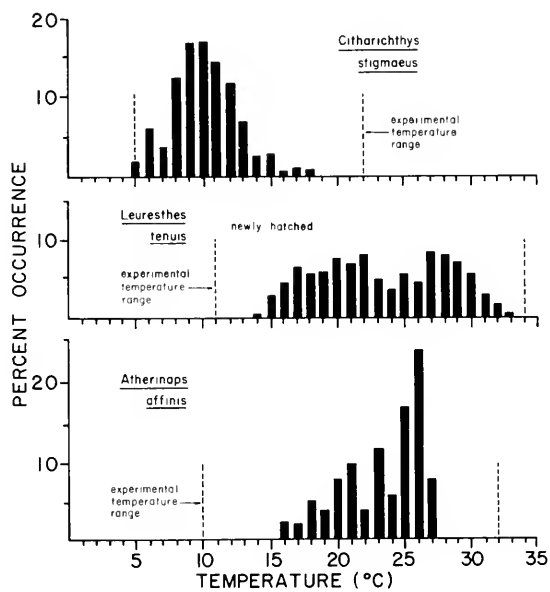

FIGURE 7.—Temperature-specific occurrences. Examples of three types of frequency distributions: normal (based on 220 fish observations), adult speckled sanddabs; platykurtic (based on 281 fish observations), newly hatched California grunion; and, skewed to the left (based on 241 fish observations), juvenile topsmelt.

normal frequency distribution (Table 1), but subsequent food deprivation resulted in selection of colder water (mean 18.7°C) and a narrower distribution (SD 3.3°C). Selection of colder water during food deprivation may be a mechanism of energy conservation by poikilothermic organisms. Other mechanisms of energy conservation, both behavioral and biochemical, have been found during starvation of herring and plaice larvae (Blaxter and Ehrlich 1974; Ehrlich 1974). The increased precision of temperature selection during food deprivation coincides with the findings of Reynolds (1977) that stress can increase precision of temperature selection. This pattern, however, of lowered selected temperature but increased precision during food deprivation was not duplicated by all species.

Comparison of data from 2 consecutive days of observation of shiner surfperch demonstrated that the temperatures they selected, as well as their tendency to school or aggregate, varied between the 2 days. The selected temperatures decreased on the second day (means 19.9° to 15.6°C and modes 19° to 16°C), but unlike California grunion the standard deviation of the mean increased (2.1° to 2.6°C). School tightness also decreased as indicated by a larger coefficient of dispersion (24 to 37%). The major preexperimental difference between the first and second day runs was that the fish were not fed before the second day of experimentation. The lowering of the preferred temperature during food deprivation followed that of the California grunion and brook trout (Javaid and Anderson 1967). Furthermore, this selection of cooler water during food deprivation agrees with the findings of Brett et al. (1969) and Brett and Higgs (1970) who showed that a limited food supply resulted in a decrease in the optimal temperature for growth, which is coincident with the final preferendum for sockeye salmon (Brett 1971). The wider preferred temperature range and reduced aggregation may reflect increased searching by hungry fish. Hunger can cause fish to increase the distance between individuals (Hunter 1965) as well as disrupt fish school integrity (Blaxter and Holliday 1958).

Larval California grunion, topsmelt, rockpool blennies, and painted greenlings selected water that was often warmer than naturally available. This behavior has several adaptive advantages but also presents potential harmful consequences resulting from man's alteration of their natural habitat. Selection of warm water by larvae will reduce the duration of the highly vulnerable yolk-sac and larval stages. In King Harbor it kept many of these larvae in the back basins that contained the largest concentration of food organisms (McGowen[5]). Furthermore, in genera such as *Hypsoblennius* that become demersal following the planktonic larval stages, selection of warm water will help the larvae to remain in the nearshore environment where they must be when they leave the planktonic community. Marshall (1966) discussed similar mechanisms by which nearshore demersal species maintain their population integrity. Rockpool blenny larvae, however, that entered water warmer than 28°C lost their equilibrium, could not extricate themselves and eventually died. This same behavioral response of entering water above a lethal temperature and not leaving it has been reported for other species (e.g., Beitinger and Magnuson 1976). Similar behavior in the field near sources of hot water such as power plant effluents may significantly affect local populations. This could be magnified as a result of predation, for it has been shown that the vulnerability of fishes to predation is increased by sublethal heat shocks (Sylvester 1972; Coutant 1973; Yocum and Edsall 1974).

Various workers (Lowe and Heath 1969; Reynolds and Thomson 1974; Reynolds and Casterlin 1976; Beitinger 1977) have reported that the final preferendum is often close to the upper lethal temperature. Frequency distributions skewed to the left such as for topsmelt (Table 1, Figure 7) are reflective of this behavior. The mode occurrence for topsmelt was 26°C, and they sharply avoided warmer water. Coutant (1975) pointed out that the upper avoidance temperature is more sharply defined than the lower one for most species. Beitinger (1977) found bluegill, *Lepomis macrochirus*, tolerated less variation in avoidance temperature near their lethal limits.

Differences in group cohesion for individual runs between nonschooling species such as adult speckled sanddabs (Figure 5) and tightly aggregating ones such as olive rockfish (Figure 6) are illustrated by comparison of the standard deviations about the run selected temperatures. Although a low coefficient of dispersion may indi-

[5]McGowen, G. E. 1977. Effects of thermal effluent from Southern California Edison's Redondo Beach Steam Generating Plant on the warm temperate fish fauna of King Harbor marina. Ichthyoplankton study report for Phase II. Annual Report for 1 March 1975-29 February 1976. Unpubl. manuscr., 46 p. Southern California Edison Res. Contract No. U0654902.

cate tighter aggregation, it could also result from individuals of a normally solitary species with a narrow preferred temperature range being compressed into a tight aggregation by a steep temperature gradient. Comparison of the coefficient of dispersion and the measures of eury- or stenothermal preference (the standard deviation about the mean selected temperature and the coefficient of kurtosis) (Table 1) helps to distinguish between behavioral aggregation and compression of individuals with stenothermal preferences. Juvenile topsmelt, for instance, aggregated closely, but the close association of the individual fish was not the result of thermal compression since they showed a wide temperature preference (Table 1). Greater caution, however, must be used in interpreting the coefficient of dispersion for species such as pile surfperch with a narrow (leptokurtic) range of preferred temperatures (Table 1). The occurrence of pile surfperch in the field at temperatures of 12°-18°C (Stephens[6]) shows that the close aggregation in the gradient was not due to thermal compaction of fish with an obligatory stenothermal preference. These fish in King Harbor were associated with the coolest water available (Stephens, see footnote 6). Coordinated laboratory and field studies provide greater understanding of the factors that affect fish populations and distributions than either investigation alone.

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[6]Stephens, J. 1977. Effects of thermal effluent from Southern California Edison's Redondo Beach Steam Generating Plant on the warm temperate fish fauna of King Harbor marina. Field study report for Phase II. Annual Report for 1 March 1975-29 February 1976. Unpubl. manuscr., 111 p. Southern California Edison Res. Contract No. U0654902.

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APPENDIX TABLE 1.—Equations and an example from an artificial data set for calculation of mean selected temperature and coefficient of dispersion. An artificial data set was used to provide a more concise presentation of the mathematical techniques. The standard deviation of the mean selected temperature is 0.7°C, and the data are neither significantly skewed ($g_1 = 0.00$, $P>0.05$) nor lepto- or platykurtic ($g_2 = 2.5$, $0.2<P<0.4$). Initial, mean, modal, and final selected temperatures were equal (13°C).

MEAN SELECTED TEMPERATURE (MST)

METHOD	EQUATIONS	EXAMPLE
STEP 1. Eliminate individual fish observations at the extreme ends of the gradient.		Eliminate the one fish that occurred in Compartment 1 at 075 min (see Artificial Data Set).
STEP 2. Determine the frequency of occurrence of individual temperatures $f(T_i)$ and the number of fish (F_i) at each temperature (T_i).	$i = 1,\ldots,n$ T_1 = minimum observed temperature T_n = maximum observed temperature	See Data Analyses for Artificial Data Set.
STEP 3. Define the valid experimental range (R) as the continuous interval in which the minimum occurrence of a temperature is at least 25% of the maximum observed temperature frequency.		R = 8-16°C (See Data Analyses for Artificial Data Set.)
STEP 4. When T_i is an element of R ($T_i \epsilon R$), calculate the relative number of fish (f_i) corrected for the variation in occurrence of each temperature.	$f_i = \dfrac{F_i}{f(T_i)}$	See Data Analyses for Artificial Data Set.
STEP 5. When $T_i \epsilon R$, calculate the corrected number of fish (f') for the range of temperatures (R) analyzed.	$f' = \sum_{i=1}^{n} f_i$	f' = 4.97 (See Data Analyses for Artificial Data Set.)
STEP 6. Compute the percent occurrence of fish (P_i) for each $T_i \epsilon R$.	$P_i = \dfrac{f_i}{f'} \times 100$	See Data Analyses for Artificial Data Set.
STEP 7. Determine the mean selected temperature (MST), when $T_i \epsilon R$.	$MST = \sum_{i=1}^{n} P_i/100 T_i$	MST = (0.20)(12°C) + (0.60)(13°C) + (0.20)(14°C) = 13.0°C (See Data Analyses for Artificial Data Set.)

COEFFICIENT OF DISPERSION (CD)

METHOD

First calculate the coefficient of dispersion for an individual run (cd_j) and then for the entire experiment (CD).

EQUATIONS

$$cd_j = \frac{2\,sd_j}{T_{jmax} - T_{jmin}} \times 100$$

where
- $j = 1,\ldots,m$
- m = number of experimental runs
- sd_j = standard deviation of the run selected temperature of the j^{th} run
- T_{jmax} = maximum experimental temperature of the j^{th} run
- T_{jmin} = minimum experimental temperature of the j^{th} run

$$CD = \frac{\sum_{j=1}^{m} cd_j}{m}$$

EXAMPLE

$$cd_{000\ min} = \frac{(2)(0.9^{\circ}C)}{15^{\circ}C - 5^{\circ}C} \times 100 = 18\% \qquad CD = \frac{(10)(18\%)}{10} = 18\%$$

(See Artificial Data Set.)

DATA ANALYSES FOR ARTIFICIAL DATA SET

i	T_i (°C)	$f(T_i)$	Fi	f_i	P_i
1	5	1	0	-	-
2	6	7	0	-	-
3	7	5	0	-	-
4	8	19	0	0	0
5	9	9	0	0	0
6	10	29	0	0	0
7	11	10	0	0	0
8	12	30	29	0.97	20%
9	13	10	30	3.00	60%
10	14	30	30	1.00	20%
11	15	10	0	0	0
12	16	25	0	0	0
13	17	7	0	-	-
14	18	13	0	-	-
15	19	3	0	-	-
16	20	2	0	-	-
				$\Sigma f_i = 4.97 = f'$	

R

ARTIFICIAL DATA SET

TIME (min)	COMPARTMENTS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	RUN SELECTED TEMP. (°C) MEAN	SD	cd (%)
000																								
TEMP. (°C)	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	13.0	0.9	18
015																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	13.0	0.9	18
030																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	13.0	0.9	18
045																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0			
NO. OF FISH	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	13.0	0.9	18
060																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0			
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
075																								
TEMP. (°C)	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	19.5	20.0			
NO. OF FISH	1	0	0	0	0	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
090																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0			
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
105																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0			
NO. OF FISH	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	13.0	0.9	18
120																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	13.0	0.9	18
135																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	13.0	0.9	18

LINEAR PROGRAMMING SIMULATIONS OF THE EFFECTS OF BYCATCH ON THE MANAGEMENT OF MIXED SPECIES FISHERIES OFF THE NORTHEASTERN COAST OF THE UNITED STATES

B. E. BROWN, J. A. BRENNAN, AND J. E. PALMER[1]

ABSTRACT

We evaluated the results of using historic bycatch (incidental catch) ratios in adjusting fishing regulations by linear programming techniques. We used both 1971 and 1973 bycatch ratios separately to assess the sensitivity of the results to the reported changes in bycatch ratios in estimating the total 1975 catch of countries fishing in the northwest Atlantic. For 4 of the 11 countries for which data were examined, the difference between the percentage of a country's species total allowable catches (i.e., those catches allowed a country by regulation) using the 1971 and 1973 bycatch ratios, was at least 20%. Only four countries were predicted to catch at least 80% of their species total allowable catches. The predicted total catches of all countries and all species was only 60% of the total species quotas. The simulated directed fisheries constituted only 70% of the total catch using 1971 bycatch ratios and only 73% using 1973 bycatch ratios. Examination of the reported 1975 catches indicated that the total allowable catches for herring were most frequently limiting a country's catch. Except for U.S.S.R., the differences between reported and simulated catches were less than 50 metric tons, with the difference less than 10 metric tons for 6 of the 11 countries. There was little difference in reported versus simulated catches between the schemes using the 1971 and 1973 bycatch ratios.

The control of fishing mortality by means of individual species catch quotas is difficult in a mixed fishery, i.e., where a significant proportion of the fishing mortality on a given species is generated as a result of the incidental catch, or bycatch, of that species in fisheries directed toward other species. Moreover, if a country is allowed to catch a specified amount of a given species by means of a directed fishery for that species, the total species catch may exceed that amount because of the associated bycatch of that species in the other fisheries.

The International Commission for the Northwest Atlantic Fisheries (ICNAF) modified its regulatory measures several times in attempts to account for bycatches of species under quota restrictions. The initial haddock quota regulations (Subarea 5 and Division 4X, Figure 1) stated that the directed fishery should cease when the accumulated catch (directed catch plus bycatch) reported to ICNAF biweekly reached 80% of the quota, anticipating that the catch after closure (a bycatch by definition) would be 20% of the quota (ICNAF 1969). When yellowtail flounder was added to the list of species under quota, the closure procedures were changed. The Assessments Subcommittee of ICNAF estimated the expected monthly bycatch after closure of directed fisheries and the decision to cease directed fishing was then made when the accumulated total catch reported to ICNAF on a biweekly basis plus the expected bycatch during the remainder of the year equalled the quota (ICNAF 1970). With the introduction of national quota allocations in 1972, the procedure again changed, requiring each country to control its directed fishery so that the sum of its directed catch and the estimated bycatches would not exceed its quota allocation (ICNAF 1972a).

The bycatch problem was acknowledged by ICNAF in its decision to establish a TAC (total allowable catch, i.e., that catch allowed a country by regulation) for all species combined that was less than the sum of the individual species TAC's for 1974 and 1975 (ICNAF 1974a). Linear programming simulations utilizing bycatch ratios from directed fisheries for all countries combined substantiated this policy (Brown et al. 1973; Anthony and Brennan 1974).

Since 1974, TAC's were set for all species (either singly or in groups) and for national catches (ICNAF 1974a, 1975a). Under this regime, it was possible to utilize linear programming more realistically to investigate the extent to which the

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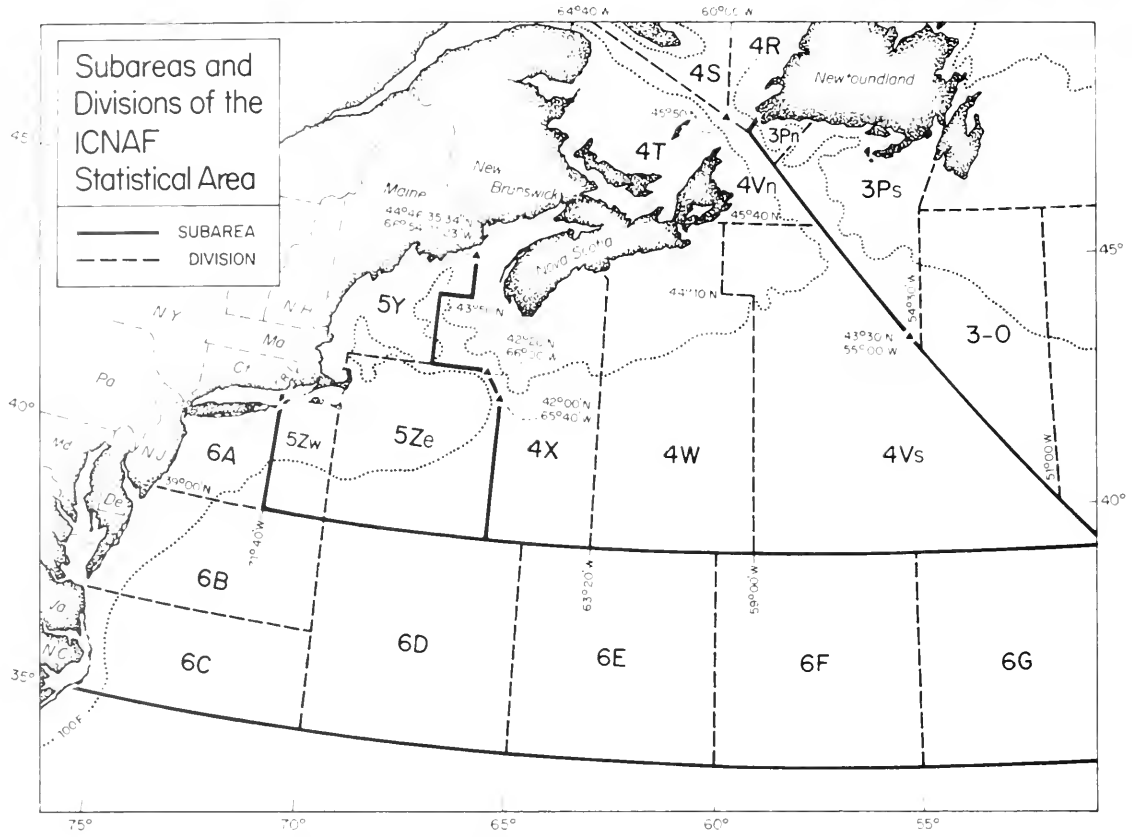

FIGURE 1.—Northwest Atlantic Ocean partitioned into ICNAF areas.

regulations in ICNAF were adequate to account for the bycatch. Simulations of 1975 catches were made utilizing bycatch ratios from both 1971 and 1973 to assess the sensitivity of the technique to differences in historic bycatch ratios. Brennan (1975) found little evidence of a decline in bycatch ratios when examined on a country-gear level over the years 1970-73. We compared the simulated catches and the reported catches on a species basis and on a country basis and examined the results to determine for which countries and species the simulations were successful.

METHODS AND MATERIALS

Data Base

Almost all countries fishing in Subarea 5 and Statistical Area 6 (Figure 1) submitted data on nominal catch (i.e., that reported landed (adjusted to live weight) by the country, not necessarily that actually caught—it is the term used in the ICNAF Statistical Records following standard United Nations Food and Agricultural Organization procedures) and effort for main species (or a species) sought. These data are published each year in tables 4 and 5 in the annual ICNAF Statistical Bulletins. The data of 1971 and 1973 (ICNAF 1972b, 1975b) were the sources of the bycatch ratios. Data of these years were reported according to the species categories given in Table 1. The nominal catches do not include fish caught and discarded at sea.

The nominal catch and effort (days fished) for 1971 and 1973 for finfish were summed over months for each target fish of the fishery (the "main species sought") categories reported in tables 4 and 5 of the ICNAF Statistical Bulletin (1972b and 1975b, respectively). Catches made with fixed gear as well as catches of Atlantic menhaden, Atlantic halibut, and large pelagic fishes, i.e., tunas, billfishes, and sharks (other

than dogfishes), were excluded. Most of these were not covered by the regulations and have <1 t (metric ton) per 100 t of directed species caught. In instances where no "main species sought" category was indicated or where landings were attributed to a mixed fishery, the monthly landings by vessel classification and gear were assigned to "species sought" categories according to the species which formed a simple plurality of the catch. The United States of America often reported mixed fisheries on groundfish species. The Union of Soviet Socialist Republics (U.S.S.R.), Poland, Japan, and German Democratic Republic (G.D.R.) typically reported their pelagic and/or squid fishery catches as mixed.

The term "fishery" as used in this paper refers to the vessels and associated catch on these "main species sought" categories. The term "species" refers to both individual species and species groups. All reported landings were thus identified by two factors: species and fisheries. Such tabulations were prepared for all nations for which data were available. For Romania, which has had an Atlantic herring fishery but did not report a directed Atlantic herring fishery in 1973, bycatch ratios for 1972 (ICNAF 1974b) were used for that species fishery. The only countries with an allocated national quota for which 1971 and 1973 data were not available and thus could not be analyzed were Italy (1971 and 1973) and France (1971).

In this paper, all catch restrictions described below will all be referred to as "quotas." To apply linear programming techniques to the bycatch problems restraints on the total catches for each species by country need to be set. For countries and for species categories reported in ICNAF Statistical Bulletins, we used restraints in linear programming (ICNAF 1974a). For countries and/or species for which ICNAF had not set specific quota allocations (but for which the quota was included in, say, "other countries" under ICNAF regulations—a country not given a specific catch quota could fish in competition with other similar countries from an "other country" allocation or "other flounder" category), we estimated these restraints by the following procedures. These were chosen so that the categories of quota allocations matched the species categories (Table 1) by which the catches were reported. We proportioned the "others" allocation category for each individual species to countries based on the 1973 nominal catch for each particular species and the catch of that species of all of the countries that did not have a national quota for the species. We proportioned the quota for "other groundfish" and "other pelagic" from the "other fish" TAC for each country. The quotas for American plaice and witch flounder were subtracted from the "other flounder" TAC for each individual country. Since the quota for pollock was set by ICNAF for Division 4VWX plus Subarea 5, national quota allocations were estimated as an average percent of the nominal pollock catches during 1971, 1972, and 1973 in Subarea 4VW and 5.

TABLE 1.—Species categories as reported to ICNAF, 1971 and 1973.

1971	1973	1973
Atlantic cod	Atlantic cod	Yellowtail flounder
Haddock	Haddock	Other flounder
Redfish	Redfish	Atlantic herring
Atlantic halibut	Silver hake	Atlantic mackerel
Silver hake	Red hake	Other pelagic
Atlantic herring	Pollock	Other groundfish
Other pelagic	American plaice	Other fish
Other groundfish	Witch flounder	Squids
Other fish plus squids		

Analysis Methods

Linear programming is a optimization method for which the effectiveness of an allocation scheme distributed over several variables is measured by the maximum or minimum value of some linear function of those variables, when those variables are subject to linear constraints. The problem considered here was to determine $X = (x_1, x_2, \ldots, x_n)$ such that

$$z = \sum_{i=1}^{n} c_i x_i \qquad (1)$$

is maximized, where for each i, c_i was the weighting coefficients of the variable x_i. In the present context,

x_i = catch of species i to be taken in directed fishery for species i,

c_i = catch of species i in all fisheries divided by catch of species i taken in directed fishery for species i ($c_i \geq 1.00$),

n = number of directed fisheries considered, and

z = total catch of all species.

Solutions $(x_1, x_2, \ldots, x_n)$ of Equation (1) were subject to the constraints for each i

$$\sum_{i=1}^{n} \hat{a}_{ij} x_i \leq b_j \qquad (2)$$

$$x_i \geq 0 \qquad (3)$$

where a_{ij} = catch of species j taken in directed fishery for species i/catch of species i in directed fishery for species i

b_j = constraint on total catch of species j, for $j = 1 \ldots m$.

The estimates of a_{ij} for each country for 1973 are presented in Appendix Table 1. Analogous tables for the 1971 data are in Brown et al. (1973).

The solution used in this paper was devised by using the Simplex Algorithm (Hadley 1963:132f) which was computed by using a Honeywell[2] computer program LINPRO; a description of this use of linear programming is given in appendix II of Brown et al. (1973). In this analysis the linear constraints were that no country would exceed its national allocation for any species (b_j). The output of the LINPRO program includes the vector X of directed catches of the species along with the resultant total catches of the species and the overall total catch.

RESULTS AND DISCUSSION

The results of each country's simulation are given in Appendix Table 2. In each case the sum of the species quota allocations exceeded the country's maximum possible catch (without violating single species constraints) as determined by the linear programming model. Table 2 lists the ratios of the simulated catches to the TAC's using 1973 and 1971 bycatch ratios. For 4 countries (Bulgaria, Canada, G.D.R., and Japan) of the 11, the percentages derived from 1971 bycatch ratios differed from those derived from 1973 fishing patterns by at least 0.20. More detailed reporting of catches (i.e., by species rather than groups) in 1973 than in 1971 and, therefore, in the analysis contributed to this change. Poland, United States, France, and Federal Republic of Germany (F.R.G.) were the only countries which could have taken >80% of the sum of their species TAC's based on 1971 or 1973 bycatch rates. The United States, however, has a significant discard of fish which is not taken into consideration in this analysis. Of the other countries considered, the effect of unreported discard would be expected to be greatest in the Spanish squid fisheries.

TABLE 2.—Comparison of maximum catches from linear programming simulation using 1971 and 1973 bycatch ratios, with sum of species "quotas" for the ICNAF area.

Country	Maximum catch—sum of species quota using: 1973 bycatch ratios	1971 bycatch ratios
Bulgaria	0.64	0.83
Canada	.54	.78
France	.52	—
Federal Republic of Germany	.97	.82
German Democratic Republic	.40	.64
Japan	.57	.17
Poland	.94	.93
Romania	.08	.05
Spain	.72	.72
U.S.S.R.	.25	.35
United States	.90	.93

Closer inspection of Appendix Tables 2 and 3 reveals the species which were the limiting factors in a country's inability to take the sum of its species quotas at present. These are the species which were caught in significant amounts as bycatch and directed catch and for which a species quota was met. The species whose catch was most frequently limiting was herring, when either 1971 or 1973 bycatch ratios was used. The next major species using 1973 ratios were pollock and "other pelagic" and using 1971 ratios were "other fish," "other pelagic," and haddock. Pollock was less limiting when 1971 ratios were used because it was combined with the "other groundfish" category, which had not been limiting.

The sum of the linear programming estimates over countries using 1971 and 1973 data are presented in Tables 3 and 4, respectively. In each case the sum of the expected maximum catches determined by the linear programming runs was only about 60% of the sum of the species quota. The simulated directed fisheries catch levels composed only 70% using 1971 bycatch ratios and 73% of the

TABLE 3.—Sum of individual country's linear programming simulation of 1975 catches in the ICNAF area, maximizing total catch (1,000 t) and using 1971 bycatch ratios. Catches of France assumed to be those using 1973 bycatch ratios.

Species sought	Total allowable catch restraint	Directed catch	Total catch
Atlantic cod	45.00	1.7	18.53
Haddock	6.00	0.0	5.23
Redfish	25.00	6.60	22.20
Silver hake	175.00	43.65	62.68
Flounders	41.00	1.32	36.25
Other groundfish	152.00	64.08	84.49
Atlantic herring	175.00	140.14	176.69
Other pelagic	311.90	189.07	210.48
Other fish plus squids	127 40	26.08	67.25
Total	1,058.30	482.64	683.81

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

TABLE 4.—Sum of individual country's linear programming simulation of 1975 catches, maximizing total catch (1,000 t), and using 1973 bycatch ratios for the ICNAF area.

Species sought	Total allowable catch restraint	Directed catch	Total catch
Atlantic cod	45.00	16.39	31.48
Haddock	6.00	0.00	5.25
Redfish	25.00	18.24	22.25
Silver hake	175.00	74.69	85.72
Red hake	65.00	11.83	26.51
Pollock	21.30	9.57	20.28
American plaice	2.70	—	1.15
Witch flounder	4.30	—	1.70
Yellowtail flounder	16.00	11.02	15.06
Other flounder	18.00	—	6.54
Other groundfish	65.70	27.38	40.96
Atlantic herring	175.00	107.38	120.01
Atlantic mackerel	285.00	127.51	150.60
Other pelagic	26.90	16.97	26.45
Other fish	56.40	9.33	33.35
Squids	71.00	25.93	40.30
Total	1,058.30	456.24	626.75

total using 1973 bycatch ratios, the rest being taken as bycatch. The highest percentage of TAC's, which were caught in directed fisheries, were for other pelagics (90%), Atlantic herring (79%), other groundfish (76%), and redfish (75%) using 1971 bycatch ratios, and for Atlantic herring (89%), silver hake (87%), Atlantic mackerel (85%), and redfish (82%) using 1973 bycatch ratios.

Referring to the individual country linear programming output tables in the Appendix, it is obvious that under 1971 and 1973 bycatch ratios, national patterns ran the gamut from almost a total mixed fishery by the U.S.S.R., and to a somewhat lesser extent by the G.D.R., to very specific fisheries of the F.R.G. and Poland.

As noted earlier, the species which was most frequently limiting to the total reported 1975 catch was Atlantic herring (6 out of 11 countries), and the countries which had the most limiting species TAC's were United States (5) and U.S.S.R. (4). Except for the catches of U.S.S.R., United States, G.D.R., and Poland, there was little difference in reported total catch minus simulated reported catch, when 1971 and 1973 bycatch ratios were used. Moreover, only for U.S.S.R were these differences $> 50{,}000$ t, and for six of the countries the differences were $< 10{,}000$ t for both schemes. The species for which the simulated and reported total catches differed most varied by country. Atlantic herring and Atlantic mackerel were the species most frequently differing in simulated vs. reported catches, but Atlantic mackerel and silver hake contributed most in metric tons to the differences. In general, and in view of the findings of Brennan (1975), the differences between schemes using 1971 and 1973 bycatch ratios were minimal, and more likely due to the different grouping of the data.

A summary of the 1975 TAC's, the 1975 reported catches, and the linear program estimates of total catch by country, is presented in Table 5. It is obvious that the overall TAC of 850,000 t for 1975 would not be attained without exceeding certain species TAC's unless bycatch was reduced, according to the simulations. The expected catches of 626,750 t using 1973 bycatch ratios and of 681,050 t using 1971 bycatch ratios are only 74% and 80%, respectively, of the 1975 total TAC. On a country basis, and using the results derived from the 1973 bycatches, it can be seen that the country total TAC's were set for 1975 at approximately appropriate levels for France and Spain (based on

TABLE 5.—Comparison of linear programming estimates of maximum total catch by overall country's total allowable catches (TAC's) in the ICNAF area. Figures in 1,000 t.

Country	1973 nominal catch of species regulated by the total TAC	Sum of species TAC's for 1975	1975 total TAC	Linear programming estimate of total catch		Actual 1975 nominal catch of species regulated on total TAC
				1973 bycatch ratios	1971 bycatch ratios	
Bulgaria	37.29	34.40	24.65	22.22	28.74	24.69
Canada	16.80	26.32	26.00	14.24	20.51	14.00
France	3.62	5.29	2.95	2.76	2.76	3.36
Federal Republic of Germany	38.28	30.89	24.85	30.05	25.31	25.10
German Democratic Republic	150.85	100.98	82.85	40.52	64.17	82.74
Italy	3.92		4.15	[1]	[1]	4.40
Japan	32.90	45.35	21.25	26.05	7.59	20.84
Poland	190.55	153.94	129.25	144.87	144.37	127.05
Romania	7.14	5.71	3.85	0.46	0.27	1.80
Spain	22.20	20.98	14.80	15.06	15.10	14.65
U.S.S.R.	449.04	366.64	301.80	93.10	127.02	313.78
United States	203.09	262.37	211.60	237.42	245.21	221.04
Total	1,155.68	[2]1,052.87	[3]850.00	626.75	[4]681.05	853.45

[1]No estimate available.
[2]Six thousand metric tons of other species not prorated to other species.
[3]Includes 2,000 t allocated to others.
[4]Due to the absence of bycatch ratios for 1971 data, estimate of France's total catch is derived from the 1973 bycatch ratios.

reported statistics, too low for the F.R.G., Japan, Poland, and United States, and too high for the other countries. In fact, summing the national total TAC's rather than the linear program estimates of country catch, when the former are limiting to obtain an overall estimated catch, results in an expected total catch of 675,000 t, only 65% of the overall TAC. The analogous expected total catch derived from 1971 bycatch ratios was 817,470 t, only 74% of the overall TAC. Bycatch may be reduced through actions initiated by fishing fleets or by regulations such as the closure to bottom trawling by larger vessels in the southern New England, Middle Atlantic, and Georges Bank areas (ICNAF 1975) for 1975 and by the similar closure in Georges Bank for 1976. The reduction of the overall TAC to 650,000 t in 1976 (ICNAF 1976) and 525,000 t in 1977 (ICNAF 1977) was designed to reduce the bycatch problem.

It should be noted, however, that despite the above potential for change as well as the inadequacies of the reporting to ICNAF, which may combine more than one directed fishery under a mixed category, there were other factors which worked in the opposite direction. The first was the inadequate recording of bycatch noted during international inspections. Some of this was discarded and not reported, and some was apparently utilized but not accurately reported on logbooks. Both the lack of reporting and any underestimates of bycatch can cause the bycatch ratios used in this analysis to be underestimated.

In mixed species fisheries, bycatch must be considered in the allocation of quotas to species and to elements of the fishery (in this example the elements are countries, but under different circumstances they could be otherwise—e.g., ports). Lack of attention to attendant bycatch may result in an unexpected overharvest of selected species or conversely the wastage of large quantities of protein depending on whether or not the directed fishery ceased when a small amount of bycatch had been taken. Linear programming provides a suitable technique for examing this problem. However, to have a refined analysis, accurate statistics as to main species sought and the composition of the bycatch including discards must be available. Lacking these, the inferences as in this paper, are directional. The specific individual estimates can be interpreted for policy decisions only when the user has the understanding of the fishery to qualitatively account for the appropriate reporting inadequacies.

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APPENDIX TABLE 1.—1973 nominal landings by country (ICNAF Subarea 5 and Statistical Area 6), expressed as ratios of bycatch to main species sought within fisheries. See text for explanation.

Species sought	Species caught															
	Atlantic cod	Haddock	Redfish	Silver hake	Red hake	Pollock	American plaice	Witch flounder	Yellowtail flounder	Other flounders	Other groundfish	Atlantic herring	Atlantic mackerel	Other pelagic	Other fish	Squids
BULGARIA																
Herring	0.006	—	0.064	0.060	0.050	—	—	—	0.010	—	—	1.000	0.243	0.049	—	—
Mackerel	0.001	—	—	0.048	0.011	—	—	—	0.003	—	0.007	0.039	1.000	0.007	0.026	0.013
CANADA																
Cod	1.000	0.214	0.009	—	—	0.081	0.003	0.002	0.004	0.011	0.125	—	—	—	—	—
Haddock	0.549	1.000	0.002	—	—	0.126	0.015	0.004	0.001	0.004	0.059	—	—	—	—	—
Other groundfish	1.087	0.700	0.027	—	—	3.472	0.012	0.005	—	0.019	1.000	—	—	—	—	—
Herring	—	—	—	—	—	—	—	—	—	—	—	1.000	0.006	—	—	—
Other pelagic	—	—	—	—	—	—	—	—	—	—	—	—	—	1.000	—	—
FRANCE																
Atlantic herring	—	—	—	—	—	—	—	—	—	—	—	1.000	—	—	—	—
Squids	—	—	—	—	—	—	—	—	—	—	0.023	—	—	—	—	1.000
FEDERAL REPUBLIC OF GERMANY																
Pollock	0.005	—	—	0.027	—	1.000	—	—	—	—	0.065	—	—	—	—	—
Other groundfish	—	—	—	—	—	—	—	—	—	—	1.000	—	0.083	—	—	0.500
Atlantic herring	—	—	—	—	—	—	—	—	—	—	—	1.000	0.010	0.008	0.010	—
Atlantic mackerel	—	—	—	—	—	—	—	—	—	—	—	—	1.000	0.094	—	0.080
Squids	—	—	—	0.001	—	—	—	—	—	—	0.463	—	0.178	0.084	0.005	1.000
GERMAN DEMOCRATIC REPUBLIC																
Pollock	0.004	—	0.002	—	—	1.000	—	—	—	—	—	0.042	0.009	—	—	—
Atlantic herring	0.001	—	0.001	0.003	—	0.001	—	—	—	—	—	1.000	0.008	—	0.211	0.005
Atlantic mackerel	—	—	—	0.001	—	—	—	—	—	—	—	0.031	1.000	0.003	0.010	—
Other fish	0.011	—	—	0.006	—	0.006	—	—	—	—	0.001	0.204	0.225	0.006	1.000	—
JAPAN																
Other groundfish	—	—	—	—	—	—	—	—	—	0.044	1.000	—	—	—	—	0.067
Atlantic herring	—	—	0.015	0.011	—	—	—	—	—	0.001	—	1.000	—	0.057	0.038	0.012
Atlantic mackerel	—	—	—	—	—	0.813	—	—	—	—	—	—	1.000	0.813	0.062	0.875
Other pelagic	—	—	0.015	0.020	—	—	—	—	—	0.003	0.003	0.007	0.017	1.000	0.055	0.334
Other fish	0.005	—	—	0.012	—	—	—	—	—	—	0.002	0.025	—	0.407	1.000	0.447
Squids	—	—	—	0.020	—	—	—	—	—	0.002	0.008	0.001	0.023	0.215	0.071	1.000
POLAND																
Red hake	—	—	—	—	1.000	0.031	—	—	—	—	—	0.047	—	0.172	0.031	—
Pollock	—	—	—	—	—	1.000	—	—	—	—	—	—	—	—	0.250	—
Atlantic herring	0.004	—	—	—	—	—	—	—	—	—	0.012	1.000	0.258	0.034	0.039	0.024
Atlantic mackerel	0.003	—	—	0.001	—	—	—	—	—	—	0.012	0.075	1.000	0.006	0.056	0.027
Other pelagic	—	—	—	—	0.142	0.025	—	—	—	—	0.039	0.025	0.352	1.000	0.167	—
Other fish	—	—	—	0.092	0.167	—	—	—	—	—	0.017	0.033	0.317	0.125	1.000	—
Squids	—	—	—	0.034	—	—	—	—	—	—	0.057	0.080	0.231	0.144	0.197	1.000

APPENDIX TABLE 1.—Continued.

Species sought	Species caught															
	Atlantic cod	Haddock	Redfish	Silver hake	Red hake	Pollock	American plaice	Witch flounder	Yellowtail flounder	Other flounders	Other groundfish	Atlantic herring	Atlantic mackerel	Other pelagic	Other fish	Squids
ROMANIA																
Herring	—	0 007	0 007	0 020	—	—	—	—	0.016	—	—	1.000	0 223	0 035	—	—
Mackerel	—	—	—	0.008	—	—	—	—	—	—	0.064	0 051	1 000	0.058	0 010	0 026
SPAIN																
Atlantic cod	1 000	0 065	—	—	0 001	0 134	—	—	—	—	0 008	—	—	—	—	—
Squids	—	—	—	—	—	—	—	—	—	—	0 003	—	—	—	—	1 000
U.S.S.R.																
Silver hake	0 005	0 001	0 034	1.000	0 236	0 003	0 001	0.001	0 002	0.004	0.062	0 069	0 303	0 006	0 188	0 073
Red hake	0.020	—	0.019	0.410	1 000	0 009	0.003	0 004	0 007	0 011	0 117	0 118	0 237	0.002	0 107	0 032
Other groundfish	0.494	—	—	0.571	0 101	—	0.002	0 012	0 035	0 058	1 000	0 164	0 148	0 036	0 031	—
Atlantic herring	0 011	—	—	0.187	0 140	—	0.003	0 002	0 004	0 007	0 100	1.000	0 227	0 001	0.110	—
Atlantic mackerel	0.010	0 005	0 017	0 147	0 094	0 017	0 002	0.003	0 001	0.005	0 051	0.301	1 000	0 003	0 082	0 017
Other pelagic	—	—	—	0.092	0.299	—	—	—	—	—	—	—	0 055	1 000	0 061	0 001
Other fish	0.068	0.003	0 010	0.147	0 245	0.126	0.024	0 026	0.006	0 056	0 675	0 099	0 250	0 020	1.000	0 059
UNITED STATES																
Atlantic cod	1.000	0.075	0.013	0.002	—	0 052	0.009	0 004	0 035	0.088	0.056	—	—	—	0 001	—
Haddock	0.343	1.000	0.006	—	—	0.087	—	0.006	0.056	0.045	0.017	—	—	—	—	0.003
Redfish	0.039	0.006	1.000	0.001	—	0.066	0.005	0.007	—	—	0.046	—	—	—	—	0 001
Silver hake	0.054	0.003	0.010	1.000	0.022	0.010	0.007	0.006	0.004	0.016	0 058	0.014	0.002	0.008	0 009	0 025
Red hake	0.023	—	—	0.241	1.000	—	—	—	0.148	0.132	0.357	0.011	0.001	0 096	0 216	0 077
Pollock	0.168	0.054	0 045	0.028	0.008	1.000	0.007	0.021	0.007	0.004	0.130	0.001	—	—	0.001	0 005
Yellowtail flounder	0.091	0.014	0.001	0.001	—	0.001	0.010	0.020	1.000	0.053	0 004	—	—	0.001	—	0 003
Other flounder	0.492	0.074	0.003	0.013	0.003	0.014	0.125	0 230	0.423	1.000	0 072	—	—	0.003	0.005	0.002
Other groundfish	0.344	0.108	0.063	0.197	0.088	0 188	0.019	0.033	0.070	0 148	1.000	0.023	0.003	0.017	0 069	0.041
Atlantic herring	0.001	—	—	—	—	—	—	—	—	—	—	1 000	0 002	0.006	—	—
Atlantic mackerel	—	—	—	0 018	0 014	0.018	—	—	0 004	0.016	0.148	0.059	1.000	0.087	0 024	0 164
Other pelagic	0.003	—	—	0 125	0.003	—	—	—	0 003	0.006	0.030	—	0.064	1.000	0 107	0 189
Other fish	0.010	—	—	—	—	—	—	0 010	—	—	—	—	—	0 160	1 000	—
Squids	—	—	—	0.015	0.002	—	—	—	—	0 091	0 110	—	0 005	0 025	0 005	1 000

APPENDIX TABLE 2.—Linear programming simulation by country in ICNAF Subarea 5 and Statistical Area 6, 1975 catches to maximize total catch (1,000 t). Simulated using 1973 bycatch ratios. Actual directed and total catches are included also.

Species sought	Total allowable catch constraint	Simulated		Actual	
		Directed catch	Total catch	Directed catch	Total catch
BULGARIA					
Atlantic cod	0.07	—	0.03	—	—
Redfish	0.50	—	0.03	—	—
Silver hake	2.00	—	0.92	1.02	1.92
Red hake	5.41	—	0.23	—	0.03
Yellowtail flounder	0.14	—	0.06	—	<0.01
Other groundfish	0.65	—	0.13	—	0.34
Atlantic herring	1.20	0.47	1.20	—	0.42
Atlantic mackerel	18.75	18.64	18.75	18.47	18.75
Other pelagic	0.75	—	0.15	—	0.39
Other fish	2.60	—	0.48	—	2.63
Squids	1.70	—	0.24	—	0.21
Total	34.40		22.22		24.70
CANADA					
Atlantic cod	4.82	0.55	1.31	1.10	1.93
Haddock	1.20	—	0.60	0.44	1.44
Redfish	0.50	—	0.02	0.01	0.06
Pollock	2.46	—	2.46	4.13	4.74
American plaice	<0.01	—	<0.01	—	0.02
Witch flounder	<0.01	—	<0.01	—	0.01
Yellowtail flounder	0.02	—	<0.01	—	0.01
Other flounder	0.03	—	0.02	—	0.05
Other groundfish	0.78	0.70	0.76	0.30	0.66
Atlantic herring	9.00	9.00	9.00	5.08	5.08
Atlantic mackerel	7.50	—	0.06	—	<0.01
Other pelagic	0.01	0.01	0.01	—	—
Total	26.32		14.24		14.00
FRANCE					
Other groundfish	0.02	—	0.02	—	—
Atlantic herring	1.87	1.87	1.87	3.34	3.34
Squids	3.40	0.87	0.87	—	—
Total	5.29		2.76		3.34
FEDERAL REPUBLIC OF GERMANY					
Atlantic cod	0.09	—	0.01	—	0.02
Silver hake	0.50	—	0.04	—	0.04
Pollock	1.60	1.60	1.60	0.10	0.15
Other groundfish	0.90	0.48	0.90	—	0.02
Atlantic herring	24.50	24.50	24.50	22.99	23.01
Atlantic mackerel	1.40	0.99	1.40	0.08	0.47
Other pelagic	0.51	—	0.35	—	1.46
Other fish	0.39	—	0.25	—	—
Squids	1.00	0.68	1.00	—	0.03
Total	30.89		30.05		25.20
GERMAN DEMOCRATIC REPUBLIC					
Atlantic cod	1.30	—	0.03	—	0.03
Redfish	0.63	—	0.02	—	0.01
Silver hake	3.10	—	0.06	—	0.04
Pollock	3.50	3.49	3.50	<0.01	0.10
Other groundfish	<0.01	—	—	—	0.07
Atlantic herring	31.90	13.00	13.75	27.00	30.90
Atlantic mackerel	56.25	20.00	20.14	47.95	48.34
Other pelagic	0.06	—	0.06	—	0.06
Other fish	2.94	—	2.90	0.12	2.18
Squids	1.30	—	0.06	—	0.90
Total	100.98		40.52		82.63
JAPAN					
Atlantic cod	0.05	—	—	—	—
Redfish	0.50	—	0.12	—	0.02
Silver hake	7.30	—	0.35	—	<0.01
Red hake	0.03	—	—	—	<0.01
Pollock	0.25	—	0.25	—	—
Other flounder	0.06	—	0.04	—	—
Other groundfish	0.10	—	0.10	0.33	1.13
Atlantic herring	1.16	1.09	1.16	1.88	1.88
Atlantic mackerel	0.80	0.31	0.65	0.08	0.20
Other pelagic	9.30	6.71	9.30	2.65	3.62
Other fish	1.50	0.37	1.50	—	—
Squids	24.30	9.89	12.58	13.25	13.99
Total	45.35		26.05		20.84
POLAND					
Atlantic cod	0.49	—	0.37	—	0.48
Redfish	0.40	—	—	—	<0.01
Silver hake	5.30	—	0.13	0.24	0.38
Red hake	2.20	2.12	2.20	—	—
Pollock	0.35	0.28	0.35	—	0.02
Other groundfish	1.40	—	1.40	—	1.11
Atlantic herring	38.40	32.14	38.40	33.05	38.46
Atlantic mackerel	90.00	81.45	90.00	68.45	74.28
Other pelagic	2.20	0.15	2.20	0.17	3.77
Other fish	6.40	0.34	6.40	—	1.71
Squids	6.80	0.45	3.42	3.25	6.84
Total	153.94		144.87		127.05
ROMANIA					
Haddock	0.01	—	<0.01	—	—
Redfish	0.34	—	<0.01	—	0.01
Silver hake	0.50	—	<0.01	—	0.12
Yellowtail flounder	0.01	—	<0.01	—	—
Other groundfish	0.15	—	0.01	—	<0.01
Atlantic herring	0.20	0.20	0.20	1.54	1.54
Atlantic mackerel	3.75	0.05	0.10	—	0.07
Other pelagic	0.13	—	0.13	—	—
Other fish	0.02	—	0.02	—	—
Squids	0.60	—	<0.01	—	0.05
Total	5.71		0.46		1.79
SPAIN					
Atlantic cod	7.09	1.49	1.49	4.07	4.07
Haddock	0.30	—	0.10	—	0.07
Red hake	0.07	—	<0.01	—	0.01
Pollock	0.42	—	0.42	—	0.10
Other groundfish	0.10	—	0.05	—	0.42
Squids	13.00	13.00	13.00	9.90	9.90
Total	20.98		15.06		14.57
U.S.S.R.					
Atlantic cod	2.50	—	0.24	—	2.43
Haddock	0.05	—	0.05	—	0.01
Redfish	1.44	—	1.44	—	1.37
Silver hake	113.30	40.20	41.22	71.38	88.88
Red hake	44.40	—	11.18	4.50	26.12
Pollock	1.26	—	0.20	—	0.19
American plaice	0.20	—	0.05	—	0.18
Witch flounder	0.20	—	0.05	—	0.20
Yellowtail flounder	0.84	—	—	—	0.08
Other flounder	0.60	—	0.20	—	0.56
Other groundfish	16.70	—	2.79	—	2.86
Atlantic herring	42.10	1.91	5.28	37.08	40.95
Atlantic mackerel	101.25	1.96	14.80	99.91	106.31
Other pelagic	4.40	4.15	4.40	—	0.68
Other fish	28.90	—	8.20	5.99	34.08
Squids	8.50	—	3.00	3.53	8.94
Total	366.64		93.10		313.84
UNITED STATES					
Atlantic cod	28.00	14.35	28.00	12.46	23.41
Haddock	4.50	—	4.50	0.86	5.09
Redfish	20.62	18.24	20.62	7.07	8.96
Silver hake	43.00	34.49	43.00	17.79	20.59
Red hake	12.90	9.71	12.90	0.11	2.43
Pollock	11.50	4.19	11.50	3.80	8.06
American plaice	2.50	—	1.10	0.26	2.19
Witch flounder	4.10	—	1.65	0.36	2.03
Yellowtail flounder	15.00	11.02	15.00	14.99	19.32
Other flounder	17.30	—	6.28	11.81	19.39
Other groundfish	44.88	26.20	34.80	10.34	19.11
Atlantic herring	24.65	23.20	24.65	35.76	36.09
Atlantic mackerel	4.70	4.11	4.70	0.54	1.65
Other pelagic	9.52	5.95	9.52	19.61	23.40
Other fish	13.60	8.62	13.60	17.02	27.65
Squids	5.60	1.04	5.60	0.21	1.67
Total	262.37		237.42		221.04

APPENDIX TABLE 3.—Linear programming simulation by country in ICNAF Subarea 5 and Statistical Area 6 of catches to maximize total catch, 1,000 t. Simulated using 1971 bycatch ratios. Actual directed and total catches are included also.

Species sought	Total allowable catch constraint	Simulated		Actual	
		Directed catch	Total catch	Directed catch	Total catch
BULGARIA					
Atlantic cod	0.70	—	0.01	—	—
Haddock	0.01	—	0.01	—	—
Redfish	0.80	—	—	—	—
Silver hake	8.00	0.88	1.82	1.02	1.92
Flounders	0.14	—	0.14	—	0.01
Other groundfish	5.06	0.78	1.78	—	0.37
Atlantic herring	1.21	—	1.20	—	0.42
Other pelagic	19.80	18.39	19.80	18.47	19.15
Other fish + squids	4.30	—	4.30	—	2.84
Total	39.41		29.74		24.70
CANADA					
Atlantic cod	4.82	—	2.76	1.10	1.93
Haddock	1.20	—	1.37	0.44	1.44
Redfish	0.80	—	0.06	0.01	0.06
Flounders	0.05	—	0.06	—	0.06
Other groundfish	3.24	2.76	2.76	4.43	5.40
Atlantic herring	9.00	9.00	9.00	5.08	5.08
Other pelagic	7.81	7.81	7.81	—	0.01
Total	28.92		20.81		14.00
FEDERAL REPUBLIC OF GERMANY					
Atlantic cod	0.09	—	—	—	0.02
Silver hake	0.50	—	—	—	0.04
Other groundfish	2.50	—	0.27	0.10	0.11
Atlantic herring	24.80	24.80	24.80	22.99	23.01
Other pelagic	1.91	—	0.84	0.08	1.93
Other fish + squids	1.09	—	—	—	0.03
Total	30.89		25.91		25.20
GERMAN DEMOCRATIC REPUBLIC					
Atlantic cod	1.30	—	—	—	0.03
Redfish	0.83	—	—	—	0.01
Silver hake	3.10	—	—	—	0.04
Other groundfish	3.50	0.84	3.50	<0.01	0.17
Atlantic herring	91.90	90.83	91.90	27.00	50.90
Other pelagic	66.31	20.23	24.53	47.98	48.40
Other fish + squids	4.24	—	4.24	0.12	3.08
Total	100.98		84.17		82.63
JAPAN					
Atlantic cod	0.06	—	0.01	—	—
Redfish	0.50	—	0.01	0.12	0.02
Silver hake	1.30	—	0.03	0.38	0.01
Flounders	0.06	—	0.01	0.04	—
Other groundfish	0.36	—	0.36	0.36	0.13
Atlantic herring	1.16	1.16	1.16	1.88	1.88
Other pelagic	10.10	4.49	4.50	2.73	3.82
Other fish + squids	28.80	—	1.91	13.84	13.99
Total	45.06		7.59		20.84

Species sought	Total allowable catch constraint	Simulated		Actual	
		Directed catch	Total catch	Directed catch	Total catch
POLAND					
Atlantic cod	0.49	—	0.14	—	0.48
Redfish	0.40	—	0.09	—	<0.01
Silver hake	5.30	—	0.09	0.24	0.38
Other groundfish	3.95	—	0.25	—	1.13
Atlantic herring	38.40	25.01	38.40	33.05	38.46
Other pelagic	92.20	85.90	92.20	68.62	78.05
Other fish + squids	13.20	1.46	13.20	3.25	8.55
Total	153.94		144.37		127.05
ROMANIA					
Haddock	0.01	—	0.01	—	—
Redfish	0.34	—	—	—	0.01
Silver hake	0.50	—	0.01	—	0.12
Flounders	0.01	—	0.01	—	—
Other groundfish	0.16	—	<0.01	—	<0.01
Atlantic herring	0.20	—	0.04	1.54	1.54
Other pelagic	3.88	0.14	0.16	—	0.07
Other fish + squids	0.62	—	0.06	—	0.05
Total	5.71		0.27		1.79
SPAIN					
Atlantic cod	7.09	1.71	4.71	4.07	4.07
Haddock	0.30	—	0.30	—	0.07
Redfish	0.01	—	—	—	—
Other groundfish	0.52	—	0.09	—	0.53
Other fish + squids	13.00	13.00	13.00	9.90	9.90
Total	20.96		18.10		14.57
U.S.S.R.					
Atlantic cod	2.50	—	0.38	—	2.43
Haddock	0.05	—	0.05	—	0.01
Redfish	1.44	—	1.44	—	1.37
Silver hake	113.90	10.00	17.73	71.38	88.88
Flounders	1.84	—	1.84	—	1.02
Other groundfish	52.36	0.14	8.14	4.50	29.17
Atlantic herring	42.10	34.46	42.10	37.08	40.95
Other pelagic	135.66	99.85	47.38	99.91	106.99
Other fish + squids	37.40	—	10.01	9.52	43.02
Total	366.84		127.02		313.84
UNITED STATES					
Atlantic cod	28.00	—	16.84	12.46	23.41
Haddock	4.50	—	4.50	0.86	5.09
Redfish	20.62	16.89	20.62	7.07	8.96
Silver hake	43.00	32.77	43.00	17.79	20.59
Flounder	38.90	1.32	34.20	27.42	42.93
Other groundfish	89.28	89.84	89.28	14.25	29.60
Atlantic herring	24.66	10.66	24.66	35.76	36.09
Other pelagic	14.22	12.56	14.22	20.15	25.05
Other fish + squids	19.20	9.86	19.20	17.23	29.32
Total	282.37		245.21		221.04

NOTES

EFFECT OF SWIMMING SPEED ON THE EXCESS TEMPERATURES AND ACTIVITIES OF HEART AND RED AND WHITE MUSCLES IN THE MACKEREL, *SCOMBER JAPONICUS*

Body temperatures of most fish typically are about the same as the water in which they swim for much of the heat generated by muscular activity is ducted away via the circulating blood and lost by convection at the gills and body surface.

Some scombrids and lamnid sharks conserve muscle heat using countercurrent vascular heat exchangers (retia mirabilia) so that temperatures are maintained significantly above ambient in the brain, eyes, red and white swimming muscles, and viscera (Carey et al. 1971; Stevens and Fry 1971; Linthicum and Carey 1972; Graham 1973). In other fishes lacking these heat conserving devices, only small temperature excesses above ambient have been recorded, but rarely more than 1°C (Stevens and Fry 1974). Since heat production must depend primarily on work output by the locomotor musculature, we have examined effects of swimming speed on the magnitude of the small temperature excesses in a "cool" scombrid not equipped with the retia exchangers, the mackerel, *Scomber japonicus* (locally the Pacific mackerel = chub mackerel).

Another important question concerning scombrid locomotion is how contractions of red and white muscle fibers are staged as swimming speed increases. It is generally thought that red muscle provides power for cruise swimming and that white muscle functions in "burst" swimming (Rayner and Keenan 1967). Red muscle is predominately aerobic and utilizes fatty acids as the major energy source whereas white muscle (which uses glycogen) usually functions anerobically (Gordon 1968; Bilinski 1974). The second objective of our study was to determine how heart rate and red and white muscle activity of *S. japonicus* are affected by swimming speed. For this purpose, electrodes were implanted into the pericardial space and in swimming muscles of fish so that simultaneous records of electrocardiograms (ECG's) and red and white electromyographs (EMG's) could be obtained.

The genus *Scomber* is a primitive member of the family Scombridae (Kishinouye 1923). It has a fusiform shape, is less heavily bodied than the skipjack tuna, *Katsuwonus pelamis*, and other tunas, but shares several characteristics with warm-bodied species: they swim continuously (swim bladders are reduced or absent), have high rates of oxygen consumption (Baldwin 1923; Hall 1930), and have high blood hemoglobin levels (Greer-Walker and Pull 1975). They are also obligatorily dependent upon ram gill ventilation as adults (Roberts 1975) and have large gill surface areas with a high diffusion efficiency (Hughes 1966; Steen and Berg 1966).

Materials and Methods

Surgical Procedures and Swimming Experiments

The general procedure was to implant either thermocouples or cardiac (ECG) and muscle (EMG) electrodes into mackerel which were then placed in a Blažka-Fry tunnel respirometer (12 cm i.d.) to swim at controlled velocities. Fifteen specimens (35-40 cm fork length (FL); 0.38-0.62 kg) were obtained from regularly replenished and maintained mackerel stocks at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA. After netting, each fish was anesthetized in a large basin of oxygenated seawater containing 0.2 g l of tricaine methanesulfonate (Crescent Research Chemical, Inc.)[1] and placed on an operating table where its gills were perfused continuously with a fast flow of oxygenated seawater containing a small amount of the same anesthetic (0.08 g l). Thermocouples (0.127 mm in diameter copper constantan, polyvinyl chloride insulation) or electrode pairs (hooked, 0.07 mm in diameter stainless-steel, epoxy insulated) were implanted within the pericardial cavity just posterior to the ventricle, and in red and white muscles just under the leading edge of the second dorsal fin.

The white muscle thermocouple tip was placed midway between the vertebral column and the lateral edge of the body at the level of the horizontal midline. Preliminary dissections confirmed that red muscle in *S. japonicus* occurs in bands

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

that are concentrated below the skin along the lateral midline and become thicker posteriorly (see also Kishinouye 1923, fig. 16; Braekkan 1959, fig. 1). To ensure that the tip of the red muscle thermocouple would remain in place, the wire was passed from near the second dorsal fin obliquely through white muscle and then into the thin red muscle band. Once inserted, its position was easily verified by gentle fingertip probing.

To facilitate positioning of the two muscle thermocouples, 3-4 cm deep holes were tapped with a 20-gage hypodermic needle. The heart thermocouple was passed into the pericardial cavity through a 17-gage needle that was subsequently withdrawn. All wires were anchored in place by skin sutures. Wire leads (1 m long) to the recorder were lap wound together, passed posteriorly, and sutured to the dorsal midline near the finlets to prevent tangling around the tail. Implanting required about 15 min after which the fish was transferred to the respirometer swimming tube where aerated water was circulated over the gills by the driving impeller at a slow speed.

Two hours recovery from anesthesia and a brief period of swim training was required before a fish could maintain station in the tube and regulate swimming speed in response to water flow. This time delay also allowed stabilization of tissue temperature at ambient conditions following surgery.

Adaptation to the swimming chamber was carried out at a basal swimming speed which is 1.5 BL/s (body lengths per second) for *S. japonicus* (Magnuson 1973). This speed is also just above the velocity required for sustained ram gill ventilation (Roberts 1975). Flow rates in the respirometer were calibrated with a ducted flowmeter (Marine Advisors, Inc. model B-7C) and controlled by altering the applied armature voltage to the impeller pump motor. Eight fish were used for excess temperature measurements and seven were used to monitor EMG (4) and ECG (3) patterns.

Calibration Procedures

Thermocouples were made by soldering together the twisted bared tips of the copper and constantan wires and sealing them with epoxy cement. The three tissue thermocouples and a reference thermocouple (for respirometer water temperature) were each connected in series (constantan leads) to an ice-bath reference couple (0°C) and to an RS Beckman Dynograph (copper leads) through a high-quality, shorting rotary-switch. This arrangement permitted rapid switching between thermocouples without opening the recorder circuit. Thermocouples were standardized in a water bath at 20°±0.05°C before and after each trial.

Paired electrodes for recording ECG's and EMG's were prepared and implanted (in the same sites used for thermocouples) as described by Roberts (1975). The ECG and EMG signals were preamplified using high impedence, probe amplifiers (Grass, P511DR) to improve the frequency response of the RS Dynograph.

Seawater was kept continuously flowing through the respirometer tube and ambient temperature was maintained within 2.0°C in each experiment by mixing warm and cold seawater at the outlet taps of the laboratory seawater system. Over the 2-mo course of experiments, respirometer temperatures ranged from 16° to 22°C.

Results

Changes in excess tissue temperatures that accompany increased swimming speed in the mackerel are best seen in a particularly successful trial with fish number 6 (Figure 1). Similar, but somewhat variable records of heart, and red and white muscle temperatures were obtained for all fish (Table 1).

While cruising at low speeds, excess temperatures reached a maximum of about 0.3°C in the red and white muscles, but doubled within 3 min swimming at enforced higher speeds (3.2-4.5 BL/s). Excess temperatures recorded in the heart averaged about one-half of the excess developed in muscles at all swimming velocities. When swimming speeds were reduced once again to slow cruising, excess temperatures returned to preburst levels within 8-15 min.

During bouts of prolonged high-speed swimming (5-6 min), water in the swimming tunnel was warmed about 1°C due to frictional heating even though a continuous exchange of seawater was maintained from the supply tap (about 15 l/min). This thermal error was minimized by rapidly accelerating the fish from slow cruising to its predetermined, burst-swimming velocity. In Figure 1 for example, the fish was accelerated from 1.4 to 3.9 BL/s in about 5 s followed by sustained swimming for 3 min, and then rapidly decelerated to 1.4 BL/s. Equilibration of tissue thermal excess (i.e., generation minus dissipation) occurred in most

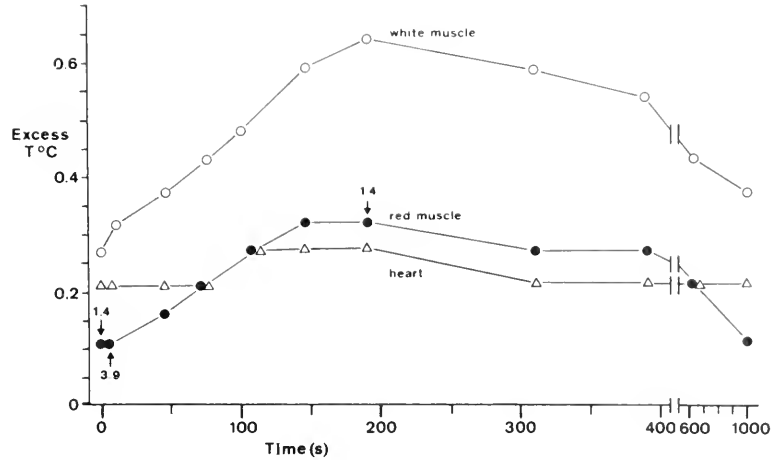

FIGURE 1.—Temperature excess in the heart and in red and white muscles recorded from *Scomber japonicus* no. 6 (35 cm FL, 0.45 kg) swimming at speeds from 1.4 to 3.9 BL/s. Arrows indicate timing and direction of speed changes. Ambient temperature, 19.5°-19.6°C.

TABLE 1.—Temperature excesses as ΔT (°C) recorded for seven *Scomber japonicus* swimming at basal and moderately fast speeds in body lengths per second (BL/s).[1]

Item	Fish number							Mean
	1	2	3	4	6	7	8	
Fork length (cm)	35.6	39.2	38.9	38.1	35.0	36.3	34.3	36.8
Weight (kg)	0.54	0.62	0.59	0.55	0.45	0.58	0.39	0.53
Highest ΔT at basal speed (1.3-1.9 BL/s) in:								
Red muscle	0.2	0.1	0.2	0.2	0.2	0.3	0.5	0.24
White muscle	0.2	0.3	0.3	0.2	0.4	0.3	0.3	0.29
Heart	0.0	0.3	0.1	0.1	0.2	0.2	[2]	0.15
Highest ΔT and swimming speeds (BL/s) in:								
Red muscle	0.9	0.75	0.55	0.85	0.3	0.5	0.8	0.66
	(4.2)	(3.2)	(3.7)	(4.2)	(3.9)	(3.8)	(4.3)	(3.9)
White muscle	0.75	0.8	0.65	0.6	0.65	0.3	0.7	0.64
	(4.2)	(3.2)	(3.7)	(3.9)	(3.9)	(3.8)	(4.3)	(3.9)
Heart	0.45	[2]	[2]	0.4	0.25	0.25	[2]	0.34
	(4.2)			(4.5)	(3.9)	(3.8)		(4.1)
Maximum trial speed (BL/s)	4.2	3.2	3.7	4.5	3.9	3.8	4.3	3.9
Water temperature, range (°C)[3]	16.1-17.0	16.5-17.0	16.8-17.8	17.1-17.5	19.5-19.6	20.5-21.0	21.1-21.8	

[1]Fish no. 5 omitted because it would not swim in the respirometer tube.
[2]Thermocouple malfunction.
[3]Starting temperature is that of the seawater supply from mid-June to mid-July.

cases within the 3-min swimming bouts. Although the thermal excess was greater in white muscle of fish number 6 (Figure 1), mean maximum temperature excesses recorded in red and white muscles of the seven mackerel were about the same (Table 1).

Variability observed in excess temperature measurements seems attributable to different performances of individual fish. Some specimens had more body fat than others and did not swim steadily. Others were affected by the trailing thermocouple cable as evidenced by their tail-beat patterns. The cable also added drag which reduced speed but probably increased total heat production at a specific speed. None of the fish trailing thermocouple cables could swim steadily above 5 BL/s, whereas fish trailing the thinner ECG and EMG cables could maintain a speed of 6 BL/s. Some of the variability in recorded thermal excesses may have also been due to the slightly differing locations of thermocouples in each fish. In addition, trauma due to thermocouple insertion, which probably interrupts normal blood flow locally may have been a factor influencing thermal convection. In a few cases, thermocouple signals changed abruptly possibly because of insulation failure at the tip due to rapid body flexing of fishes at higher swimming speeds.

A wide range was found in heart rates of mackerel cruising at 1-1.5 BL/s (mean, 106; range, 80-140 beats/min). With acceleration to 4-5 BL/s, the mean heart rate increased by 54% (mean, 130; range, 112-150), but rapidly returned to the resting rate within a few minutes of deceleration.

Body Temperature

This article starts with a brief overview of the topic. It then goes on to describe the various methods used to measure body temperature, including both invasive and non-invasive techniques. The article also discusses the factors that can affect body temperature, such as exercise, environmental conditions, and illness. Finally, it concludes with a discussion of the importance of maintaining a stable body temperature for overall health and well-being.

One of the most common methods for measuring body temperature is the oral thermometer. This device is placed under the tongue and measures the temperature of the blood flowing through the arteries in the mouth. Oral thermometers are generally considered to be accurate and reliable, but they can be affected by factors such as eating or drinking hot or cold beverages shortly before taking the measurement.

Another method for measuring body temperature is the rectal thermometer. This device is inserted into the rectum and measures the temperature of the surrounding tissues. Rectal thermometers are considered to be the most accurate method for measuring body temperature, but they are also the most invasive and uncomfortable. They are typically used in infants and young children, as well as in adults who are unable to cooperate with other methods.

a warm vein to an artery. Between parallel and closely positioned arteries and veins, either segmental vessels or postcardinal vein and dorsal aorta, could reduce convective heat transport. For example, Stevens and Sutterlin (1976) demonstrated a mechanism of this type that transferred heat directly from afferent to efferent gill arteries in the sea raven, Hemitripterus americanus.

Fish body temperatures are not uniform. In most species, including the warm-bodied forms, the highest thermal excesses occur in deep muscles (both red and white) where body thickness is maximum (Lindsey 1968; Carey et al. 1971; Graham 1975). For this reason, white muscle temperatures in the mackerel might be higher in more anterior regions of the body (i.e., around the first dorsal fin) where the white muscle mass and body thickness are greater. By contrast, higher temperatures in red muscle would not be expected because in Scomber this tissue is a thin band along the side of the body, only reaching maximum thickness as the body tapers toward the caudal peduncle (see figures in Kishinouye 1923 and Braekkan 1959).

Red and White Muscle Activity at Different Swimming Speeds

We were unable to determine a specific velocity where white muscle is recruited for swimming in the mackerel. At very low speeds, tail beats often became erratic or excessively strong. This may have been due to the added cable drag. Also, the basal speeds for fish in this study coincide with their minimum velocity needs for ram gill ventilation (Roberts 1978), which may have elicited struggling at slow speeds. Our EMG's do show low amplitude, synchronous potentials in both red and white muscles that were correlated with tail beats from very slow speeds up to about 2 BL/s. Amplitudes of EMG's in both muscle types seemed to reach a maximum for steady swimming at 3-4 BL/s, demonstrating that white fibers are active well within the range of sustainable cruising velocities for this species and that red muscle remains active at high speeds.

Neither patterns of motor innervation of red and white muscle fibers (focal or distributed) of scombrid myotomes nor the nature of their electrical responses seem to be known. Whether the compound potentials we recorded represent all-or-none spikes, abortive spikes, or partial [illegible] in membrane potentials (local potentials) or some combination is also unknown.

We suggest that the amplitude changes recorded from both the red and white fibers as the fish accelerated represent fiber recruitment. White muscle electrodes were located close to the vertebral column, well removed from the lateral strips of red muscle, so detection of red fiber potentials was unlikely. Amplitude variations detected in both muscle types during single tail-beat cycles was considerable. These variations were attributed to movement artifacts and possible propagation of potentials from nearby the electrodes.

A recently completed dissertation study in the [illegible] laboratories has demonstrated clearly that EMG's of red muscle in striped bass (Morone saxatilis) and in bluefish (Pomatomus saltatrix) also grade in amplitude with increasing swimming speed up to about 3 BL/s (L. A. Freadman, Graduate Student, Department of Zoology, University of Massachusetts, Amherst, MA 01003, pers. commun., September 1977). But onset of white muscle activity in these species does not appear until the transition to burst-swimming velocities—a pattern of red and white muscle activity that resembles the herring (Bone 1975).

Red and white muscle fibers have different anatomical, physiological, and biochemical characteristics that relate directly to their roles in the swimming of different fishes (George 1962; Bone 1966; Pritchard et al. 1971; Johnston et al. 1977). In some species, red muscle functions over a wide range of speeds whereas white muscle is used only in burst swimming (Bone 1966). [illegible] in the activity of red and white muscles, [illegible] involvement of white [illegible] as swimming [illegible] increases, has been observed in many species [illegible] (Bone 1966; [illegible] Rayner and Keenan 1967; [illegible] 1971; Hudson 1973; [illegible] 1977) and carp (Johnston et al. 1977). The relative contribution of these muscle fibers to swimming [illegible] species-specific [illegible] requirements for cruise swimming and burst activity. [illegible] that, as in Scomber, white muscle fibers are often [illegible] swimming speeds [illegible] and are not exclusively reserved for high speed burst swimming (Johnston et al. 1977).

For scombrids, which swim continuously and rely upon forward motion to ventilate their gills, the existence of a relatively high speed for the division of labor between red and white muscles, has been assumed primarily on the basis of work done by Rayner and Keenan (1967). These investigators concluded that in the skipjack tuna, red muscle alone powered cruise swimming and white muscle only became active at burst velocities. The initial objective of Rayner and Keenan's study was to demonstrate contractile properties of red muscle, and to this end they blocked white muscle activity (pentobarbital) and worked exclusively with tranquilized (propriopromazine) or sedated fish. Moreover, their specimens were restrained in a fixed position and artificially ventilated by perfusion tubes in the mouth. Thus the movements by these skipjack tunas that were identified as "low frequency swimming," were in fact only casually related to the swimming requirements for gill ventilation and hydrostatic equilibrium; both are controlling factors in normal swimming (Magnuson 1973; Roberts 1975).

Our results with *S. japonicus* contrast in that they show both red and white muscles function in low-speed swimming. Also, Dizon and Brill (A. E. Dizon, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. Pers. commun., September 1977) recorded red and white EMG's from yellowfin tuna, *Thunnus albacares*, and found that white muscle activity begins at swimming velocities of <3 BL/s—a speed only slightly above the minimum for hydrostatic equilibrium and well below maximal burst capabilities (Magnuson 1973). These observations indicate that in fast-swimming scombrids, patterned staging of red and white muscle activity may differ in that activity begins in white fibers at very low speeds, and that both red and white muscle remain active throughout a wide range of sustainable speeds as well as at burst velocities. Implicit in this idea is the presence of a high scope for aerobic activity in scombrid white muscle which has been recently demonstrated for the skipjack tuna (Guppy et al. in press). Also required by the hypothesis are specializations in red muscle for high-speed contraction which is supported by the findings of Johnston and Tota (1974) that high levels of myofibrillar ATPase occur in the red muscle of bluefin tuna, *T. thynnus*.

What physiological advantage might be gained by a 1°C thermal excess during fast swimming? Assuming a Q_{10} of 2 then a 10% increase in metabolism would afford about a 2-3% rise in swimming speed, but an insignificant change in overall swimming efficiency (Webb 1971). An interesting speculation is that the extensive heat-exchanging vascular network used for endothermy in the scombrids may have initially evolved to meet the high oxygen requirements of red and white myotomal muscle. More metabolic heat is produced during aerobic respiration and natural selection may have proceeded toward a vascular design that maximized oxygen delivery, yet augmented muscle function by conserving heat and insulating the swimming musculature from ambient conditions.

Acknowledgments

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THERMAL BEHAVIORAL RESPONSES OF THE SPECKLED SANDDAB, *CITHARICHTHYS STIGMAEUS*: LABORATORY AND FIELD INVESTIGATIONS

The speckled sanddab, *Citharichthys stigmaeus*, is a small bothid flatfish that is common in southern California (Ford 1965; Stephens et al. 1974). These authors and Helly[1] have suggested that temperature may have a significant effect on localized population abundances and distributions of speckled sanddabs. No studies to date, however, have examined in detail the relationship between temperature and fish behavior and distribution.

We designed this work to study the speckled sanddab population in King Harbor, Redondo Beach, Calif. This harbor (Figure 1), which receives the thermal effluent from an electricity generating station as well as cold upwelled water from the adjacent Redondo Submarine Canyon, contains a highly diversified thermal environment (Stephens 1972).

[1]Helly, J. J., Jr. 1974. The effects of temperature and temperature selection on the seasonality of the bothid flatfish, *Citharichthys stigmaeus*. Honors Thesis, Occidental Coll., Los Ang., 34 p.

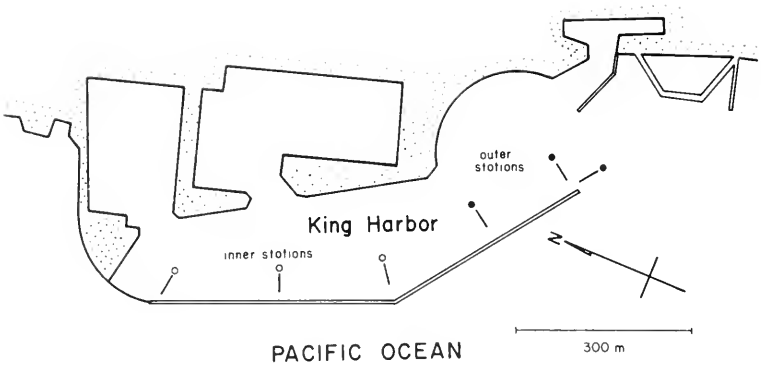

FIGURE 1.—Location of field sampling stations for speckled sanddabs in King Harbor, Redondo Beach, Calif.

Methods

We collected adult speckled sanddabs between August 1975 and January 1976 with a 3-m otter trawl. The fish were transported to the laboratory in aerated seawater and acclimated to a range of normally occurring temperatures (10.0°-19.7°C) according to the methods of Ehrlich et al. (1979). Prior to acclimating the speckled sanddabs, we removed the gill isopod *Livonica vulgaris* individually with forceps. During holding and acclimation, we fed the fish to satiation daily with live and frozen *Artemia salina*. The behavioral responses of the fish to temperature were studied using a 3.6-m long horizontal gradient and employing the techniques of Ehrlich et al. (1978). Each experiment lasted for 7-8 h with observations every 15 min. We shifted isotherm positions during each experiment to separate selection of temperature from preference for a given position within the experimental chamber.

Speckled sanddab abundance and distribution were studied using timed diver transects at six stations (Figure 1). Two divers swimming side by side for 5 min traversed each 6-m wide transect. They recorded the species and number of individuals observed in the same area. The transects by each pair of divers were run in duplicate on a monthly basis at each station from September 1974 through February 1976 and quarterly thereafter. In the analyses, we used the largest number of individual fish counted by either diver, but the average count of the two independent observations was used for estimates of large groups of fishes. The divers recorded the temperature at least twice during each transect, with thermometers readable to 0.5°C.

Results and Discussion

We examined the effects of acclimation temperature, size, and sex of speckled sanddabs on their temperature selection during 11 experiments (Table 1). The presence of some skewed temperature-specific frequency distributions (Table 1) precluded comparison of the results with parametric statistics. We tested these distributions for homogeneity using a Kruskal-Wallis test (Steel and Tor-

TABLE 1.—Temperatures selected by speckled sanddabs in laboratory experiments.

Date	No. test animals	No. fish observations	Standard length (mm) Mean	Standard length (mm) SD	Sex	Acclimation temperature (°C)	Selected temperature (°C) Mean	Selected temperature (°C) SD	Selected temperature (°C) Mode	Coefficient of skewness (g_1)	Coefficient of kurtosis (g_2)
21 Aug. 1975	9	265	96.3	0.6	not noted	14.0	10.5	3.4	10	0.493*	2.788
15 Dec.	8	230	91.5	1.3	not noted	10.0	12.3	4.5	9	0.543*	2.824
18 Dec.	8	218	88.5	3.2	M	19.7	10.5	4.1	8	0.673*	2.928
22 Dec.	9	220	90.3	3.5	F	18.9	10.1	2.6	9-10	0.427	3.438
5 Jan. 1976	9	210	77.1	4.0	M	15.2	10.9	2.6	11	0.220	3.512
8 Jan.	9	251	82.0	6.7	F	15.2	10.4	3.2	8-9	0.465	3.036
9 Jan.	9	250	82.0	6.7	F	15.2	11.6	3.6	8	0.573*	2.673
26 Jan.	6	162	76.3	5.6	M	12.0	9.9	4.3	8	0.400	0.592*
27 Jan.	6	167	71.5	2.7	M	12.0	10.5	2.5	9-10	0.291	2.372
29 Jan.	6	157	73.2	2.6	M	12.0	11.1	3.0	9	0.724*	2.538
30 Jan.	6	160	75.5	5.1	M	12.0	9.8	2.5	8	0.422	2.078

*$P < 0.05$.

rie 1960) and detected no significant differences ($\chi^2_{10\,df} = 15.99$, $P>0.05$). The overall mean selected temperature from pooled data was 10.8°C (SD = 3.1°C), and the mode was 9°C; 70% of all occurrences were in the range of 8°-13°C (Figure 2). The frequency distribution, however, was significantly skewed towards warmer temperatures (Figure 2).

Brett (1971) showed that the preferred temperature coincided with the optimal temperature for growth of sockeye salmon, *Oncorhynchus nerka*. Crawshaw (1977) found that physiological responses are often optimized in a zone of efficient operation rather than at a peak, and temperature preference reflects this. We are not aware of any work on the effects of temperature on the physiology of speckled sanddabs.

Considering the work of Brett (1971) and Crawshaw (1977), it is not unreasonable to suspect that speckled sanddabs may have a range of temperatures (approximately 8°-13°C) for efficient growth. The skewness may partially be due to activity increasing with temperature that could have resulted in occasional excursions into a greater number of compartments (temperatures) than at colder temperatures. Ehrlich et al. (1978) also suggested that skewness of a temperature-specific frequency distribution could result from preferred temperatures approaching lethal limits. These limits are not known for speckled sanddabs. DeWitt (1967) suggested that skewness of distribution could result from the regulation of body temperature by the animals depending on ". . . detection of deviations from a set point of some rate process bearing a direct exponential relation to body temperature. . . . Since physiological activity bears a direct exponential relation to temperature, the corresponding body-temperature distribution for the animals concerned would necessarily be negatively skewed." Speckled sanddabs, however, show a positively skewed mesokurtic distribution. A mesokurtic frequency distribution is not overly peaked (leptokurtic) or flat (platykurtic). Ivlev and Leizerovich (1960) and Ehrlich et al. (1979) used kurtosis to quantify the strength or precision of the preference: leptokurtic distribution indicates greatest preference.

The peak abundance of speckled sanddabs in King Harbor occurred from winter through spring and early summer when bottom temperatures were low (Figure 3). During the late summer and fall breakdown of stratification, warm bottom water was associated with a pronounced decrease in the number of fish observed. Stephens et al. (1974) found a similar decrease in abundance of speckled sanddabs during destratification in Los Angeles Harbor. Figure 3 also shows that the lower winter and early spring temperatures dur-

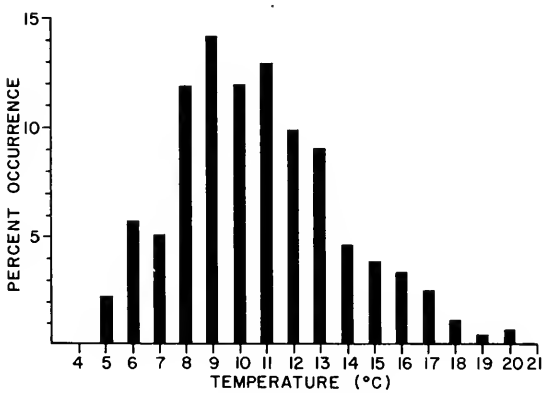

FIGURE 2.—Temperature-specific occurrences of speckled sanddabs, based on pooled data from 2,290 fish observations. The frequency distribution was significantly skewed toward warmer temperatures ($g_1 = 0.571, t_{99\,df} = 2.33, 0.01<P<0.025$) but was mesokurtic, that is not overly peaked or flat ($g_2 = 3.078, t_{99\,df} = 1.59, 0.1<P<0.2$).

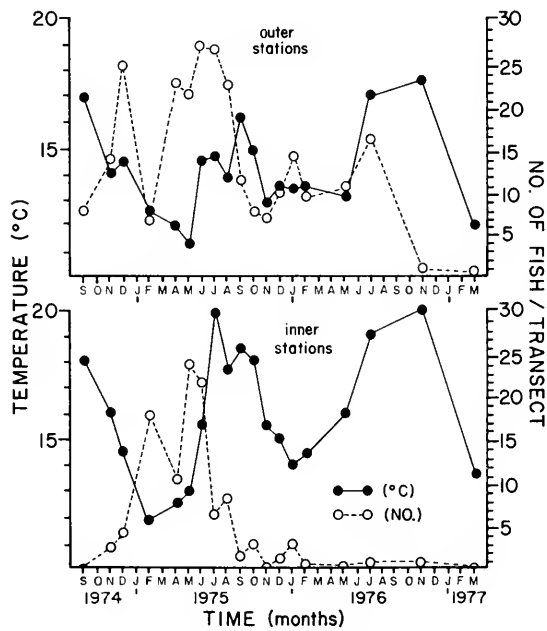

FIGURE 3.—Bottom temperatures and number of speckled sanddabs per transect at inner and outer stations in King Harbor, September 1974 to March 1977.

ing 1974, as compared with 1 yr later, coincided with a larger population of speckled sanddabs. The population density variability shown in Figure 3 results, at least in part, from the patchy distribution of the fish. Even at the time of year of greatest density the occasional transect found no fish. When fish were observed at these times of year, however, the numbers were high.

We grouped the abundance of speckled sanddabs per transect data according to the observed field temperature at the time of the survey to help explain the distribution of the fish (Table 2). The mean abundance per transect was determined for each observed field temperature (11°-20°C), and we calculated the percent occurrence at each temperature after correcting for the variation in occurrence of each temperature. This correction was accomplished by dividing the fish abundance at each temperature by the number of times the temperature occurred. We compared the temperature-specific field distribution with the temperatures selected in the laboratory by speckled sanddabs as a step in trying to understand the effect of temperature on field distributions. The laboratory data of temperature-specific occurrences was recalculated using only data for fish that were observed at 11°C or higher temperatures as if we had only sampled that part of the population occurring above 11°C (Figure 4). Statistical analysis of the arc sine transformed frequency distributions revealed no significant difference between laboratory and field data ($\chi^2_{9\,df} = 10.75$, $0.25<P<0.50$). We found a significant correlation between percent occurrence (arc sine transformed) and field temperature ($r_{8\,df} = -0.869$, $P<0.01$) of the data in Table 2. This high degree of correlation indicates that 76% ($r^2 \times 100$) of the variation in the field occurrence of speckled sanddabs in King Harbor seems explained by temperature. The similarity in temperature-specific distributions for the laboratory and field data (Figure 4) indicates that speckled sanddabs in King Harbor represented only that portion of the population found in warm water. Comparison of Figures 2 and 4 indicates that the greatest density of these fish may occur outside of the harbor in deeper, colder water. Furthermore, these fish in King Harbor do not appear to be a subpopulation endemic to this harbor. This would be in agreement with Taylor (1957) who suggested that there is but one popula-

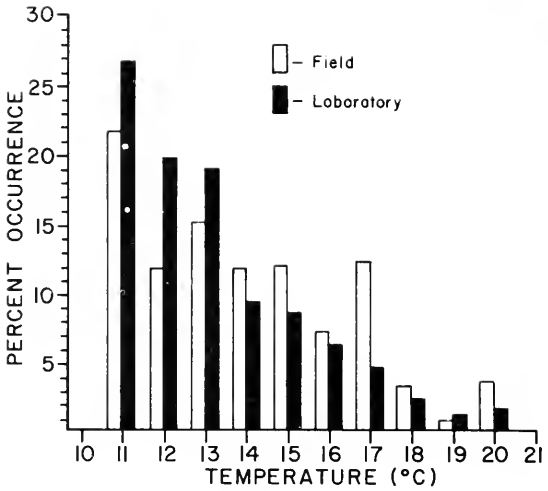

FIGURE 4.—Correspondence of temperature-specific occurrences of speckled sanddabs in the laboratory and field. The frequency distribution for the laboratory data was obtained from Figure 2 using only data for fish that occurred at 11°C or higher, which matched the range of observed field temperatures.

TABLE 2.—Frequency of occurrence of temperatures and speckled sanddabs in King Harbor, Redondo Beach, Calif.

Parameter	11°C	12°C	13°C	14°C	15°C	16°C	17°C	18°C	19°C	20°C
Temperature occurrences (X)[1]	1	5	6	9	3	5	2	5	1	2
Fish abundance (Y)[2]	21.8	18.0	24.0	4.2	1.2	2.7	8.0	0.0	0.8	6.5
		10.5	24.7	3.0	27.0	21.8	16.6	8.5		0.8
		7.0	7.0	0.7	7.8	0.2		1.5		
		23.0	10.3	0.0		0.5		3.0		
		0.5	14.5	14.0		11.5		1.0		
			10.8	25.0						
				27.3						
				22.8						
				9.5						
ΣY	21.8	59.0	91.3	106.5	36.0	36.7	24.6	14.0	0.8	7.3
$\Sigma Y\,X$	21.8	11.8	15.2	11.8	12.0	7.3	12.3	2.8	0.8	3.6
% occurrence[3]	21.9	11.9	15.3	11.9	12.1	7.3	12.4	2.8	0.8	3.6

[1] X is number of surveys that occurred at the indicated temperature
[2] Y is number of fish observed per transect during each survey that occurred at the indicated temperature.
[3] % occurrence = $[(\Sigma Y\,X)/\Sigma(\Sigma Y\,X)] \times 100$, where $\Sigma(\Sigma Y\,X) = 99.4$. It is coincidental that this number approximates 100.

tion of speckled sanddabs over its entire open coast range.

Biotic and abiotic factors, in addition to temperature, must be considered when relating temperature preference data to field situations. Factors such as the presence of predators or prey, nutritive condition, light levels and/or physical substrate can influence the temperature selected under natural conditions (Fleming and Laevastu 1956; Brett 1970, 1971; Blackburn and Williams 1975; Beitinger and Magnuson 1975). Stephens (in press) reported that the speckled sanddab prefers sand (outer stations in King Harbor) rather than mud substrate (inner stations in King Harbor). These types of parameters are probably particularly responsible for the 22% variation in field occurrences that was not explained by temperature. In the laboratory where we controlled these variables, we found a higher correlation ($r_{8\,df} = -0.976$) between fish occurrence and temperatures, which accounted for 95% of the variation in fish position.

Based on the laboratory data, it appears that the water in King Harbor is usually warmer than that preferred by speckled sanddabs. This is particularly true if one considers the modal selected temperature (9°C). Reynolds (1977) suggested that the mode is the best indicator of fish's thermal preference. Occurrence of speckled sanddabs in King Harbor, where their modal preferred temperature was not observed on any of the surveys indicates that this harbor (particularly the inner part) may be a marginal area for this species. We observed a high rate of parasitism by the isopod *Livonica vulgaris* in King Harbor on speckled sanddabs (virtually 100% infection), compared with the lower levels (approximately 25% infection) observed in this species collected in La Jolla, Calif. (Ford 1965). This appears to support our hypothesis that this area may be of marginal value to speckled sanddabs and that they may be under stress and more susceptible to infection. Snieszko (1974) reported such a relationship between stress and infection for some fish species.

Acknowledgments

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MERCURY AND SELENIUM IN BLUE MARLIN, *MAKAIRA NIGRICANS*, FROM THE HAWAIIAN ISLANDS

In a previous study, nine species of pelagic and inshore fish caught in Hawaiian waters were analyzed for total and organic mercury (Rivers et al. 1972). In all but one species the organic mercury was >80% of the total, a finding consistent with other mercury values reported (Kamps et al. 1972; Westöö 1973). In muscle and liver tissues of blue marlin, *Makaira nigricans* Lacépède, however, only a small portion of the total mercury was found to be organic mercury. Additional studies on marlin landed during fishing tournaments in 1972 (Schultz et al. 1976) and 1973 (Schultz and Crear 1976) revealed low levels of organic mercury in six other tissues. These studies also showed that the difference between total and organic mercury was indeed inorganic mercury. G. Westöö (National Swedish Food Administration, Stockholm. Pers. commun., 1972) had previously identified the organic fraction as methyl mercury.

An assessment of mercury is complicated by the presence of selenium. Selenium has been shown to reduce the toxicity of mercuric chloride and methyl mercury in laboratory animals when given as selenite, selenomethionine, or as selenium present in tuna (Parízek et al. 1971; Ganther and Sunde 1974). The presence of selenium in tuna, a principal food item of marlin (Naughton[1]), indicates that it should also be present in marlin.

For this report, nine tissues from blue marlin were analyzed for selenium, total mercury, and organic mercury.

Materials and Methods

Samples of muscle, liver, kidney, spleen, pyloric caecum, stomach, gill, gonad, and blood were collected from 46 marlin landed during a fishing tournament in Kailua-Kona, Hawaii, during August 1974. The tissues were ground with Dry Ice[2] in a blender and stored in acid-washed plastic vials.

The organic extraction was carried out as described by Rivers et al. (1972), i.e., a benzene extraction of the methyl mercury was reextracted with cysteine, oxidized with permanganate, and reduced to elemental mercury with stannous ion prior to being volatilized into the flameless atomic absorption apparatus. Total mercury digestions were performed (Rivers et al. 1972) but with 10 ml of concentrated nitric acid instead of 30 ml. All analyses were made with a Perkin-Elmer 303 atomic absorption spectrophotometer equipped with a vapor chamber (Manning 1970).

Selenium was determined by a fluorometric technique (Watkinson 1966), as modified by S. Nishigake (Tokyo Metropolitan Research Laboratory of Public Health, Tokyo, Japan. Pers. commun., 1975), i.e., following sample digestion with nitric and perchloric acids, the selenium was complexed with 2,3-diaminonaphthalene and this fluorescent compound then extracted into cyclohexane. All analyses were made using a Turner Model 110 fluorometer equipped with a primary filter at 369 nm and a secondary filter at 522 nm.

[1]Naughton, J. J. 1973. To all billfishermen. (Summary report of 15th Hawaiian International Billfish Tournament, 27-31 August 1973), 9 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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

Results

A summary of mercury and selenium concentrations in the marlin is given in Table 1. Average total mercury and selenium values were greatest in kidney (26.33 mg/kg Hg, 23.42 mg/kg Se) and least in blood (0.18 mg/kg Hg, 1.29 mg/kg Se) and gill (0.32 mg/kg Hg, 1.29 mg/kg Se). Average methyl mercury was highest in muscle (0.40) mg/kg) and lowest in blood (0.04 mg/kg) and gill (0.06 mg/kg). The percentage of organic to total mercury ranged from 1% in kidney to 27% in gonad. The molar ratio of mercury to selenium ranged from 0.06 in blood to 0.62 in muscle. (Molar ratio is computed here using sample average statistics of combined male and female data.)

An analysis of variance revealed significant differences ($P<0.05$) in total mercury between males and females for all tissues except gill and blood. A similar pattern was found for selenium. The organic mercury levels were not statistically different ($P>0.05$) between the sexes. In earlier studies on marlin caught from the same area during fishing tournaments in 1971, 1972, and 1973, mercury concentrations in both sexes were found to be similar.

Table 2 presents correlation coefficients for body weight and tissues. In most cases, the relationships are positive and highly significant. Figures 1-6 illustrate the dependence of mercury and selenium on weight and on each other.

Discussion

The data clearly demonstrate that methyl mercury concentrations are low relative to total mercury in blue marlin. Westöö (pers. commun.) and Nishigaki (pers. commun.) confirmed this low percentage in our samples based on subsamples sent to them. Nishigaki has also confirmed our selenium results.

In a study of 37 Pacific blue marlin (50-238 kg, average 109 kg) from Japanese waters, Nishigaki (pers. commun.) found total mercury levels ranging from 0.02 to 13.0 mg/kg (average 2.83 mg/kg) and methyl mercury ranging from 0.02 to 1.28 mg/kg (average 0.57 mg/kg). Selenium values for 11 marlin ranged from 0.52 to 1.99 mg/kg, averaging 0.97 mg/kg. These values are similar to our findings for mercury and selenium in marlin from Hawaiian waters.

TABLE 1.—Summary of mercury and selenium data in 46 blue marlin from the Hawaiian Islands by sex.[1]

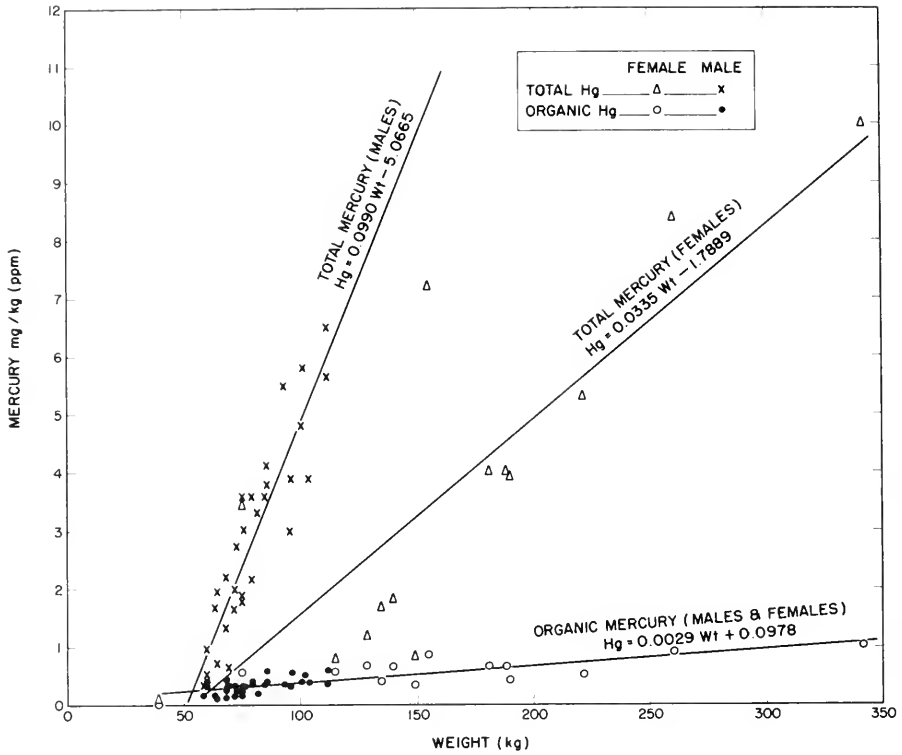
	Total Hg (mg/kg)				Organic Hg (mg/kg)				% organic Hg of total Hg	Se (mg/kg)				Hg/Se molar ratio
	Mean			Range	Mean			Range		Mean			Range	
Tissue	M & F	M	F	M & F	M & F	M	F	M & F	M & F	M & F	M	F	M & F	M & F
Muscle	3.12	2.83	3.76	0.09-10.00	0.40	0.32	0.58	0.02-1.02	13	1.98	1.88	2.21	0.63-5.32	0.62
Liver	11.58	12.53	9.46	0.13-39.20	0.26	0.21	0.38	0.09-0.76	2	17.47	20.36	11.06	2.50-61.12	0.26
Kidney	26.33	26.25	26.53	0.18-77.00	0.22	0.16	0.35	0.04-0.86	1	23.42	25.33	19.06	2.63-56.25	0.44
Spleen	6.93	6.34	8.21	0.08-17.60	0.18	0.12	0.30	0.02-0.66	3	9.31	9.12	9.73	0.63-24.25	0.29
Stomach	1.27	1.33	1.16	0.06-3.00	0.12	0.08	0.21	0.03-0.47	9	2.91	3.16	2.39	1.35-4.03	0.17
Pyloric caecum	1.83	1.74	2.03	0.17-4.50	0.30	0.22	0.49	0.08-0.98	16	4.92	5.10	4.52	2.28-10.10	0.15
Gill	0.32	0.26	0.44	0.08-0.96	0.06	0.03	0.11	<0.01-0.34	19	1.29	1.31	1.26	0.71-2.21	0.10
Gonad	0.40	0.30	0.68	0.03-2.15	0.11	0.06	0.25	0.03-0.65	27	2.14	1.97	2.60	1.24-3.80	0.07
Blood	0.18	0.18	0.18	0.02-0.53	0.04	0.04	0.05	<0.01-0.11	22	1.29	1.33	1.19	0.72-2.30	0.06

[1]Weights of 32 males ranged from 58 to 112 kg (average 80); 14 females weighed 39, 75, and 115-342 kg (average 166). Average for all samples was 106 kg.

TABLE 2.—Correlation coefficient of mercury, selenium, and weight in 46 blue marlin from the Hawaiian Islands by sex.

	Total Hg wt			Organic Hg/wt	Organic/ total Hg	Se/wt			Total Hg/Se	Organic Hg/Se
Tissue	M & F	M	F	M & F	M & F	M & F	M	F	M & F	M & F
Muscle	0.69**	0.90**	0.83**	0.79**	0.72**	0.68**	0.88**	0.85**	0.93**	0.61**
Liver	0.23	0.76**	0.69**	0.76**	0.13	0.00	0.68**	0.38	0.80**	−0.08
Kidney	0.49**	0.83**	0.79**	0.87**	0.42**	0.32*	0.79**	0.73**	0.91**	0.30*
Spleen	0.61**	0.88**	0.75**	0.84**	0.51**	0.45**	0.72**	0.61*	0.87**	0.41**
Stomach	0.38*	0.77**	0.82**	0.81**	0.35*	−0.27	0.18	0.15	0.32*	−0.33*
Pyloric caecum	0.59**	0.83**	0.82**	0.86**	0.59**	−0.11	0.32	−0.10	0.25	−0.14
Gill	0.86**	0.70**	0.90**	0.88**	0.77**	0.04	0.08	0.16	0.21	−0.14
Gonad	0.85**	0.75**	0.95**	0.82**	0.76**	0.15	−0.10	−0.53	0.10	0.25
Blood	0.28	0.32	0.57*	0.36*	0.44**	−0.04	−0.17	0.49	0.44**	0.09

*$P<0.05$.
**$P<0.01$.


FEMALE MALE
TOTAL Hg
ORGANIC Hg
TOTAL MERCURY (MALES)
Hg = 0.0990 Wt − 5.0665
TOTAL MERCURY (FEMALES)
Hg = 0.0335 Wt − 1.7889
ORGANIC MERCURY (MALES & FEMALES)
Hg = 0.0029 Wt + 0.0978
MERCURY mg / kg (ppm)
WEIGHT (kg)

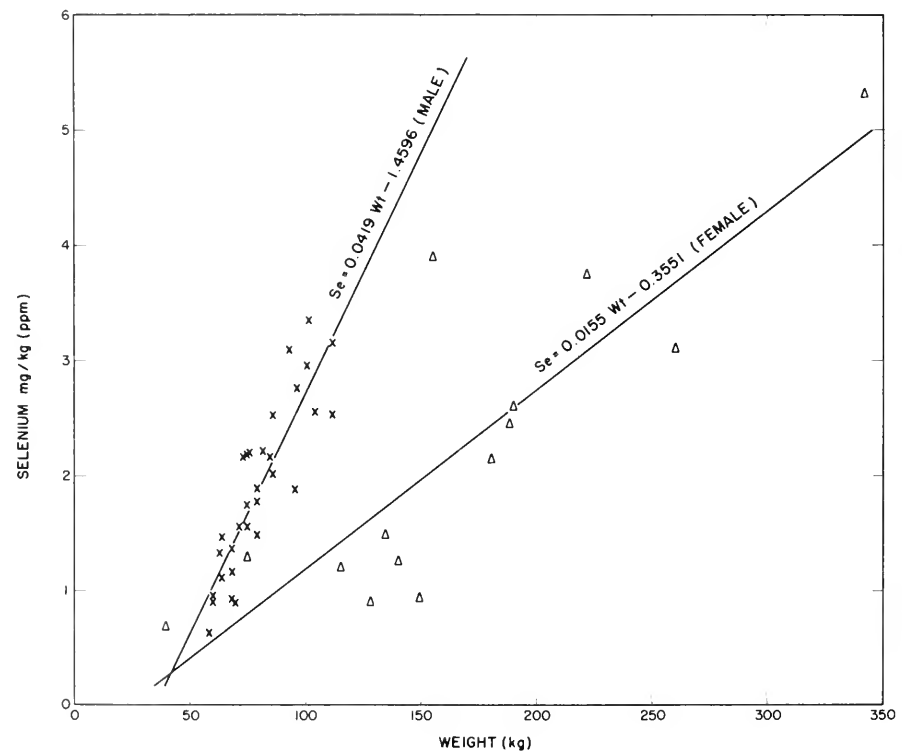

Se = 0.0419 Wt − 1.4596 (MALE)
Se = 0.0155 Wt − 0.3551 (FEMALE)
SELENIUM mg / kg (ppm)
WEIGHT (kg)

FIGURE 1.—The relationship of total and organic mercury in muscle tissue of 46 blue marlin from the Hawaiian Islands to fish weight.

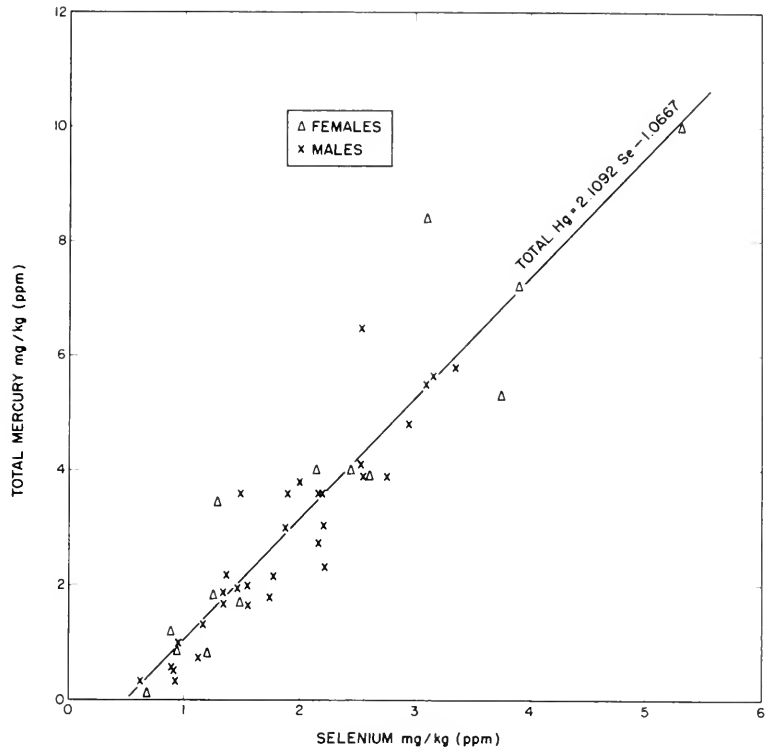


FIGURE 3.—Relationship between total mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

FIGURE 2.—Relationship between selenium in muscle tissue and weight of 46 blue marlin from the Hawaiian Islands.

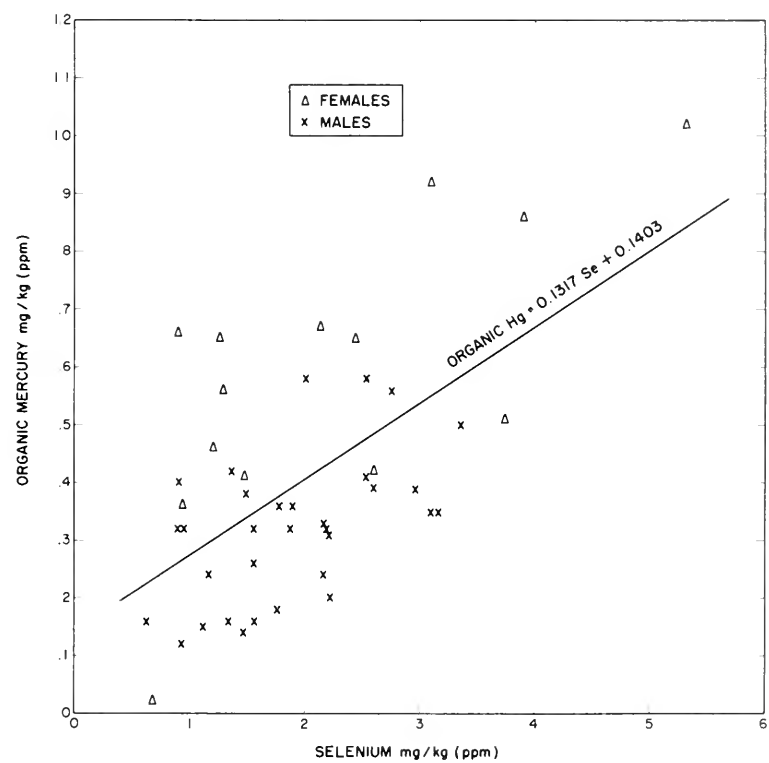


FIGURE 4.—Relationship between organic mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

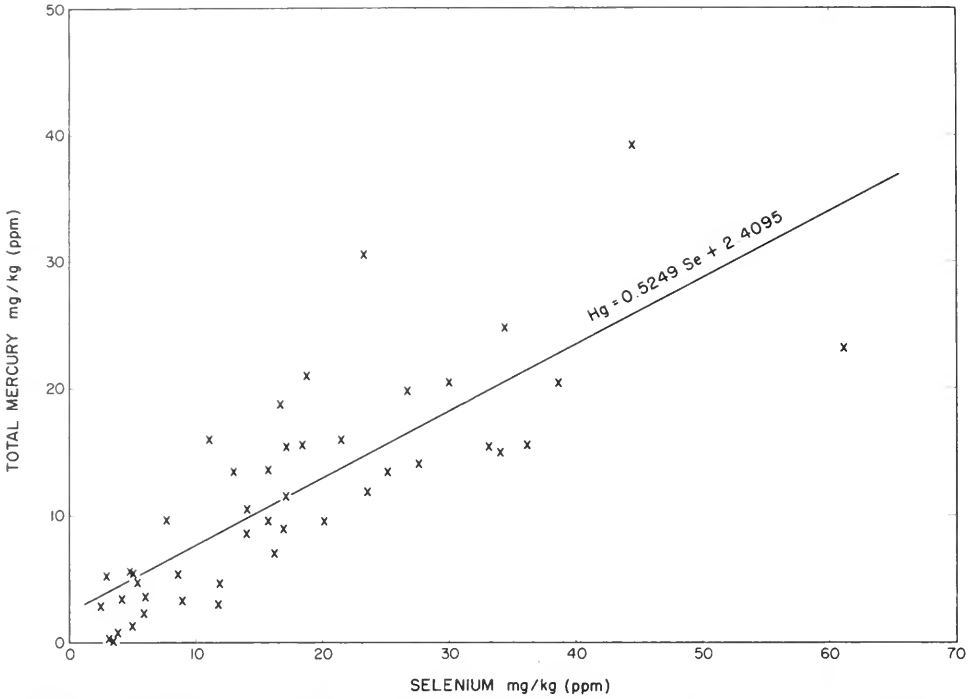


FIGURE 5.—Relationship between total mercury and selenium in liver of 46 blue marlin from the Hawaiian Islands.

Concentration through the food chain is apparently the reason for the elevated levels of mercury found in the marlin. Stomach contents examined in 76 blue marlin captured in 1973 showed that the most common food items were tuna, mostly *Katsuwonus pelamis* (38% occurrence); mackerel scad, *Decapterus pinnulatus* (36%); squid (21%); spiny puffer, Diodontidae (19%); and dolphin, Coryphaenidae (12%) according to Naughton (see footnote 1).

Mercury levels were reported for yellowfin tuna, *Thunnus albacares*, 0.54 mg/kg; skipjack tuna, *K. pelamis*, 0.38 mg/kg; and for dolphin, *Coryphaena hippurus*, 0.25 mg/kg; by Rivers et al. (1972). These are pelagic species and as such, are exposed to the same amount of mercury in their physical environment; yet all have mercury levels nearly an order of magnitude less than that of the marlin. In addition, their mercury content was essentially all methyl mercury.

If most of the mercury entered the marlin via the food chain as methyl mercury it would seem that demethylation to inorganic mercury had occurred. Conversion of methyl mercury to inorganic mercury has been shown to occur in bluegill (Burrows and Krenkel 1973) and in rats (Norseth and Clarkson 1970).

It is indicated in Figure 1 that the mercury is accumulated with size but at different rates for males and females. This observation contrasts with previous year's results in which no sex-related concentration disparities were found (Shultz and Crear 1976; Shultz et al. 1976). The reason for this year's anomaly is unclear and not enough information is available to determine if we are dealing with more than one population.

Selenium levels in the marlin are presented in Table 1 and show an increase with weight and age (Figure 2). The high correlation of mercury and selenium with weight (Table 2), and the observation that selenium modifies the activity of mercury in experimental animals, indicate that they are highly correlated with each other, as is seen in Figures 3-6. The precise nature of the mercury-selenium interaction is not known, although a number of suggestions have been advanced. Pařízek et al. (1971) demonstrated with rats that the protective effect of selenite against mercuric chloride was not related to an increase in mercury excretion but to a decrease, resulting in a change

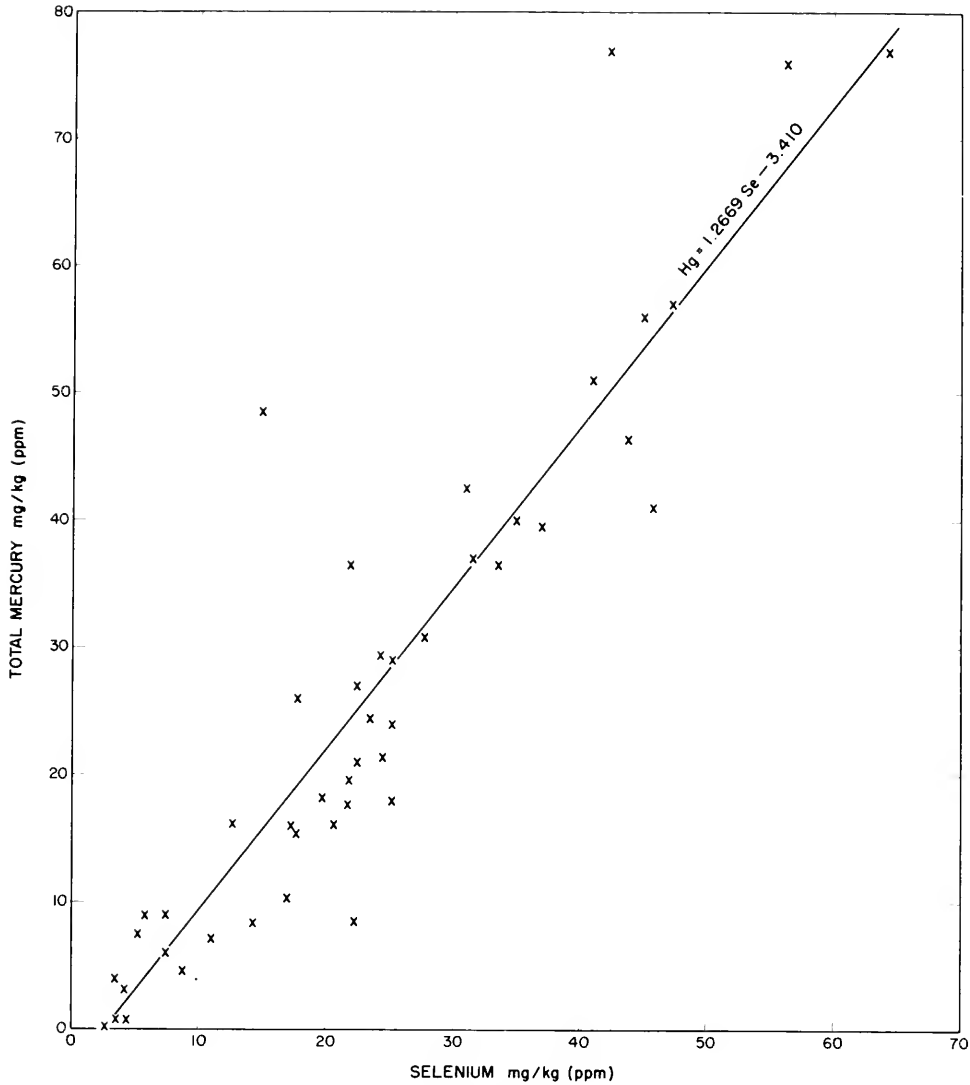


FIGURE 6.—Relationship between total mercury and selenium in kidney of 46 blue marlin from the Hawaiian Islands.

in organ distribution of mercury. The kidneys and intestines lost mercury while the testes gained mercury relative to the controls. In addition, mercury in the macromolecular fraction of blood plasma increased after addition of selenite. Burk et al. (1974) found a similar increase of mercury in plasma protein when mercuric chloride was administered simultaneously with selenite. This was not the case when mercuric chloride or selenite was injected alone. Their experiments using dialysis of rat plasma protein indicated that selenium and mercury are bound in a 1:1 molar ratio to a single protein, with selenium attached to the protein through a sulfhydryl group and mercury attached to the selenium. They also observed a time lag after injection of selenite before detection of protein binding during which the selenite was apparently metabolized to another form. Lunde (1970) has found selenium to be associated also with proteins in marine organisms.

The molar ratio of average total mercury to average selenium in muscle is 0.62. Subtracting the methyl mercury to obtain inorganic mercury (Schultz and Crear 1976), the ratio reduces to 0.54.

Ganther et al. (1972) reported that the mercury to selenium molar ratio for high-mercury tuna (can tuna) (average 2.87 mg/kg) approaches 0.5. They also noted that the mercury and selenium increments between low-mercury tuna (0.32 mg/kg) and high-mercury tuna were about in a 1:1 molar ratio, implying they are accumulated together.

The total mercury-selenium relationships observed in marine mammals and man are similar to those found in tuna. Koeman et al. (1973) found a 1:1 molar ratio in the livers of seals, *Phoca vitulina*, porpoises, *Phocoena phocoena*, and dolphins, *Tursiop truncatus*, *Delphinus delphis*, *Lagenorhynchus obscurus*, and *Sotalia guianensis*. Regression analyses of their data give an average slope of 2.7 ± 0.2 or 1.1 ± 0.1 on a molar basis for mercury-selenium interactions ($r = 0.932$). Interestingly, they found that only 2 to 14% of mercury in the liver and 2 to 13% in the brain was recovered as methyl mercury. Post-mortem studies on humans exposed to high inorganic mercury (from a mercury mine) showed a 1:1 molar ratio of mercury to selenium ($r = 0.998$) in tissues which had accumulated high amounts of mercury, i.e., thyroid, pituitary, kidney, and brain (Kosta et al. 1975). They noted, however, that this ratio did not exist for a nonexposed group in which mercury and selenium levels were insignificant. Elevated mercury levels were apparently responsible for increasing the selenium concentrations such that, in many cases, the molar ratio of mercury to selenium increments over normal levels approached 1:1 (selenium was low in the mine environment: 1 mg/kg versus 100 mg/kg Hg—in contrast to the relative enrichment of selenium in the diet of tuna and marine mammals). The levels of methyl mercury in organs of the exposed group were low, implying that no significant in vivo methylation occurs in man.

Because selenium is high in the marlin (average 1.98 mg/kg in muscle, 17.47 mg/kg in liver, 23.42 mg/kg in kidney), the possibility of selenium toxicity should not be discounted. Aptly, though, mercury has been shown to mitigate the toxicity of selenium in rats and chicks (Parízek et al. 1971; Hill 1974).

In an earlier study, it was indicated that cooking did not remove either methyl or total mercury from marlin fillets (Schultz and Crear 1976). Higgs et al. (1972) have found that baking does not remove selenium from flounder or chicken although some loss was reported from boiling two vegetables. It does appear then that mercury (muscle average 3.12 mg/kg) and selenium (muscle average 1.98 mg/kg) concentrations in raw fillet are representative of that in cooked fish.

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RECENT RECORDS OF *CALLINECTES DANAE* AND *CALLINECTES MARGINATUS* (DECAPODA: PORTUNIDAE) FROM NORTH CAROLINA WITH ENVIRONMENTAL NOTES

Temperature and latitudinal distributions of the genus *Callinectes* are best known for *C. sapidus* Rathbun (Williams 1974; Norse 1977). The northern limits of *C. danae* Smith and *C. marginatus* A. Milne Edwards are listed as Bermuda and southern Florida, with one specimen of *C. marginatus* from North Carolina regarded as a temporary range extension (Williams 1974). We report the taking of two specimens of *C. danae* and six specimens of *C. marginatus* by 12.2-m (40-ft) otter trawl in and near the Cape Fear River estuary, N.C. All specimens have been deposited at the Institute of Marine Sciences, University of North Carolina, Morehead City, N.C. Measurements listed are of carapace width in millimeters including lateral spines.

Two specimens of *C. danae* (UNC 2766, ♂ 115; ♂ 113), 1 *C. marginatus* (UNC 2765, ♂ 97), 6 *C. ornatus* Ordway, and 7 *C. similis* Williams were captured by trawl in the Intracoastal Waterway on 19 September 1977, just south of the Carolina Beach Inlet, on a sand-shell bottom 4 m deep in water of 36‰ surface salinity and 26°C. Four *C. marginatus* (UNC 2763, ♀ 92; ♂ 103; ♂ 62; ♂ 81) were also caught at this location on 14 September 1977, along with 30 *C. ornatus*, 35 *C. similis*, and 10 *C. sapidus*. Bottom salinity was 20‰, and bottom temperature was 26.5°C. Several other small specimens of *C. marginatus* (40-60 mm) were observed, but not retained in this trawl. A sixth specimen of *C. marginatus* (UNC 2764, ♀ 91), 1 *C. ornatus*, 30 *C. similis*, and 20 *C. sapidus* were collected in the intake canal of the Carolina Power and Light Company generating plant in the Cape Fear River estuary west of buoy 19 on 11 October 1977. Bottom type was silty-sand at depth of 4 m. Surface salinity was 31‰ and surface water temperature was 17°C.

The present record of *C. danae* represents a northward range extension of 1,000 km, from Biscayne Bay, Fla., to the Cape Fear River. Williams (1974) noted that it occurs in a wide range of salinities and habitats. However, Norse (1977) believed *C. danae* prefers lower salinities, from studies in the Caribbean.

The six specimens of *C. marginatus* bring the total recorded in North Carolina and north of southern Florida to seven. Shallow environments over a wide range of substrates are preferred in a salinity range of 19-32‰ and temperature range of 22°-30°C (Williams 1974). Norse (1974) has inferred a preference for higher salinities by *C. marginatus*; note, we obtained four of the six specimens at 20‰ and a fifth was captured inside the Cape Fear estuary where salinities fluctuate widely.

Callinectes danae, *C. marginatus*, and *C. ornatus*, with the exception of two specimens of the latter from Charleston, S.C., are now recorded from Florida, North Carolina, and Bermuda. Another species which occurs in Florida and Bermuda, *C. exasperatus* Gerstaecker, has yet to be taken in

North Carolina. The northerly distribution for these species may be indicative of larval transport patterns via currents, i.e., Gulf Stream (Williams 1974). Another significant element, as proposed by Norse (1977), is the presence of summer temperatures in excess of 20°C required for the hatching of eggs and larval development.

Acknowledgments

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ANALYSIS OF CHLORINATED HYDROCARBON POLLUTANTS: A SIMPLIFIED EXTRACTION AND CLEANUP PROCEDURE FOR FISHERY PRODUCTS

Fishery scientists wishing to quantitate chlorinated hydrocarbons find a multitude of methods only marginally appropriate to the routine analysis of marine fishery products. This paper is a laboratory manual, delineating details of a simple, rapid, and reliable method for the extraction and cleanup of samples of fish, fishery products, and paper for analysis of chlorinated hydrocarbons, such as PCB,[1] dieldrin, and DDT and its metabolites TDE and DDE. The procedures can be adapted to a great variety of sample types. The method is economical since small amounts of solvents are used and the equipment and glassware are relatively inexpensive and readily available.

Chlorinated hydrocarbon analysis in marine fishery products is an extremely complex procedure requiring extensive knowledge and many years of experience to perfect. A number of specialized problems, uncommon in the preparation of foodstuffs and freshwater fish for analyses of chlorinated hydrocarbons by the established methods, occur during the isolation of such materials from marine fish and fishery products. For example, the official method of the Association of Official Analytical Chemists (Horowitz 1970; Porter et al. 1970) often requires 1½ days for the initial extraction of marine fish oil because of intractable emulsions. After purification, the final extracts still contain substances which cause the rapid loss of sensitivity of the electron-capture detector and decomposition of the column packing in the gas-liquid chromatographic system. The procedure described in this paper eliminates extraction of fish oil and provides final extracts freer of extraneous substances. In the course of analyzing over 2,000 samples we have found it suitable for routine analysis of marine fishery products.

The method was first developed by Robert Reinert (Reinert 1970; Snyder and Reinert 1971). We have refined it to maximize recovery of chlorinated hydrocarbons and have adapted it to new types of samples, such as fishmeal and carbonless carbon paper. We have described the procedure in detail because of the ultimate purity and freedom from unanticipated contaminants required of extracts for gas chromatography with an electron-capture detector. Data from samples of typical fishery products analyzed by us using the methods described in this paper were comparable to the data obtained by a number of other laboratories[2] following their usual procedures.

Preliminary Information

The accuracy and precision of analyses for chlorinated hydrocarbons are assured only if careful attention is given to the procedural details and the time factors involved in the various steps.

[1]Abbreviations used in this paper: DDE—*p, p'*-dichlorodiphenyldichloroethylene; DDMU—*p, p'*-dichlorodiphenylchloroethylene; DDT—*p, p'*-dichlorodiphenyltrichloroethane; IPA—isopropyl alcohol; PCB—polychlorinated biphenyls (Aroclor 1254 was used as the standard for PCB); and TDE—*p, p'*-dichlorodiphenyldichloroethane. The *o, p'*-isomers of DDT and its metabolites act similarly to the more common *p, p'*-isomers used here.

[2]See Acknowledgments for the list of laboratories.

Time

For a set of eight samples: Extraction of oil, none; extraction of other samples, 4 h (or less); cleanup, 1 h; separation of DDT and PCB, 4 h; and transfer and dilution of samples for gas-liquid chromatography, 1-2 h.

Reagents

Analytical standards: U.S. Environmental Protection Agency, Health Effects Research Laboratory, Environmental Toxicology Division, Research Triangle Park, N.C.

Aroclor[3]1254: Monsanto Company, St. Louis, Mo. (Aroclor 1254 was used as the analytical standard for PCB because it represented the PCB most typically found in our samples. Snyder and Reinert (1971) tested both Aroclor 1254 and Aroclor 1260. The suitability of the procedure for PCB of other degrees of chlorination would need to be verified.)

Sodium sulfate: anhydrous, reagent grade. If the blank indicates the sodium sulfate is contaminated, rinse with petroleum ether or hexane and dry before use.

Solvents: distilled-in-glass grade, Burdick & Jackson, Muskegon, Mich. (The suitability of other "pesticide" or "nanograde" solvents would need to be determined.)

Florisil: 60/100 mesh P.R. grade, Floridin Company, Pittsburgh, Pa. Store in the dark in tightly closed, screw-cap, flint glass jars, and use without further activation.

Silica gel: grade 950, 60/200 mesh, desiccant, Davidson Division, Grace Chemical Company, Baltimore, Md. (The performance of other silica gels would have to be evaluated.)

Carborundum chips: 16 mesh. Use as a boiling aid in all evaporation steps. (Whenever ebullition is interrupted, new chips are necessary.)

Aluminum foil: domestic grade.

Teflon wash bottles: Nalgene Co., Rochester, N.Y. Use for adding small amounts of solvents in the boildown and chromatographic procedures. Discard the contents of the wash bottle if left longer than a day.

Glassware

Glassware: borosilicate (DDT and TDE decompose on contact with flint glass).

Glass wool: borosilicate fiber glass, Corning 3950 or equivalent. Use directly from the package.

Graduated centrifuge tubes: 50-ml, Kimax 45164 or equivalent, and stoppered 13-ml, K-410550, Kontes Glass Co., Vineland, N.J., or equivalent.

Modified micro Snyder column: Kontes K-569251 or equivalent.

Chromatographic columns: 7 mm i.d. × 150 mm and 9 mm i.d. × 150 and 250 mm glass tubing. (All tubes are without stopcocks.)

Storage bottles: 23-ml screw-cap, borosilicate specimen bottles, Prescription Containers, Inc., Brooklyn, N.Y., with Teflon cap liners, 2390-H62, Arthur H. Thomas Co., Philadelphia, Pa.

Pipettes: Class A. Use for preparation of standards.

Pipettes: disposable glass. Use for quantitative dilution and transfer of samples.

Pipettes: disposable glass, Pasteur capillary, Kimax 72000 or equilavent. Use for sample transfer. (Disposable pipettes are preferred for handling samples in order to eliminate cross contamination.)

Equipment

Virtis homogenizer: Macro, Model 23 or 45, with stainless steel blades, Teflon cap, and 10-50 ml glass homogenizer flasks (No. 16-207), Virtis Co., Gardiner, N.Y., or equivalent. (Bearing lubricants contaminate samples.)

Tube heater: Kontes K-720000. (It is convenient for evaporating solutions in 13-ml centrifuge tubes.)

Plastic and Rubber

Avoid materials, such as gloves, flexible tubing, and polyethylene bags, which often contain PCB or substances which interfere with quantitation by gas chromatography with an electron-capture detector. (Teflon is the only plastic suitable for these analyses.) Wrap samples in aluminum foil for shipment to the laboratory.

Washing Procedure

Chlorinated hydrocarbons and some of the substances in samples adhere tenaciously to glassware. To prevent contamination of future samples, rinse glassware with an organic solvent immediately after use, and then soak in water until washing.

[3]Mention of trade names or companies does not imply endorsement by the National Marine Fisheries Service, NOAA.

Wash all glassware (and spatulas) in the hottest water practical and rinse thoroughly also with very hot tapwater. (Unless an all-glass still and piping system is available, tapwater is preferable to distilled water because stills often contain plastic tubing and sealing compounds containing PCB.) Bake glassware overnight at 225°-250°C to reduce residual contamination. Cover glassware with aluminum foil. Rinse 3-5 times with petroleum ether or hexane immediately before use. Keep containers covered with foil or stoppers except during evaporation or chromatography to exclude dust, etc.

Procedure For DDT and PCB

The details in time and quantity of chemicals are given only as general guidelines. The exact parameters of these procedures vary with ambient temperature, humidity, altitude, etc. They must be adjusted in each laboratory to optimize recovery, cleanup, and separation of desired components.

Caution

All procedures involving benzene must be performed in a well-functioning hood.

Blank

Carry out the complete procedure as described below without any test sample (omit step 1 under Extraction) to assure that the blank is substantially below the level to be determined. Evaporate the final solutions to 2 ml and quantitate the residues, typically <0.001 ng/μl DDT, TDE, and DDE and <0.01 ng μl PCB. (Incompletely washed glassware and new batches of reagents are common sources of high blanks.)

Recovery

Carry out the complete procedure with solutions of standards of known concentration in the range anticipated for the samples to assure quantitative recovery. (Some loss of chlorinated hydrocarbons always occurs in the absence of proteins and lipids, which act as keepers. A minimum recovery of 80% is essential. Doping samples originally containing very low levels of chlorinated hydrocarbons gives results which better reflect the accuracy of the method: 85% or higher recovery of DDE, TDE, DDT, and PCB, and 80-85% recovery of dieldrin and endrin.)

Extraction

1) Weigh approximately 10 g of the material (see Procedure Variations for exceptions), to be analyzed into a Virtis flask and record exact weight to the desired degree of accuracy.

2) Add 20 ml of a 1:1 IPA/benzene mixture to the flask.

3) Homogenize at about 23,000 rpm for 5 min.

4) Rinse homogenizer blade and Teflon cap with hexane so that the hexane drips into the Virtis flask. Fill the flask with hexane nearly to the bottom of the flask neck.

5) Place the Virtis flask in a hot-water bath (ca. 85°C) or sand bath. (An electric fry pan with a layer of sand covered with water provides an economical heating bath.) Boil moderately for at least 45 min, adding hexane whenever the level falls to about one-third of the flask capacity. (If the solution boils too rapidly, material will be lost in the spray. The rate of boiling must be adequate to distill all the H_2O, IPA, and benzene from the flask, because they interfere with the cleanup.) When adding hexane, do it so as to rinse down the sides of the flask as well. Keep the water level in the bath and the hexane level in the flask adjusted so that the flask does not become buoyant and tip over. After 45 min of boildown, reduce the volume of the solution to about 20 ml (ca. 1 cm from the bottom of the flask). Cool. If a layer of water separates, add Na_2SO_4 and allow to stand 1-3 min.

6) Filter through a funnel plugged with glass wool into a 50-ml graduated centrifuge tube. Rinse the flask with three or four 5-ml portions of hexane and pour the rinse solutions through the filter into the centrifuge tube.

7) Concentrate the extract in a hot-water bath to desired volume (20-25 ml), record volume, and pour most of extract into a 23-ml borosilicate screw-cap bottle (with Teflon-lined cap) containing 1 g Na_2SO_4. (The extract can be stored in this condition for extended periods.) (If the extract, prior to concentration, still contains traces of H_2O or IPA, as indicated by cloudiness, add hexane while concentrating in order to remove the H_2O or IPA.)

Oil Determination

8) Pipette exactly 1 ml of the extract into a tared aluminum weighing dish and allow it to

evaporate 4-6 h at room temperature to minimum weight. (Since marine oils oxidize, the weight of oil begins to rise again after a few hours.) Weigh the residue, which contains the oil in 1 ml of extract.

Cleanup

9) Prepare a Florisil column by filling a 9 mm i.d. × 150 mm glass tube, plugged with glass wool, with ca. 5 cm of Florisil. Wash the column with at least 15 ml of hexane added 1 ml at a time. Allow the hexane level to drop to 1-2 mm, but not to dryness. Pipette 1 ml of the extract onto the column. For samples with very high oil content (refer to step 8 for the amount of oil in 1 ml of the extract), adjust the volume placed on the Florisil so that no more than 0.1 g, and preferably no more than 0.08 g, of oil is placed on the Florisil. Elute with 1-ml portions of hexane; collect the first 12-13 ml of the eluate in a 13-ml graduated centrifuge tube. (Note: Once the Florisil has been wetted, it must always have solvent above it.)

10) If DDT and PCB are not going to be separated, concentrate (in a tube heater) the eluate to an appropriate volume for gas-liquid chromatographic analysis.[4] If separating DDT and PCB, evaporate the eluate to slightly less than 1 ml.

Separation of DDE, TDE, and DDT from PCB

Quantitation of TDE and DDT is often difficult and quantitation of the PCB is usually impossible unless the DDT family is separated from the PCB. Separation is achieved by chromatography on silica gel. The behavior of DDT and PCB during solid-liquid chromatography is very similar, and obtaining optimal separation requires careful control of all the parameters of the procedure. Even so, DDE does not separate entirely from PCB. Therefore, the DDE in the PCB fraction is quantitated[5] and included with that in the DDT fraction.

Evaluate the degree of separation of DDE, TDE, and DDT from PCB by chromatographing standard solutions of these compounds according to the procedure described below. Adjust the time and temperature of activation, the degree of rehydration, the amount of silica gel, and the volume of the pentane fraction to obtain the optimum separation of DDT and TDE from PCB; that is, to maximize the amount of PCB in the pentane fraction and the amount of DDT and TDE in the benzene fraction.

11) Activate the silica gel by heating at 215°C for 16 h. (The time and the temperature are adjusted to obtain an arbitrarily, but consistently activated product with suitable separating characteristics, since complete dehydration occurs over a long period of time.) Cool to room temperature in a desiccator. Rehydrate by placing 98 g silica gel in a glass-stoppered bottle and adding 2 g distilled water. Stopper the bottle and shake and tumble until the water is evenly distributed. Allow the silica gel to equilibrate for 2-4 h before use.

12) Place a portion of this prepared silica gel in a beaker and cover with pentane. Let stand 5-10 min to return to room temperature. (Because the chromatographic columns do not contain stopcocks, a special technique is required for packing.) Quickly transfer silica gel to a glass-wool-stoppered column, 9 mm i.d. × 250 mm long, wet with pentane. (A disposable transfer pipette with the narrow part of the tip removed works quite well for transferring the silica gel slurry.) Tap the column gently to facilitate packing. Make sure that there is always enough pentane above the column to allow the silica gel to settle slowly in order to eliminate air bubbles and prevent the top of the column from running dry. Pack the column to a height of ca. 8 cm. (Throughout the whole separation procedure the silica gel must always have solvent above it and must be free of bubbles and cracks, which interfere with the desired separation. If the column runs dry or cracks, discard it.) Rinse the column with 15-20 ml of pentane.

13) Allow the pentane level to descend to 1-2 mm (not dry) and place the Florisil eluate (ca. 1 ml) on the column with a Pasteur capillary pipette. Rinse the Florisil eluate tube with three or four 1-ml portions of pentane, and transfer each rinse successively to the column. After the sample and rinses have been adsorbed, fill the tube with

[4]For a detailed description of gas chromatography of chlorinated hydrocarbon pollutants, see the Pesticide Analytical Manual (1977), available from Management Methods Branch, DMS, ACA, HFA-250, 5600 Fishers Lane, Rockville, MD 20857, or National Technical Information Service (NTIS), Springfield, Va. The manual provides extensive background on residue analysis.

[5]Although DDE elutes from the gas-liquid chromatograph at the same time as one of the PCB peaks, measurement of the other five intense PCB peaks provides accurate quantitation of PCB. Use the amount of PCB in those peaks to determine the size of the peak overlapping the DDE and correct the apparent total DDE (actually DDE plus PCB) to obtain the true DDE concentration. The electron-capture detector is so much more sensitive to DDE than PCB, that the correction affects the accuracy of DDE determination only to a small extent. Consequently the variability in amount of DDE in the pentane fraction does not markedly affect the accuracy of DDE analysis.

pentane. Collect 42 ml of pentane eluate in a 50-ml graduated centrifuge tube. (This fraction contains PCB and some DDE.)

14) After the appropriate volume of pentane eluate has been collected, place a second 50-ml graduated centrifuge tube under the silica gel column. Then fill the tube with benzene. Collect 35 ml of benzene eluate. (This fraction contains most of the DDT complex.) (DDE elutes very rapidly with benzene. If benzene is added to the column before the second centrifuge tube is in place, the DDT complex will often be found in the pentane fraction.)

15) Concentrate each fraction in a boiling water bath to less than the desired final volume and quantitatively transfer with hexane to a volumetric flask of the desired final volume. (The 50-ml centrifuge tubes are not very accurate volumetric containers.) Proceed with gas-liquid chromatographic analysis (see footnote 4).

Notes on DDT/PCB Separation Procedure

1) Elution with hexane instead of pentane during the silica gel chromatography fails to provide the necessary separation of DDT from PCB. Hexane is reported to contain variable amounts of benzene, which would obviously affect an already delicate separation. Use of UV-quality pentane or hexane has been recommended by others, and might allow use of hexane in warm weather.

2) For high residue level samples, evaporation of the Florisil eluate to ca. 1 ml is not necessary; instead an appropriate aliquot is used. However, no more than 1 ml of the eluate should be placed on the silica gel column because the hexane may contain benzene.

Procedure Variations

Plankton and Other High-Moisture Samples

Plankton do not homogenize well using the standard procedure. They also contain water in excess of the amount that 20 ml of 1:1 IPA/benzene can absorb. Addition of Na_2SO_4 before homogenization overcomes both difficulties. Na_2SO_4 not only absorbs water, but also serves as a grinding aid.

To the weighed sample of plankton add 25 ml of 1:1 IPA/benzene; then add 25 ml hexane and 10-15 g Na_2SO_4. Homogenize 5 min and proceed as usual.

During the 45-min boildown, scrape the material on the bottom of the flask. Pile up the solids to leave areas of the flask bottom in direct contact with the solvent to improve boiling action and prevent bumping. Cool. If water separates, add Na_2SO_4.

Filter through glass wool and proceed as usual (step 6 under Extraction).

In order to compensate for the low residue level usually found in plankton, place 2 ml of the extract on the Florisil column for cleanup.

Fishmeals or Dry Feeds

If the standard extraction procedure is used for meals and animal feeds, the finely ground meal forms a layer on the bottom of the Virtis flask which causes bumping and loss of solvent during the 45-min boildown. Extraction with hexane provides as good recovery as IPA/benzene. This substitution allows omission of the boildown.

1) Homogenize sample with 20 ml of hexane. Wash down Virtis blades and Teflon top with minimal amount of hexane. Add 10 g Na_2SO_4.

2) Immediately filter through glass wool tightly wadded to remove as much of the solids as possible. Wash flask and funnel with a minimal amount of hexane so that the volume of the centrifuge tube is not exceeded (35-40 ml).

3) Stir to mix and centrifuge at 1,500 rpm for 45-60 min at 10°C. (There should be about 35 ml of clear solution with less than 1 ml of solids.)

4) Record volume, subtracting 50% of the volume occupied by the solids. (Although this involves an approximation, the error involved should be no more than 2%.)

5) Decant the supernatant liquid into a storage bottle containing 1 g Na_2SO_4. Proceed with Florisil cleanup (step 9 under Cleanup).

Fish Oil

Homogenization and extraction of oil are unnecessary.

1) On an analytical balance weigh accurately about 2 g of oil into a 50-ml graduated centrifuge tube.

2) Dilute to about 20 ml with hexane and swirl to dissolve the oil completely.

3) Record the volume.

4) Place in a storage bottle, containing 1 g Na_2SO_4, and proceed with the usual cleanup (step 9 under Cleanup).

NOTE: For greater accuracy in oil analysis, weigh accurately about 2.0-2.5 g oil into a 25-ml volumetric flask. Dilute to volume with hexane. Shake thoroughly. Place sample in storage bottle and proceed at step 9 under Cleanup.

Paper

This procedure is included because occasionally fishery samples come in contact with contaminated packaging and labelling materials, such as carbonless carbon paper and cardboard. Although the procedure has not been validated by collaborative studies, it provides guidelines for an analysis relevant to fishery studies.

Cut the paper (or cardboard) into small pieces, approximately 1 cm on a side, with a scissors or office paper cutter, which has been cleaned thoroughly with iso-octane or hexane. Mix the paper thoroughly and weigh ca. 7 g into a Virtis flask. Add 15 ml distilled water and mix thoroughly with the paper. Allow the mixture to stand 2-5 min, stir again, and dilute with portions of 1:1 IPA benzene to a total of 70 ml. Homogenize the mixture briefly at low speed. Push the paper down with the Virtis blades, then homogenize briefly. Repeat the process until the paper is completely homogeneous, approximately 10 min total homogenization time. Follow the usual boildown and Florisil procedures.

Procedure For Dieldrin and Endrin

Saponification[6] and Extraction

1) Weigh 10 g of material to be analyzed into a 250-ml Erlenmeyer flask. For oil, use only 2 g.

2) Dissolve 10 g of KOH in 6 ml distilled water. Slowly dilute with 34 ml of ethyl alcohol (95 or 100%). Swirl until clear.

3) Pour the alcoholic KOH over the sample and heat in a water bath without boiling for 20 min; the exact temperature is not critical.

4) Allow the mixture to cool. Pour the liquid portion into a 250-ml separatory funnel and rinse out the Erlenmeyer flask with 50 ml of water, divided into 4 or 5 portions. Avoid pouring any solids into the separatory funnel. For finely powdered samples like meal, filter the sample through a wad of glass wool and rinse the glass wool carefully with each rinse.

5) Add 15 ml hexane to the separatory funnel and shake for 2 min. Open the stopcock several times during shaking to relieve the pressure buildup. Allow the layers to separate completely, usually about 30 min.

6) Drain off the aqueous layer into the Erlenmeyer flask from which it came. Pour the hexane layer into a 30-ml beaker. Do not let any water escape into the beaker. Cover the beaker tightly with aluminum foil.

7) Pour the aqueous layer back into the separatory funnel and repeat step 5.

8) Drain off the aqueous layer and discard it.

9) Return the hexane extract in the beaker to the separatory funnel. Rinse the sides of the beaker with 1 ml hexane. Add the hexane wash to the extract in the separatory funnel.

10) Wash the hexane extract with 10 ml water by rotating the separatory funnel gently to avoid emulsion formation. *Do not shake.* Allow the layers to separate and discard the aqueous layer.

11) Pour the hexane layer into a 50-ml graduated cylinder. Do not transfer any water to the cylinder. Record the volume. Pour the extract into a 23-ml borosilicate screw-cap bottle (with Teflon-lined cap) containing 1 g Na_2SO_4.

Cleanup

12) Prepare a Florisil column by filling a 9 mm i.d. × 150 mm glass tube, plugged with glass wool, with ca. 4 cm of Florisil. Or use a 7 mm i.d. × 150 mm tube containing ca. 5 cm of Florisil. (The longer column of adsorbent may give slightly better cleanup.) Wet the Florisil with benzene and wash it with 4 to 5 ml benzene added 1 ml at a time. Wash it next with 10 ml hexane (or more) added 1 ml at a time. Pipette 2 ml of the hexane extract onto the column. Put a 12-ml graduated centrifuge tube under the column. Elute with hexane added 1 ml at a time. Collect the first 12 ml of hexane eluate, which contains DDMU (the dehydrochlorination product of TDE), DDE, and PCB. (They may be quantitated if desired.)

Place a second 12-ml centrifuge tube under the column. Change eluant to benzene; add it 1 ml at a time. Collect the first 10 ml of eluate. Place a modified micro Snyder column on the centrifuge tube to prevent loss of residues during evaporation. Concentrate the eluate containing dieldrin and endrin to an appropriate volume (1-3 ml) for

[6]Saponification in the presence of some proteinaceous materials has been reported to cause degradation of dieldrin. As stated above, recovery studies are always important.

gas-liquid chromatographic analysis (see footnote 4).

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GROWTH OF JUVENILE SPOT PRAWN, *PANDALUS PLATYCEROS*, IN THE LABORATORY AND IN NET PENS USING DIFFERENT DIETS

Floating net pens have been used to culture Pacific salmon, genus *Oncorhynchus*, in the marine waters of the West Coast since 1969 (Mahnken 1975). Although it has been a monoculture effort to date, use of a companion crop species such as the spot prawn, *Pandalus platyceros* Brandt, could diversify and enhance this industry.

In 1975 the National Marine Fisheries Service selected the spot prawn to examine as a potential companion species to net pen-reared salmon. The spot prawn was selected as a candidate for several reasons: 1) it has a rapid growth rate and large size compared with other pandalids (Butler 1964); 2) it can be successfully cultured to maturity in captivity (Prentice 1975); 3) it will reproduce in captivity, often for two consecutive years (Rensel and Prentice 1977); 4) it is gregarious and is normally not cannibalistic; 5) it adapts to vertical or horizontal substrates; and 6) it scavenges for, and accepts, a wide variety of foods (Wickins 1972).

Coincident to investigating the prawn as a companion crop to salmon, several prawn diets were evaluated with prawns held in tanks and net pens at the NMFS Aquaculture Experiment Station on Puget Sound near Manchester, Wash. These experiments were conducted using diets made up of underutilized marine species or fishery byproducts that are available to most salmon farmers.

Materials and Methods

The spot prawns used in the experiments were laboratory-reared progeny of females captured in Hood Canal, Wash. Three concurrent experiments with juvenile prawns (<1 yr of age) began 10 July 1975 (Table 1).

Experiment A was conducted in the laboratory where prawns were held in flowing seawater tanks at 110 animals/m^2 of immersed substrate. Four diets were evaluated: 1) steamed mussel, *Mytilus edulis*, meat; 2) chopped salmon that had died in nearby net pens; 3) feces and pseudofeces from the Pacific oyster, *Crassostrea gigas* (eight oysters per replicate having a mean weight (total) of 153 g); and 4) no food (control). Diets 1 and 2 were fed every other day while diet 3 was always present in varying amounts. A sample of 10 prawns for each of four replicates was measured during each of

TABLE 1.—Growth and survival of juvenile *Pandalus platyceros* during three tests.

Experiment	Location	Diet	No. of replicates	Start of experiment: No. of prawns in each replicate	Start of experiment: Mean weight (g)	60 days after start of experiment: Mean survival (%)	60 days after start of experiment: Mean weight (g)	End of experiment: No of days	End of experiment: Mean survival (%)	End of experiment: Mean weight (g)
A (prawns alone)	Laboratory tanks	Mussel	4	25	0 72	82	2 52	90	74	3 14
		Salmon	4	25	0 62	83	2 27	90	71	2 61
		Oyster wastes	4	25	0 69	64	1 06	(1)	(1)	(1)
		No food	4	25	0.64	26	1 07	(1)	(1)	(1)
B (prawns alone)	Net pens	Mussel	2	200	0 64	98	3 14	365	69	10 30
		Salmon[2]	2	200	0 63	98	2 79	365	64	10 61
C (prawns and salmon)	Net pens	Variety of feeds[3]	1	100	0 64	93	3 42	206	93	8 60

[1]Terminated at 60 days.
[2]Includes net-fouling organisms.
[3]Includes salmon mortalities, uneaten fish feed (Oregon moist pellets), salmon feces, and net-fouling organisms

three 30-day sampling periods. Carapace lengths[1] and individual wet weights (nonblotted) were measured to the nearest 0.5 mm and 0.01 g, respectively. In all experiments growth data were analyzed by one-way analysis of variance and survival by chi-square tests.

In Experiment B, prawns were held in two net pens measuring 1.2 × 1.8 × 1.8 m and constructed of knotless nylon web (6.8-mm stretched measure mesh). Each pen was vertically divided into three equal compartments (6.5 m^2 of substrate each) with only the outer two being stocked with prawns. The prawns were stocked at a density of 30.8/m^2 of immersed substrate. The net pens were covered with black plastic to prevent bird predation and to reduce light intensity. Two dietary treatments were evaluated, mussel meat and salmon. Each treatment consisted of two replicates and was fed exclusively on one of the two diets. Feed was to excess every other day.

A sample of 50 prawns/replicate (100/treatment) was measured for length and weighed during each of eight sampling periods, except during the last three periods in which all survivors were measured and weighed. The prawns were sampled at the beginning of the experiment and 32, 60, 88, 146, 205, 292, and 365 days later.

In Experiment B, in addition to evaluating the diets, we studied the net cleaning ability of the prawns and the value of the organisms on the net (i.e., the net fouling organisms) as a supplementary food source. Samples of net fouling organisms were taken from inside and outside of a compartment containing prawns (test) and inside and outside of one not containing prawns (control). The nets were selected at random, and each sample consisted of all the organisms on the net within the area of two 20-cm-diameter circles; one circle was at 0.25-m depth, and the other was at 1.0-m depth. The material collected was identified, enumerated, and measured volumetrically. The nets were sampled during November 1975 and March 1976.

In Experiment C, juvenile prawns were stocked in a net pen with coho salmon, *Oncorhynchus kisutch*, (age-group 0) that averaged 20 g each. A single net pen (without dividers) having a substrate area of 10.8 m^2 was used. Prawn density was 9.3/m^2 of substrate, and salmon density was 82 m^3 of water. The salmon were fed Oregon moist pellets at 3% body weight/day; however, no feed was provided for the prawns other than what they could scavenge. All the prawns were measured at each of seven periods: at the beginning of the experiment and 15, 33, 60, 89, 146, and 206 days later.

Care was taken to standardize culture conditions such as lighting, substrate type, and water temperature within each experiment. This was not practical between experiments because of inherent differences between laboratory and net pen work.

Stocking density differed between experiments, but its impact on growth and survival (agnostic behavior and feeding dominance) was minimized by distributing an excess of food throughout the rearing enclosure. In several years of behavioral observations we have rarely seen overtly agressive or cannibalistic behavior in spot prawns.

Results and Discussion

Mussel-fed juvenile prawns had the best survival and growth rate of all the prawns raised in the laboratory tanks (Experiment A); 74% of the

[1]Carapace length is defined as the distance from the base of the eyestalk to the posterior middorsal edge of the carapace.

prawns survived, and they had a final mean weight of 3.14 g (Table 1). The prawns fed salmon were significantly smaller ($P < 0.01$) than the mussel-fed group. However, the growth of prawns in both the mussel and salmon diet groups equaled or exceeded the growth reported for a natural population in British Columbia (Butler 1964).

Growth was similar between oyster waste and no food diet groups (Table 1), but survival was significantly different ($P < 0.01$), 64% for oyster waste and 26% for no food supplement. Prawns fed oyster wastes or receiving no food grew at a slower rate than the prawns in the other two diet groups; this portion of the study was terminated after 60 days.

The poor growth of prawns fed oyster wastes contrasts with the good growth of lobster *Homarus americanus* fed algae and oyster wastes in a sewage enriched raceway system (Mitchell 1975). In that study intermediate organisms that fed on the solid wastes of oysters were also available as a food source for juvenile lobsters. In our study, raw unfiltered seawater was used, but cleaning the tanks twice weekly prohibited the establishment of intermediate organisms.

Prawns in the net pens (Experiment B) grew significantly faster than those in the laboratory (Experiment A) for both mussel- ($P \leq 0.01$) and salmon-fed ($P > 0.01$) treatments (Table 1). Further, there was no significant difference in the growth ($P > 0.10$) or survival ($P > 0.25$) of prawns fed mussel or salmon in the pens as there had been in the laboratory tanks.

In the net pens, the presence of net fouling organisms as an additional food source for the prawns could explain the improved growth over that seen with the same basic diets used in the laboratory. Net fouling organisms could have provided nutritional requirements that were deficient in the basic diets as provided in the laboratory.

Prawns in both diet groups were observed removing organisms that were on both the inside and outside surfaces of the net pens using their second periopods. The amount of net fouling organisms was reduced by the prawns in these en-

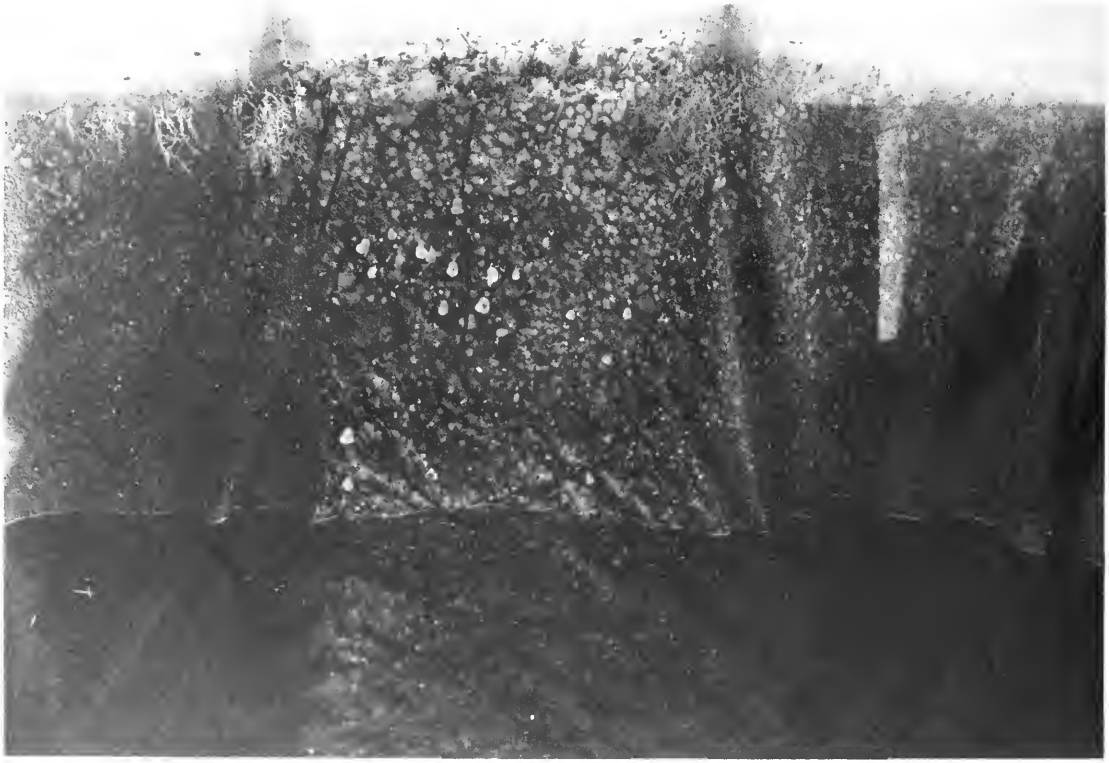

FIGURE 1.—Webbing of a three-chambered net pen showed reduced fouling in the right and left chambers (spot prawns present) compared with the center chamber without prawns.

closures (Figure 1, Table 2). The largest amount of organisms occurred at the shallower depths of the nets as in Moring and Moring's (1975) study of salmon net pens at the same site. Mussels, ascidians, and tubicolous polychaetes, *Spirorbis* sp., contributed the most fouling in the control chambers (without prawns). Except for a few *Spirorbis* sp., the net pen chambers with spot prawns were completely clean. Little algal growth was present due to the reduction of light by the black plastic covers.

Rearing prawns and salmon in the same net pen (Experiment C) proved encouraging. After 6½ mo of culture the growth of these prawns (Figure 2) exceeded that of the monoculture Experiment B ($P < 0.01$) and that reported for a natural population (Butler 1964). Survival was 93% and not significantly different ($P > 0.95$) from that of Experiment B.

There was no evidence of adverse salmon/prawn interaction. The types of food available to the prawns when reared with salmon included: dead fish, uneaten fishfood pellets, fish feces, and net-fouling organisms. The relative contribution of each was unknown.

A limiting factor to stocking juvenile prawns in commercial salmon net pens is the requirement that the prawns must be large enough to prevent them from going through meshes of the net. Smaller "nursery" nets of reduced mesh size could be hung inside the main salmon nets until the prawns reach a suitable size (about 4 g, or 3 mo of age).

Several advantages might accrue from using a scavenger, such as the spot prawn, as a companion crop in salmon culture. In Experiment B a reduction in net fouling was seen in net pens with prawns (Table 2, Figure 1). This reduction will aid salmon culture because it would allow greater water circulation within the enclosure, thus increasing dissolved oxygen levels and flushing of

TABLE 2.—Displacement volumes (milliliters) of fouling organisms on the inside and outside surfaces of net pens with and without *Pandalus platyceros* from July 1975 to March 1976. All pen chambers were clean at the start of the experiment. Sample area was 314.2 cm² of vertical mesh.

Location of sample	Depth of sample (m)	Net pen compartment with prawns		Net pen compartment without prawns	
		Nov 1975	Mar 1976	Nov 1975	Mar 1976
Inside of net	0 25	0 40	0 00	26 40	41 55
	1 00	0 00	0 00	10 50	12 03
Outside of net	0 25	0 25	0 50	9 00	17 00
	1 00	0 10	0 40	6 00	11 53

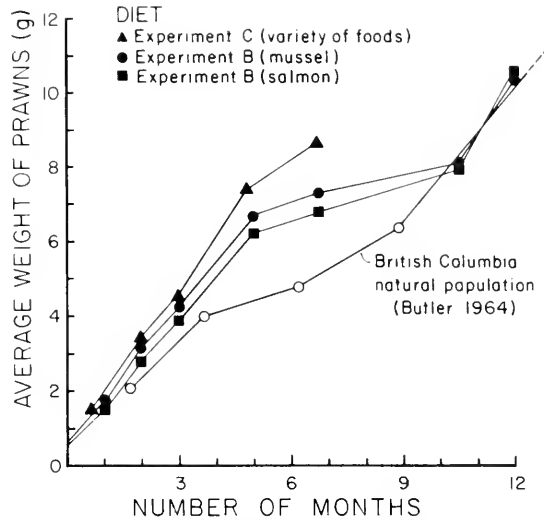

FIGURE 2.—Growth of juvenile *Pandalus platyceros* in net pens compared with a natural population.

metabolic wastes from the pens. A reduction in net maintenance cost might also be realized. Experiments B and C demonstrated that fish in the presence of net-fouling organisms was an acceptable food for the prawn (Figure 2); the utilization of dead salmon by a scavenger would be a valuable conversion of an otherwise unused protein and would reduce the labor needed to remove salmon mortalities from the system.

Further experiments are needed to determine proper stocking densities of prawns and salmon to maximize growth rates, survival, and to make optimum use of the net cleaning activities of the prawns. Further, while our studies showed that a single diet fed to prawns in the laboratory was not adequate for rapid growth, other studies (Kelly et al. 1976) have shown that combination raw diets could produce adequate growth. These combination diets need to be evaluated in the net pen system.

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LARVAL LENGTH-WEIGHT RELATIONS FOR SEVEN SPECIES OF NORTHWEST ATLANTIC FISHES REARED IN THE LABORATORY

Growth is an important connecting link in the functional influence of biotic and abiotic factors on the dynamics of fish populations. Length-weight relations are used by fishery scientists to describe the growth characteristics of species or populations and as a basis of evaluating the consequences of environmental influences on growth. Length-weight relations are also used in assessing production when combined with age and growth information and in determining length or weight in a situation where either one or the other is unknown due to sampling procedures.

Studies of the early life of fishes are receiving increasing emphasis, particularly with regard to growth and survival in the larval stage. Survival during this period is thought to be minimal and potentially variable from year to year. Small changes of tenths of a percent in mortality have the potential to produce orders of magnitude differences in eventual adult populations. Larval growth can be influenced due to food limitations and varying abiotic factors (Houde 1974; Lasker 1975; Laurence 1977). Because of these facts, fishery scientists are particularly concerned with two aspects: 1) quantifying variable larval growth and survival, relating it to subsequent year-class recruitment, and applying it to traditional stock-recruitment relationships where recruitment has often been considered constant; and 2) the potential use of this type of information in evaluating the increasing effects of pollution or other environmental perturbations because of the fragility and sensitivity of larvae to changing or altered environmental variables.

Solutions to these problem areas require quantitative knowledge of growth parameters of larval fishes, and length-weight relations can be helpful in providing information or establishing relationships between pertinent sets of data. It is generally thought that weight[1] is a better measure of absolute growth of fish larvae than length as well as the prime determinant of condition when combined with length. Many species exhibit allometric or disproportionate length-weight growth. This is especially true during the period of metamorphosis when some species display varying or unusual body proportions with age (Blaxter 1969) and length does not increase in proportion to increasing weight. Additionally, recent attempts to construct models of larval survival, as influenced by environmental variables and density dependent feeding relationships, require weight determinations for estimates of biomass and caloric turnover between larval and prey trophic levels.

There is an extensive data base to asses larval fish growth and survival based on ichthyoplankton collected on survey cruises during the last 75 yr by marine laboratories throughout the world. Unfortunately, almost all of these data are in standard or total length measurements as they are much more easily and rapidly taken than dry weights. The difficulty involved in obtaining dry

[1]Weight for species in this research refers to dry weight. Dry weight is the most accurate for fish larvae because accurate wet weights are difficult to obtain and yield variable results on organisms as small as fish larvae.

weights of young stages has been overcome to a certain degree with the advent of experimental laboratory programs at a few research facilities during the last 10 yr.

The experimental larval fish program at the Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, has been studying growth, metabolic, and trophodynamic factors for a number of important commercial and sport species, and it is the object of this report to present larval length-weight relations for seven species including Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; scup, *Stenotomus chrysops*; Atlantic herring, *Clupea harengus*; winter flounder, *Pseudopleuronectes americanus*; summer flounder, *Paralichthys dentatus*; and yellowtail flounder, *Limanda ferruginea*. The larval length-weight relations presented here are previously unreported in the literature for six of the seven species with the exception of the Atlantic herring, which is included because it represents the only data available for western North Atlantic stocks.

Materials and Methods

All larvae were obtained from experimental spawning of adults in the laboratory and reared by techniques reported by Smigielski (1975a, b) and Laurence (1975). The length-weight data were collected coincident with a variety of experimental studies on larval growth, survival, metabolism, and feeding reported by Laurence (1974, 1977, 1978, and as yet unpublished).

In all cases the data were collected from larvae reared at prey concentrations in the range of 0.5 to 3.0 organisms/ml. Concentrations of 0.5 and above have been shown to be adequate for normal growth in the studies cited above. Rearing temperatures were optimum for growth and survival or within a 3°C nonlethal range about the optimum depending upon the experiment from which the data were taken. Optimum temperatures determined in laboratory studies for rearing the seven species were 7°C for cod and haddock, 8°C for winter flounder, 10°C for herring and yellowtail flounder, 16°C for summer flounder, and 18°C for scup.

Length measurements were taken from the tip of the snout to the end of the notochord in the preflexion stage. During flexion of the notochord measurements were taken to a line vertically perpendicular to the tip of the notochord until the hypural bones became prominent or exceeded the line vertically perpendicular to the notochord tip. At this time, a standard length measurement to the posterior end of the hypural plate was recorded. Since the original experiments were not designed for developmental anatomy purposes, the different flexion stages were not recorded coincident with the length and weights.

Lengths were recorded to the nearest 0.1 mm with a filar ocular micrometer. Dry weights were determined after rinsing larvae in distilled water, pipeting onto a glass Petri dish, and drying to a constant weight at 60°-90°C for 24 h. Individual dry weights were recorded to the nearest 0.1 μg on a gram electrobalance.

All measurements were made on post yolk-sac larvae that were freshly sacrificed and unpreserved. The data points for each species represent lengths and weights for individual larvae except for winter flounder and haddock. The data for these two species are the means of lengths and weights for samples of 10-25 larvae collected on a weekly basis during different experiments. The experimental procedures precluded the matching of individual lengths with weights for these two species.

Regression equations and associated parameters were calculated as geometric mean, functional regressions using log base 10 transformed data according to the methods of Ricker (1973) rather than using the previously standard predictive, regression techniques. Ricker demonstrated the advantages of using functional rather than predictive regression calculations to reduce bias in length-weight conversions where the populations of measurements are typically open ended, where only a portion of the length and weight distributions are represented, and where the variability may be more inherent in the biological material itself rather than the means of measuring length and weight.

Results and Discussion

The exponential relation between length and weight for all seven species are presented in linearized form by logarithmic transformation in Figures 1-7. The larvae studied in this research are from different taxonomic families (Clupeidae, Gadidae, Sparidae, Bothidae, and Pleuronectidae), represent different adult life styles (pelagic and demersal), develop in a range of different temperatures, and demonstrate different patterns of metamorphosis from larval to juvenile stages.

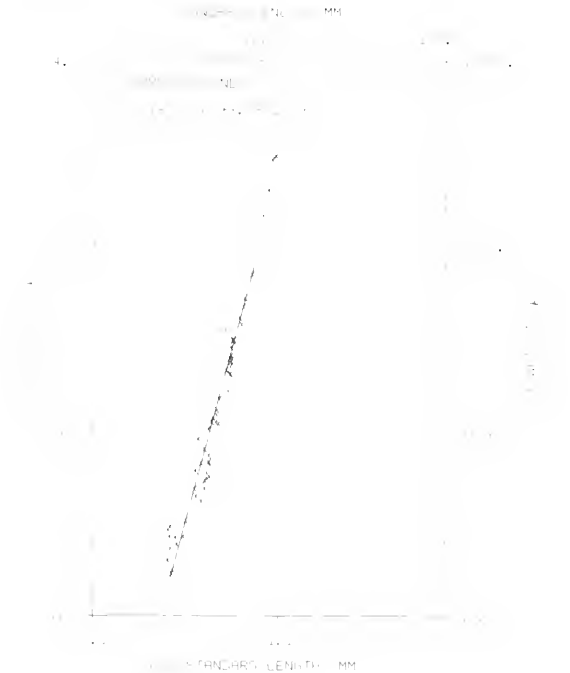

FIGURE 1.—Standard length-dry weight relationship of larval summer flounder.

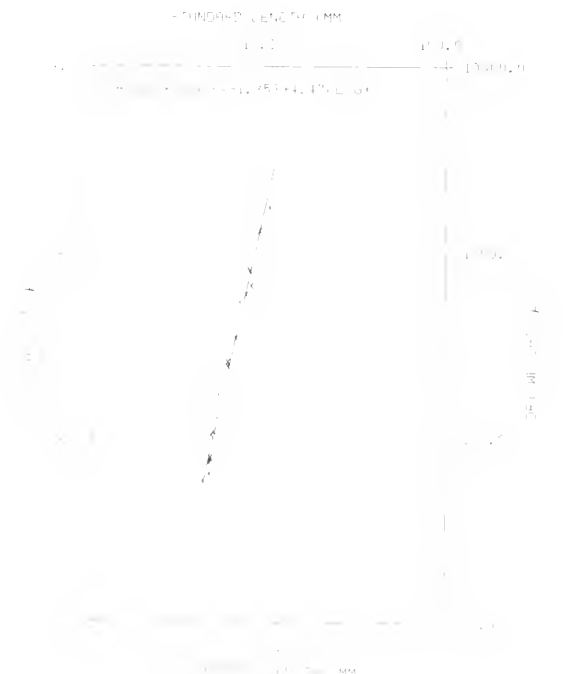

FIGURE 2.—Standard length-dry weight relationship of larval haddock. Points represent means for length and weight of samples of 10-25 larvae.

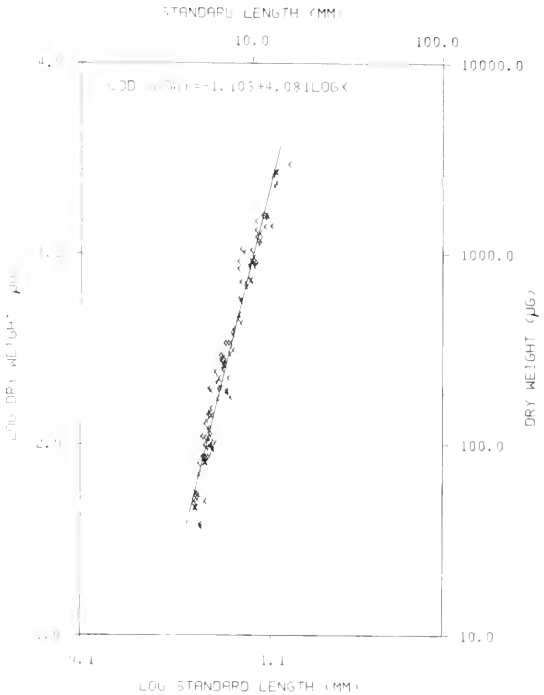

FIGURE 3.—Standard length-dry weight relationship of larval cod.

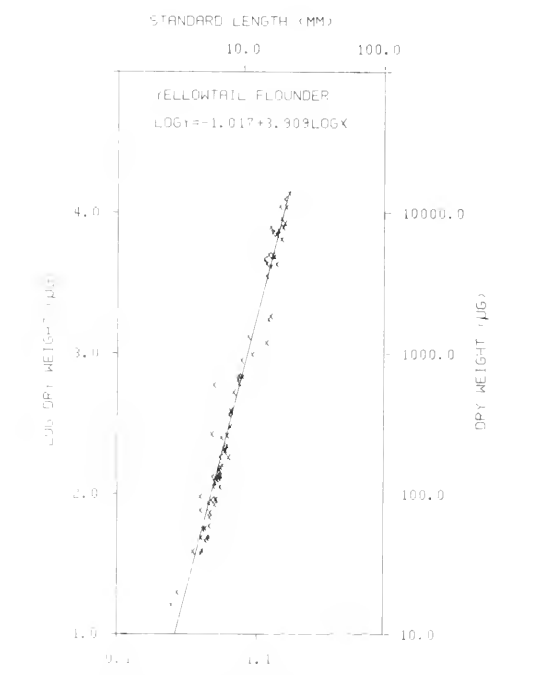

FIGURE 4.—Standard length-dry weight relationship of larval yellowtail flounder.

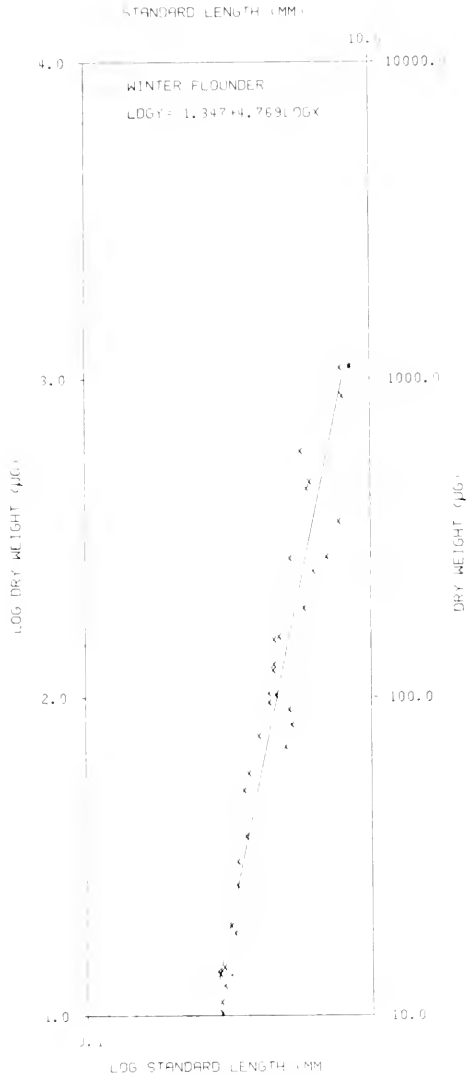

FIGURE 5.—Standard length-dry weight relationship of larval winter flounder. Points represent means for length and weight of samples of 10-25 larvae.

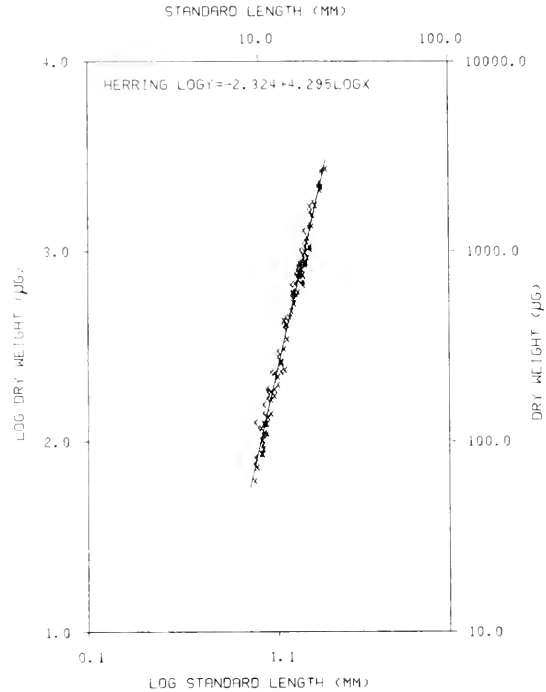

FIGURE 6.—Standard length-dry weight relationship of larval Atlantic herring.

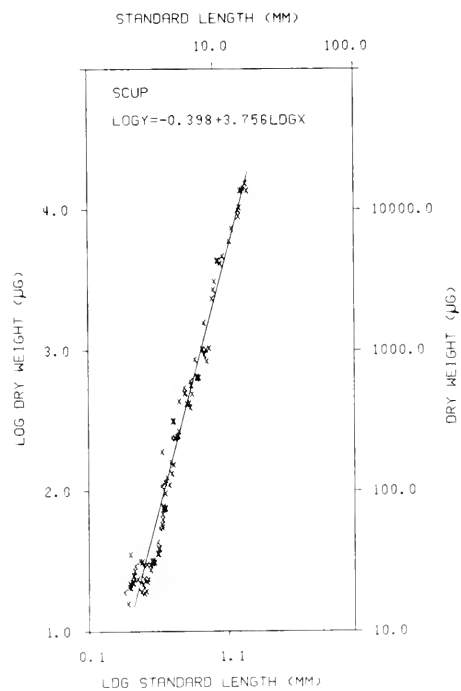

FIGURE 7.—Standard length-dry weight relationship of larval scup.

In spite of these differences, a visual examination of the length-weight regression equation coefficients and associated parameters for all species reveals no obvious correlations with the differences (Table 1). It would not be prudent to statistically test for differences or associations between the species because data for haddock and winter flounder were averaged. Ricker (1973) cautions that averaging changes the variances associated with the variables, particularly the independent variable, so that a comparison between

TABLE 1.—Regression parameters for length-weight relations of seven species of laboratory-reared larval northwest Atlantic fishes.

Larval species	Number sampled	Correlation coefficient	Coefficient of determination	Regression coefficient	Standard error of regression coefficient	95% C.I. about regression coefficient
Summer flounder	57	0 997	0 994	3 780	0.039	3.702-3 858
Yellowtail flounder	80	0 995	0 990	3 909	0.044	3.821-3 953
Herring	98	0 997	0 993	4 295	0 037	4 221-4 369
Scup	100	0 997	0 993	3 756	0 028	3 692-3 820
Cod	104	0 997	0 995	4 081	0.029	4 023-4 104
Haddock[1]	23	0 997	0 995	4 476	0.071	4 328-4.624
Winter flounder[1]	36	0 991	0 982	4 769	0.110	4.545-4 993

[1]Data represent means for length and weight of samples of 10-25 larvae

averaged and unaveraged data is not valid: although he does not discredit the use of averaged data by itself. Also, seven species, some of which are closely related taxonomically, probably do not constitute enough cases for drawing conclusions about functional differences. Consequently, these length-weight relations should properly be considered individually as empirically derived relations for each particular species.

The length-weight relation of fishes usually approximates the cube law relationship in which the weight is proportional to the cube of the length (Beckman 1948; Rounsefell and Everhart 1953). This is usually true for adult fishes; however, results of this research imply that it is not necessarily so for larvae. All the length exponents for the species investigated in these studies were >3.6 with a mean value of 4.152. It would seem then that the dry weight of larval fishes may be more closely proportional to length to the fourth power rather than cubed. Length-weight relations for fish larvae are scarce in the literature. Examination of the data available ($\log_{10}$ formulation) seems to substantiate that the length exponent is always greater than three and more closely approximates four. Marshall et al. (1937) presented a total length-dry weight equation for larval herring, the only species with data available to compare with this study, equivalent to $\log W = -5.6990 + 4.52 \log L$. The length exponent is >4 and similar to the value of 4.295 for herring in this research. Ehrlich et al. (1976) also presented a similar standard length-dry weight relation for Firth of Clyde herring larvae ($\log W = -5.7052 + 4.5710 \log L$) as well as a relationship of $\log W = -4.3043 + 3.9155 \log L$ for larvae of plaice, *Pleuronectes platessa*. Stepien (1976) reported a standard length-dry weight relationship for larval sea bream, *Archosargus rhomboidalis*, of $\log W = -0.5144 + 4.2816 \log L$, and Lasker et al. (1970) reported a standard length-dry weight relationship for northern anchovy larvae, *Engraulis mordax*, of $\log W = -3.8205 + 3.3237 \log L$.

It is acknowledged that variables such as temperature and feeding conditions can influence growth and complicate length-weight relations. These factors may have contributed to some variability in the present study. However, it is felt that these influences were minimized by the experimental feeding levels and temperatures which were within ranges for adequate growth and survival, and any changes in length or weight were most likely mitigated together causing little effect on the form of the length-weight relation. This is supported in studies of haddock larvae (Laurence 1974) where condition factors were similar and randomly associated with prey concentrations >0.5 organisms/ml.

The use of larval length-weight relations for extrapolation may result in some underestimation or overestimation at the smallest and/or largest sizes due to changes in growth rates for yolk-sac or metamorphosing larvae. Farris (1959) suggested that growth rates of larval marine fishes could be separated into three different phases; the first two prior to yolk absorption and the third following. Zweifel and Lasker (1976) presented a mathematical interpretation of larval growth with age defined by the Laird-Gompertz growth function. They noticed two growth cycles; one extending from hatching to yolk absorption and the other following yolk absorption. This variability in the small sizes is probably not inherent in the data of this study because larvae were not included until yolk was absorbed and active feeding had commenced. Some variability may be present in the upper range of sizes in these length-weight relations. In some cases data for larger larvae are not as extensive as for smaller larvae. Also, the majority of the largest individuals for each species were either undergoing or had completed metamorphosis where changes in growth rates of length or

weight might cause allometry. Zweifel and Lasker (1976) briefly considered the length-weight relation in terms of a modified Gompertz-type relation and noted overestimation problems in extrapolation at the largest sizes.

Length-weight relations have merit, but their usefulness is greatly enhanced when combined with other studies, particularly those on age. Length-weight by itself does not necessarily imply rate of change because of the potential influence the environment may have on changing growth with time. However, when correlated with age and compensated for change in rate due to biotic and abiotic influences, length-weight studies can be an important component in estimating growth, survival, and population production.

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EFFECT OF THERMAL INCREASES OF SHORT DURATION ON SURVIVAL OF *EUPHAUSIA PACIFICA*

Euphausiids are an important source of food for many valuable species of fish including herring, cod, pollock, and salmon. Cooney (1971) reported that *Euphausia pacifica* was the most abundant species associated with the diffuse scattering layer at all locations in Puget Sound, Wash. He found that during the day euphausiids are most abundant between depths of 50 and 100 m and that at night most of the population migrates into the upper 50 m. Cooney's findings indicate that great numbers of euphausiids could be drawn through

the condenser cooling systems of thermal nuclear power plants where they would encounter a sizable thermal shock.

Zooplankton entrained in a power plant cooling system located in a saltwater environment could be subjected to an average temperature increase ranging from 12° to 16°C (Coutant 1970). In some plants, the increases are as high as 19°C. Maximum temperatures would be reached in <1 min in the condenser and would be maintained for at least 9 min in a diffuser discharge system and at almost maximum temperature, for possibly up to 21 min, in a discharge canal system. Other factors that could cause damage to euphausiids in a cooling system include pressure changes, abrasion, and toxic substances.

I simulated the thermal conditions encountered in a cooling system to determine the temperature increases that *E. pacifica* could resist for short periods (15 and 30 min). This information can be applied to the design and operation of cooling systems to protect zooplankton.

These studies were conducted at the National Marine Fisheries Service's Mukilteo Field Station, Washington, during 1971-74.

Methods

Euphausiids for these experiments were captured during daylight hours in Port Gardner of northern Puget Sound, Washington, between Mukilteo and Gedney Island. A 10-m net with 333-μm aperture Nytex[1] netting was towed at a depth of about 60 m at a rate of 4.6 km/h. Tows were usually of a 5-min duration. A 946-ml glass bottle was used as a collection receptacle to protect the animals.

As soon as the net was retrieved, the catch (consisting mostly of euphausiids) was divided between two or three 18.9-l Nalgene carboys filled with fresh seawater and covered with black polyethylene sheeting to exclude light. The catch was taken immediately to the laboratory, usually <2 km away, where the euphausiids were separated from other organisms in the catch and placed in 5-l battery jars (23 × 14 × 17 cm) of fresh seawater. They were then placed in a dark, low-temperature incubator set at their previous ambient seawater temperature where they were held before and after testing.

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

The test apparatus consisted of a series of 5-l battery jars filled with seawater that were maintained at specific temperatures by immersion heaters activated by temperature controllers (Craddock 1976). The jars were in a primary bath of running seawater at ambient temperature and air was continuously bubbled into the jars to eliminate stratification.

Test containers for holding the euphausiids were polyvinyl chloride boxes of 5 cm^3 with two opposing sides having 4-cm diameter cutouts covered with 333-μm aperture Nytex netting to allow free water circulation. Styrofoam glued to the boxes provided flotation (Figure 1).

The temperature-time regime to which the euphausiids were subjected was designed to simulate their passage through a condenser cooling system. Coutant (1970) depicted a hypothetical temperature-time course for organisms entrained in condenser cooling water and discharged by diffuser or by discharge canal. An animal could be subjected to maximum temperature increases for up to about 10 min in a diffuser and up to about 20 min in a discharge canal system. Relative to his study, I chose 15- and 30-min exposure tests to represent the longest exposure that might be encountered. To simulate these conditions, test euphausiids were subjected to a given temperature ranging from 14° to 29°C for 15 or 30 min, starting from temperatures of 11° or 9°C. Euphausiids used as controls were always kept at the prevailing ambient temperature (approximately the same as the subsurface temperature of Puget Sound). Five 15-min tests were conducted during June-July 1971, four 30-min tests were run during June-August 1971, and two 15-min tests were made during March-April 1974.

The euphausiids were held 18 h or longer before testing to eliminate handling mortality and were then counted into test containers in seawater while the secondary baths were being raised to the test temperatures. Either 5 or 10 euphausiids were tested in each container, depending upon the numbers available for that particular test.

When all secondary baths became equilibrated at the test temperatures, the boxes containing the euphausiids along with a small amount of water were placed in the test baths. Water in the test containers was within 0.5°C of the test temperature in an average of 28 s after introduction. At the end of the exposure period, the test boxes containing the euphausiids were removed from seawater at the test temperature and placed in fresh seawa-

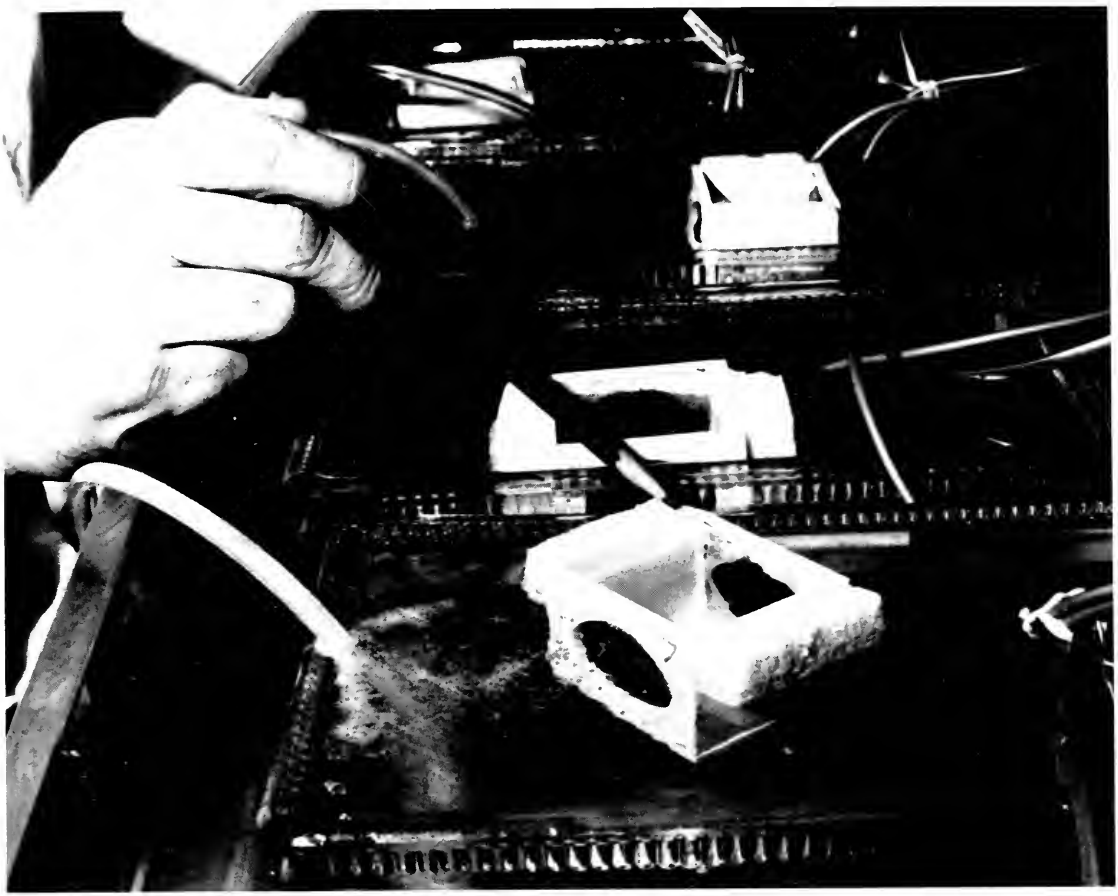

FIGURE 1.—Test chambers and apparatus for testing thermal effects on *Euphausia pacifica*.

ter at the acclimation temperature and maintained in the low temperature incubator. All lots were checked for mortality at 5, 10, and 15 min after introduction to the test temperature when the duration of the exposure was 15 min and also at 20 and 30 min after introduction for the 30-min exposure. All were again checked at 1, 24, and 48 h after testing. The 48 h survival was taken as diagnostic for the TL_{50}'s.

Temperature effects were evaluated on the basis of mortality during tests and 48 h after testing. Forty-eight hours was assumed to be a reasonable holding period to check for delayed mortalities—yet not long enough to cause mortality due to confinement and lack of food. A euphausiid was considered dead if no movement of the thoracic appendages, pleopods, or antennae could be detected using 3× magnification. I modified the term median tolerance limit (TL_{50}) to indicate the maximum 15- or 30-min exposure temperature survived by at least 50% of the experimental animals 48 h after testing. This should be considered the maximum temperature-time combination resisted.

Lengths of the test animals between the extreme tips of the rostrum and telson were taken at the end of each test. The mean-lengths of the euphausiids tested at the various seasons ranged from 12.11 to 18.37 mm (Table 1). The actual range was from 9 to 27 mm. Those tested in the early part of June were the largest; they exceeded those tested later in June by an average of 6.26

TABLE 1.—Sizes (millimeters) of *Euphausia pacifica* tested.

Dates	Mean	Range	Dates	Mean	Range
1971			1974		
June 2-9	18 37	14-26	Mar 12	14 15	10-20
July 21-30	12.11	9-16	Apr. 12-16	13 85	10-23
Aug 4-11	13 14	10-19			

mm. Those tested in August, March, and April had an average spread of only 1.01 mm.

Results

Controls in the different tests suffered no mortality during the exposure period except the June-July tests, where the 15-min group lost 7% of controls by the end of 48 h and the 30-min group lost 10% by the end of 48 h. The data were corrected to reflect the loss of the controls in the June-July tests, using the method of Tattersfield and Morris (1924) as reported by Sprague (1969).

Acclimation temperature influenced resistance. The TL_{50} of euphausiids given a 15-min exposure to elevated temperature was 25°C for those acclimated to 11°C; it was 23°C for those acclimated to 9°C. Exposure to 26°C resulted in survivals of 32% and exposure to 27°C resulted in almost immediate death (<15 min). In the 15 min 9°C acclimation test (March-April 1974), the TL_{50} was at 23°C and 47% were still surviving 48 h after exposure at 24°C. However, 15 min after exposure to 25°C, only 13% remained alive and all were dead in <15 min at 26°C. Figure 2 depicts the survival after a 15- and 30-min exposure to elevated temperatures and after a 48-h holding period.

Increasing the duration of exposure to test temperatures from 15 to 30 min when the ambient temperature was 11°C decreased the TL_{50} by 1° to 24°C. Of those tested at 25°C, only 44% survived 48 h after testing. At 26°C, only 2.5% survived the 30-min test period. None survived the test period at 27°C.

The logistic model was fitted to the data from the three different thermal shock tests. The probability of survival was taken to be the form P [survival at temperature x] $= 1/(1+e^{ax+b})$ where $e = 2.718$. This is the so-called logistic model and a and b are parameters which are estimated using the data. In the 15-min exposure of June-July 1971, $\hat{a} = 0.6544$ and $\hat{b} = -16.4138$; in the March-April 1974 exposure, $\hat{a} = 0.9568$ and $\hat{b} = -22.2860$; whereas in the 30-min exposure July-August 1971, $\hat{a} = 0.5173$ and $\hat{b} = -12.2572$. The estimates of TL_{50} and an approximate 95% confidence interval for it follow for the three tests: 1) 25.08°C, 24.51°-25.65°C; 2) 23.29°C, 22.76°-23.82°C; and 3) 23.69°C, 22.95°-24.44°C.

There was no obvious difference in the effect of a

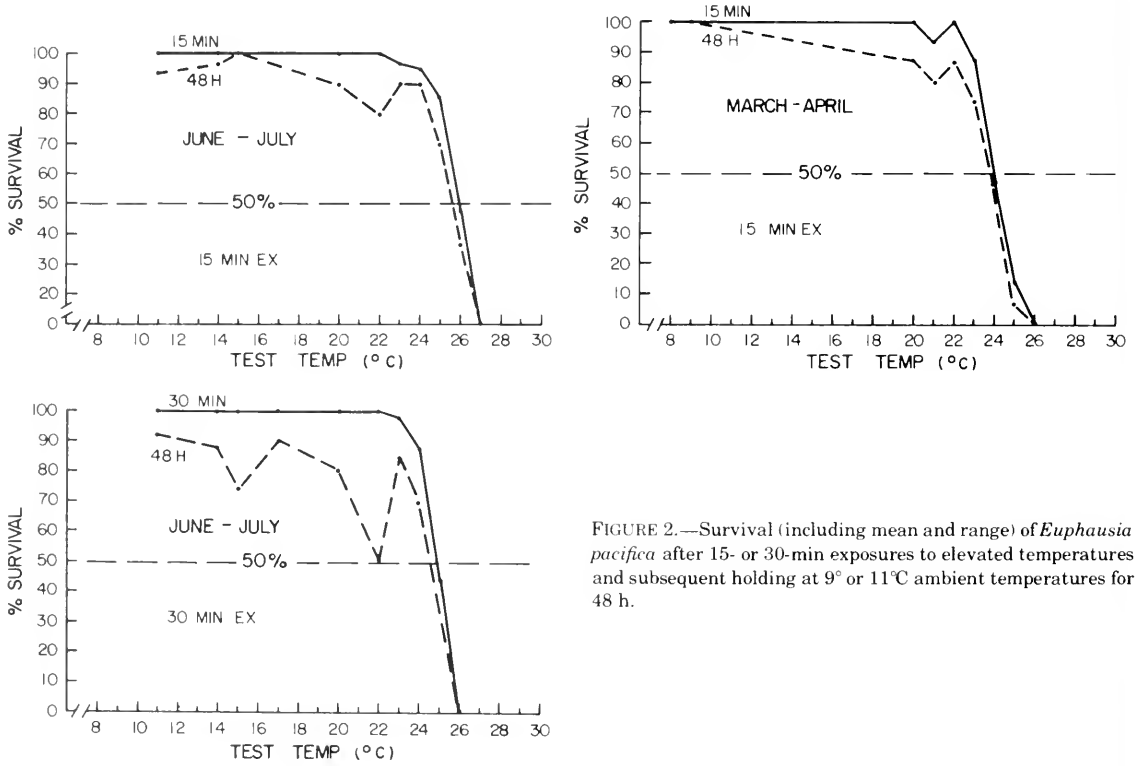

FIGURE 2.—Survival (including mean and range) of *Euphausia pacifica* after 15- or 30-min exposures to elevated temperatures and subsequent holding at 9° or 11°C ambient temperatures for 48 h.

short exposure to increased temperature on the largest or the smallest euphausiids tested. Two out of three groups tested for 15 min in early June (the largest euphausiids) exceeded 50% mortality after exposure to 26°C as did the two groups tested in late July (the smallest euphausiids).

Discussion

The intake of a condenser cooling system may entrain large quantities of euphausiids—depending to some extent on the depth of the intake, the season of the year, and even the time of the day. During the summer, fall, and winter, the young euphausiids make diurnal vertical migrations from the 50- to 100-m strata, rising daily to the surface during the dark hours. After sexual maturity in the early spring they descend even deeper until they inhabit depths over 200 m during their second winter. The following spring they rise to the surface for the second time to breed. The young euphausiids thus spend much of their first year at depths above 50 m, and older adults are again near the surface in the spring (Ponomareva 1963).

Gilfillan (1972) pointed out that *E. pacifica* is widely distributed and is abundant in water having differing temperature characteristics. His studies showed that *E. pacifica* from the Pacific Ocean were more easily stressed by changes in temperature and salinity than those from the west entrance of Strait of Juan de Fuca—which, in turn, were more readily stressed than those from Saanich Inlet. His results indicate that *E. pacifica* from inner Puget Sound would be among the most resistant to thermal stress of these different groups.

Temperatures encountered by euphausiids in Puget Sound normally vary only slightly from the surface to 100 m and deeper. From October through about May there is usually no change in temperature from the surface to 100 m, whereas in the summer the surface to 10 m or less may be a few degrees warmer (Lincoln and Collias[2]).

Seasonal temperature variations in most of Puget Sound are also small, ranging from a low of 7° or 8°C in February to 11°C in late July, August, and September. Even considering their vertical migrations in summer, euphausiids are normally subjected to only slight temperature fluctuations and, therefore, the mortalities observed at simulated condenser cooling temperatures are not surprising.

Once entrained in a condenser cooling system, the euphausiids would encounter an abrupt temperature increase of 12°-16°C (Coutant 1970), which could increase temperatures above the ambient temperature of Puget Sound to the critical range for survival. There are periods from July through September when surface temperatures may reach or exceed 15°C in portions of Puget Sound (Lincoln and Collias see footnote 2). Normally, surface temperatures do not exceed 14°C. Cooney (1971) noted high surface temperatures in June of 16.7°-19°C. These temperatures could result in condenser cooling temperatures of 27°C and above, which this study found to be 100% lethal in a very short time.

Data from this study indicate that even a short passage time through a condenser (15 min) at temperatures of 23°-24°C could kill from 11 to 53% of the euphausiids by thermal causes alone. The added loss due to abrasion, pressure, and toxic substances is unknown.

To minimize damage to the euphausiid populations, condenser cooling system intakes should be located deep enough to take advantage of the coldest cooling water available to minimize temperatures in the system. A very deep intake (just below 100 m) would probably minimize the entrainment of euphausiids. A surface intake would be especially harmful because of the higher surface temperatures and because of the swarming of euphausiids on the surface. Plant lights at night could cause the surface swarming.

[2]Lincoln, J. H., and E. E. Collias. 1970. Skagit Bay Study Progress Report No. 3. Univ. Wash. Dep. Oceanogr., Seattle, Ref. M70-111, 88 p.

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LUNAR SPAWNING OF THE THREADFIN, *POLYDACTYLUS SEXFILIS*, IN HAWAII[1]

Recent evidence indicates that lunar spawning rhythms are more common in fishes than was once thought. Johannes (1978) listed 50 species of teleost fishes with lunar spawning rhythms, most of them tropical and all of them marine or catadromous. In the course of developing methods for culturing the threadfin, *Polydactylus sexfilis* (Cuvier and Valenciennes), we found that this species displayed a lunar spawning rhythm (May 1976). The lunar pattern of spawning had been indicated by a previous field study (Lowell 1971) and is consistent with fishermen's lore (Hosaka 1944), but proof was lacking and details of the rhythm were unknown. In this paper we present detailed information on the lunar spawning of *P. sexfilis* along with observations of spawning behavior, using results from captive fish.

Polydactylus sexfilis is a much sought-after food fish in Hawaii and supports an important sport fishery as well as a small commercial fishery (Rao[2]). Information on the life history of this species (Lowell 1971; Morris and Kanayama[3]) indictates that spawning takes place close to shore. The larvae and juveniles lead a pelagic existence for about 3 mo, juveniles moving to shallow inshore areas at fork lengths (FL) between about 50 and 100 mm. The fish become sexually mature males at 20-25 cm FL and subsequently undergo a sex reversal, passing through a hermaphroditic stage and becoming functional females between 30 and 40 cm FL. Adults inhabit inshore rocky and sandy areas, frequently in zones of turbulence.

Methods

Juvenile *P. sexfilis* were captured by seine on reef flats along windward Oahu in September and October 1970 and reared to sexual maturity in tidal ponds at Coconut Island, in Kaneohe Bay, Oahu. The fish were daily fed chopped squid or smelt, commercial trout chow (40% protein), or trout chow supplemented with chopped squid. In May 1973, 30 mature fish (18 females and 12 males) were transferred to a 18-m^3 nylon net enclosure suspended from Styrofoam[4] floats and anchored off the leeward (southwest) side of Coconut Island. In June and July 1973, a small number of these fish were removed to laboratory tanks and used in experiments on hormone-induced spawning. During this work, ovarian biopsy samples were examined which contained residual eggs and indicated that the fish had been spawning spontaneously. In order to monitor any such spawning, an airlift egg collector was installed (May et al.[5]) in the center of the net in July 1973 and operated continuously (except for a few days when equipment malfunctioned) between 14 July 1973 and 31 December 1975. *Polydactylus sexfilis* produces pelagic eggs, so that the collector obtained a sample of eggs at each spawning. Every morning the entire contents of the collector were harvested and examined under a dissecting microscope, and the number of *P. sexfilis* eggs was estimated by sub-

[1]Contribution No. 552, Hawaii Institute of Marine Biology.

[2]Rao, T. R. 1977. Enhancement of natural populations of moi (*Polydactylus sexfilis*) in Hawaii through the release of hatchery-reared juveniles - a feasibility study of sea ranching. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 33, 46 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

[3]Morris, D. E., and R. Kanayama. 1964-69. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Projects No. F-5-R-11 to F-5-R-17, Div. Fish Game, State of Hawaii. Division of Fish and Game, Honolulu, Hawaii.

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

[5]May, R. C., G. S. Akiyama, and M. T. Santerre. 1976. A simple method for monitoring the spawning activity of fish in net enclosures. International Milkfish Workshop-Conference, May 19-22, 1976, Tigbauan, Iloilo, Philipp. Working Pap. 10, p. 133-138. Southeast Asian Fisheries Development Center, Kalayaan Building, Dela Rosa corner Salcedo Sts., Makati, Metro Manila, Philipp.

sampling. In 1976 and 1977, the collector was operated only during the spawning periods, which were predictable on the basis of data collected during the previous years. Eggs of *P. sexfilis* were distinguished from occasional eggs of other species by their diameter (800-825 μm) and by comparing hatched larvae with larvae obtained from hormone-induced spawnings; the identification was further corroborated by rearing larvae to the juvenile stage on several occasions. Since *P. sexfilis* undergoes a male-female sex reversal, additional males were added to the population each year to maintain a female to male sex ratio between 1:1 and 1.5:1 during the spawning season. In 1976, additional males were not added until the third spawning month, so data on spawning were not available for the first two spawning months of that year. At the end of this study in December 1977, the population of spawners numbered 57.

In order to determine the exact time of day when spawning occurred, water was sampled from the holding net continuously with a centrifugal pump at 10 l/min and passed through a small collecting basket (500-μm nylon mesh) on a barge anchored next to the net. The collecting basket was monitored visually, and the time when eggs first appeared was noted. The superstructure of the barge provided a barrier between the observer and the holding net, so that activities associated with monitoring the basket did not disturb the spawners in the net.

Results

Lunar Spawning Rhythm

Eggs of *P. sexfilis* were first observed in the collector from 23 to 25 July 1973. Subsequently the fish were found to spawn at night over a period of 3-7 (in one instance, 10) days once each month, always in proximity to the last quarter phase of the moon (Figure 1), and in a spawning season that extended from May or June to October (Table 1). Because the lunar month is 29.5 days long and does not coincide exactly with the calendar month, the calendar dates of spawning (Table 1) were generally 1-3 days earlier in each succeeding month. The first spawning of each monthly series was usually preceded by 1 or 2 days on which the fish fed less actively than normal. Counts of *P. sexfilis* eggs from the collector were made in August 1973, and thereafter. Judging from the samples obtained by the collector, relatively few eggs

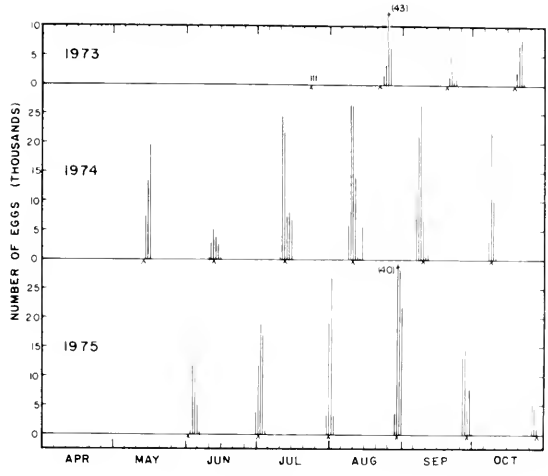

FIGURE 1.—Numbers of *Polydactylus sexfilis* eggs obtained by the airlift egg collector between August 1973 and October 1975. In July 1973, eggs were noted on 3 days but were not counted. Carets indicate the time of the last quarter phase of the moon.

TABLE 1.—Dates on which eggs were produced by captive *Polydactylus sexfilis* during study period. For each spawning month, the upper date is the first observed day of spawning, the lower date the last day.

Year	Spawning month					
	I	II	III	IV	V	VI
1973	(1)	(1)	(1)	22 Aug.	19 Sept.[2]	18 Oct.[2]
				25 Aug.	22 Sept.	21 Oct.
1974	13 May	9 June	9 July[2]	7 Aug	5 Sept	6 Oct
	15 May	14 June	14 July	13 Aug	10 Sept	9 Oct.
1975	1 June[2]	29 June	29 July	27 Aug	25 Sept.[2]	25 Oct.
	5 June	3 July	1 Aug	30 Aug	29 Sept	27 Oct
1976	(1)	(1)	17 July	15 Aug	13 Sept [2]	13 Oct
			20 July	18 Aug.	16 Sept.	16 Oct.
1977	9 May	7 June[2]	6 July	4 Aug	3 Sept	1 Oct
	14 May	11 June	11 July	13 Aug	7 Sept.	5 Oct

[1]Data not available
[2]Collector malfunctioned on previous day; initial spawning day possibly earlier.

were produced on the first and last days of spawning, with a peak usually on the second or third day (Figure 1). However, because the eggs collected represented only a sample of the total number of eggs produced, it is possible that the peaks reflected some sampling variability.

The time of spawning relative to the lunar cycle appeared to change as the spawning season progressed. The first spawning series of the year always began (Figure 2) on the day of the last quarter (in one case the egg collector malfunctioned prior to the last quarter, and it is possible that the first day of spawning occurred earlier). In subsequent months the series began 1-4 days prior to

the last quarter (Figure 2). In April 1974 the collector obtained several thousand eggs over a 3-day period about 12 days before the last quarter; although the eggs were of the same diameter as *P. sexfilis* eggs, the larvae were not reared for positive identification. In view of the consistency of subsequent spawning data, and the low ovarian weights which two previous studies found in *P. sexfilis* in April (Lowell 1971; Morris[6]), we believe these were eggs of another species.

Some of the eggs found in the collector were transparent, buoyant, and developing normally, while others sank and were opaque and obviously not viable. Among the spawnings in which 1,000 or more eggs were collected, an average of 52% of the eggs were viable (range, 0-98%). The airlift collector apparently damaged the eggs to some extent. For example, on 13 June 1974, when 75% of the eggs from the collector were viable, eggs obtained by dip net at the time of spawning showed over 90% viability. It is not known how many of the fish in the net participated in each spawning or whether the same fish spawned each month, although Kanayama[7] believed that individual *P. sexfilis* spawned more than once in a season.

[6]Morris, D. E. 1964. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-11, Div. Fish Game, State of Hawaii, 15 p. Division of Fish and Game, Honolulu, Hawaii.

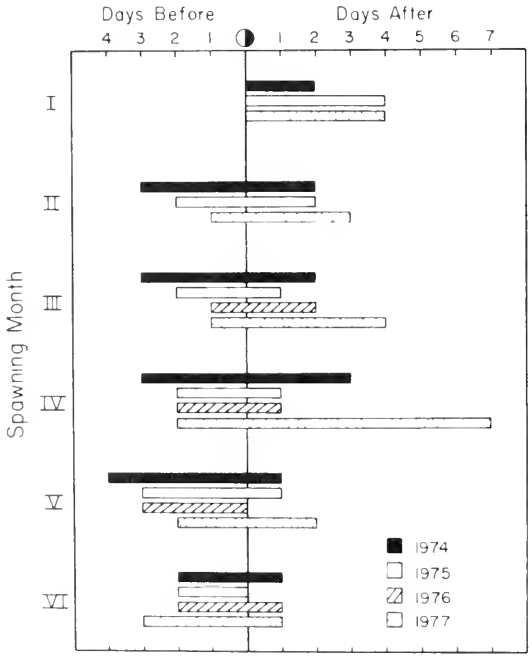

FIGURE 2.—Duration of spawning of *Polydactylus sexfilis* relative to the time of the last quarter (◑) for the six spawning months in 1974, 1975, and 1977. Data are given only for the last four spawning months of 1976.

Time of Spawning

The developmental stage of eggs found in the collector in the morning indicated that spawning had occurred shortly after sunset. Visual monitoring of water sampled continuously from the net on 34 spawning nights showed that with few exceptions the fish spawned between 2030 and 2130 h (Figure 3, Table 2). The times recorded were those when eggs were first observed in the collector; it is possible that additional spawnings took place slightly later on the same night, and behavioral observations (see below) indicated that this may have been true on at least some nights. The time of spawning did not vary with the time of sunset (Figure 3) and appeared unrelated to the time of moonrise (which occurred generally between 2300 and 0400 h during the spawning season).

[7]Kanayama, R. 1967. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-15, Div. Fish Game, State of Hawaii, 9 p. Division of Fish and Game, Honolulu, Hawaii.

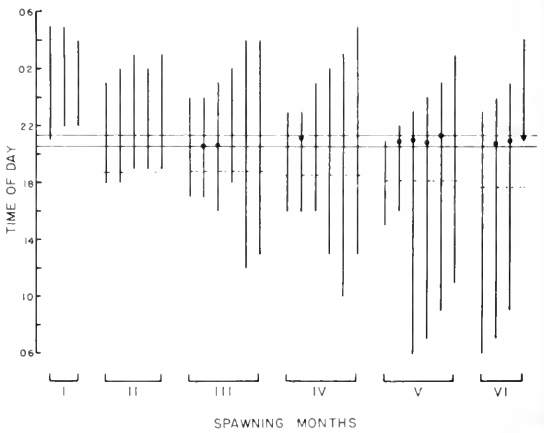

FIGURE 3.—Times of spawning of *Polydactylus sexfilis* during the six spawning months (roman numerals) of 1974 in relation to the tidal cycle. Dots indicate observed times of spawning in 1974, and the horizontal lines delineate the time of spawning as indicated by data from 1974, 1975, and 1977 (see Table 2). Dotted horizontal lines show the times of sunset in 1974. Vertical lines for each spawning night indicate time between the evening high and low tides, i.e., the duration of the outgoing tide, as measured by a tide gage at Coconut Island in 1974.

TABLE 2.—Times of first spawning in a captive population of *Polydactylus sexfilis* on nights in 1975 and 1977. Where a single time is given, the egg collector was examined continuously; in other cases, the collector was examined at intervals of 5-15 min. Numbers in parentheses indicate times of peak fish activity, presumed to be the exact time of spawning.

Date	Time of first spawning	Date	Time of first spawning
1975.		26 Sept	2045-2100 (2052)
2 June	2115-2118	27 Sept.	2054-2100
3 June	2110-2115	28 Sept.	2050-2054 (2053)
4 June	2110-2115	29 Sept.	2135-2140 (2138)
5 June	2115-2120	26 Oct.	2050-2100 (2056)
30 June	2115-2120	27 Oct.	2105-2110 (2107)
2 July	2125-2130 (2127)	1977	
3 July	2140-2145	7 June	2105
30 July	2045-2100 (2058)	9 July	2147
31 July	2120-2125	10 July	2140
28 Aug	2115-2118 (2117)	6 Aug	2050
29 Aug	2129	4 Sept	2103
30 Aug	2115-2118 (2117)	3 Oct.	2038

Data from a tide gage located at Coconut Island were available for 1974 and showed that spawning nearly always took place on the outgoing tide (Figure 3). Although tide gage data were not available for subsequent years, tides predicted from tide tables showed patterns similar to the 1974 tide gage data. For 1975, 1976, and 1977, the time of spawning (i. e., 2030-2130 h) was compared with predicted tides and again found to occur mostly during the outgoing tide. Spawning occurred on the outgoing tide in 73% of the spawning nights during 1974-77.

Spawning Behavior

Observations of spawning behavior were made initially by watching bioluminescence caused by the fish's movement; later, direct observations were made by shining lights on the water at the time of spawning. The level of activity of the fish gradually increased beginning around 2015 h and culminated in the spawning act as determined by the appearance of eggs in the centrifugal pump samples. Occasionally the fish broke the surface of the water during the period of increased activity. During courtship the fish swam rapidly around the net in a circular manner in groups of two or three. They appeared to be chasing one another, and often one fish would contact another from behind, either dorsally or ventrally, with snout. Spawning appeared to take place between pairs rather than among larger groups of fish. Increased activity usually continued for 20 or 30 min after eggs were first noted.

Discussion

The captive population of *P. sexfilis* was clearly spawning with a well-defined lunar rhythm. Other evidence implies that this is a natural behavior for this species. Lowell (1971) set gill nets weekly in certain shoal areas of Oahu from April to August 1970 and reported that exceptionally large catches of *P. sexfilis* per effort occurred "after the full moon and continuing until the last quarter (1 week duration)," and because of the stage of gonadal development among fish in such catches, he termed them "spawning runs." In July 1970, female fish caught 3 days before the last quarter all had well-developed ovaries, but fish caught 4 days after the last quarter had spent ovaries. Fishermen seem to have been aware of the habits of *P. sexfilis* for a long time: Hosaka (1944:117) stated, "Moon light nights are best for moi (= *P. sexfilis*) fishing, and this is especially true when the moon is in the last quarter phase."

Spawning at the time of the last quarter phase of the moon appears to be rare among fishes. Of the 50 lunar spawners which Johannes (1978) listed, only two besides *P. sexfilis* spawned on the last quarter; both of these are species of *Amphiprion*, and one spawned on the first as well as the last quarter. Since the various species covered in Johannes' list occurred in different geographic locations, the variations in spawning days, taken together with variations in spawning times, could reflect local adaptations such as would occur if egg or larval survival were related to tides or currents.

The coincidence of spawning in *P. sexfilis* with the outgoing tide indicates that the remarkably precise timing of spawning may act as a mechanism for offshore dispersal of eggs and larvae. Lowell (1971) noted that there was a strong, oceanward current at his sampling site during falling tide, when he estimated spawning occurred, and results of ichthyoplankton surveys indicated that *P. sexfilis* eggs and larvae are not found in inshore waters in Hawaii (Leis and Miller 1976; Miller et al.[8]; Watson and Leis[9]). Johannes (1978)

[8]Miller, J. M., W. Watson, and J. M. Leis. 1973. Larval fishes. *In* S. V. Smith (editor), Atlas of Kaneohe Bay, a reef ecosystem under stress, p. 101-105. Univ. Hawaii Sea Grant Tech. Rep. 72-1. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

[9]Watson, W., and J. M. Leis. 1974. Ichthyoplankton of Kaneohe Bay, Hawaii: a one-year study of the fish eggs and larvae. Univ. Hawaii Sea Grant Tech. Rep. 75-1, 178 p. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

pointed out that spawning on outgoing tides is a common phenomenon among coastal marine fishes in the tropics, and he believed it evolved as a strategy for ensuring that eggs and larvae are transported away from the heavy concentration of predators in shallow water. Johannes noted that nocturnal spawning is also common in tropical reef fishes and serves to reduce predation both on the eggs and on the spawners.

The first *P. sexfilis* spawning of the year appears to be anomalous in that it occurs relatively late with respect to the last quarter. If offshore transport confers an important selective advantage on *P. sexfilis*, the lateness of the first spawning is maladaptive because it results in release of eggs early relative to the outgoing tide (see Figure 3). The initial phase of the spawning season may thus result in few viable offspring and could represent a gradual initiation of the main spawning season, delayed perhaps by the lower water temperatures which usually prevail during the first spawning month (Bathen[10]).

No observations on the spawning behavior of a polynemid fish have been published previously. In *P. sexfilis* the sexes apparently pair and spawn after a brief courtship involving rapid following and nosing of one fish by another. The spawning behavior of this species is similar in many respects to that of the Pacific bonito, *Sarda chiliensis*, including behaviors described by Magnuson and Prescott (1966) as "circle swimming," "tail nosing," and "following." The circling behavior noted among *P. sexfilis* may have been imposed by the confinement of the net enclosure, but *S. chiliensis* also showed tight circling behavior at the time of gamete release in a very large tank at Marineland of the Pacific, and circling prior to spawning occurs naturally in mullets (Helfrich and Allen 1975) and some (perhaps many) other tropical fishes (R. E. Johannes, Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96844. Pers. commun., December 1977). The circling behavior during spawning observed in captive *P. sexfilis* thus may not be abnormal for this species but may, as Magnuson and Prescott (1966) theorized for *S. chiliensis*, serve to enhance the probability of fertilization.

[10]Bathen, K. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 14, 353 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

Acknowledgments

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THE ROLES OF PRIOR RESIDENCE AND RELATIVE SIZE IN COMPETITION FOR SHELTER BY THE MALAYSIAN PRAWN, *MACROBRACHIUM ROSENBERGII*[1]

Behavorial dominance, territoriality, and their relationship to survival and population density have been the subject of extensive research (reviewed by Brown and Orians 1970; Itô 1970; Brown 1975). Generally dominance (behavioral) hierarchies imply some form of ranked order (reviewed by Marler and Hamilton 1966; Eibl-Eibesfeldt 1970; Itô 1970) whereby the alpha animal(s) has preferred access to food, shelter, or mates. Dominance may develop within a short time after an initial encounter (Dingle and Caldwell 1969), is partially controlled by differences in relative size (Marler and Hamilton 1966), and in some species is modified by relative location in space (Brown 1963). This latter modification is related to Noble's (1939) original concept of territory. Noble referred to territory as "any defended area." This area could serve as a "retreat" (in contrast to a sexual or nesting area) that "is occupied because it is familiar and defended because any newcomer is irritating to the resident."

Such space-related aggressive behavior has been reported in numerous animals (Brown and Orians 1970). Territorial behavior can be related to "defense" of 1) a breeding area (Buechner 1961; Watson 1964); 2) a renewable resource such as food (Stimson 1970); or 3) a physical shelter (Crane 1958; Reese 1964; Fielder 1965; Hughes 1966; Dingle and Caldwell 1969). Often the outcome of such a defensive action is exclusion of the intruder by the resident. Since this area is "familiar" to the resident and unfamiliar to the "newcomer," it follows that the resident has some type of advantage. This "prior resident effect" has been observed in a number of species (Braddock 1945, 1949; Miller 1958; Hughes 1966; Baird 1968; Dingle and Caldwell 1969; Selander 1970). Thus in many animals, spacing behavior is a powerful mechanism that can regulate resource utilization and influence distribution patterns.

Many of the above-mentioned studies and reviews dealt with animal populations in natural open systems subject to both immigration and emigration. In contrast, aquaculture systems are closed and deal with confined high-density populations. In the case of *Macrobrachium rosenbergii*, ponds are stocked with postlarvae, and harvesting of adults begins 9-12 mo later. The same space-related behavioral mechanisms observed in open systems may be operating in these high-density ponds. Circumstantial evidence indicates that this is occurring in ponds containing *M. rosenbergii*. Animals of the same age exhibit large variation in size at the end of several months of growth (Fujimura nad Okamoto 1970). Malecha (1977) reported that small *M. rosenbergii* can greatly increase their size when larger animals are absent. This has been called the "Bull Effect" by Fujimura and Okamoto (1970). Similar observations have been reported for carp (Nakamura and Kasahara 1955, 1961; Wohlfarth and Moav 1972), trout (Brown 1946), and salmon (Symons 1971). One hypothesis advanced by Nakamura and Kasahara (1961) is that the larger animals are outcompeting the smaller subordinates for food.

Macrobrachium rosenbergii is a large freshwater prawn. Its native distribution ranges from Pakistan to Papua, New Guinea, and Palau (Johnson 1960; McVey 1975). Usually it is found in fresh and brackish streams and pools. The eggs hatch near ocean waters, and the adults are found up to 200 km from the coast (Ling 1969). Generally males are thought to stay in upstream waters while the females undergo a seasonal migration, moving downstream and into brackish waters (Raman 1967). Relatively little is known of *M. rosenbergii's* behavioral ecology but Raman (1964) reported juveniles "hiding in crevices or among submerged plants along river banks." In order to understand how social behavior affects resource utilization by *M. rosenbergii*, three experiments were conducted in which shelter was the limiting resource, and relative size and prior residence were measured as variables.

Methods

The three experiments consisted of: a prior resident experiment, a simultaneous introduction experiment, and a control experiment. The prior resident experiment was used to test for the role of prior residence and relative size in competition for shelter. The simultaneous introduction experiment tested for the role of relative size on competition in the absence of a "prior resident effect." The control experiment tested for the effect of handling and capture.

[1]Contribution No. 544 from the Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii.

Water conditions were maintained via an air lift filter. The animals were fed a dry pellet diet approximately every other day (see diet #5, Balazs et al. 1973). A 12-12 photoperiod with one-half hour twilight lighting at "sunrise" and "sunset" was employed.

Prior Resident Experiment

Earlier experiments revealed a form of shelter preference or selection operating in *M. rosenbergii* (Peebles 1977). The shelters used in this experiment were identical to those most frequently selected by animals in the earlier experiments. One shelter was placed in each experimental tank. A shelter consisted of six concrete bricks arranged into a double open ended square tunnel (19.3 × 19 × 11.4 cm tall).

Refuge other than the shelter was eliminated by the use of oblong experimental tanks (137 × 75 × 92 cm deep) and the suspension of the air lift filters just below the water surface (the usual position for these filters was on the bottom). Water depth was 34 cm.

Adults from commercial ponds were placed in two separate holding tanks, where they were kept for no longer that 1 wk. Two animals were removed, one each from the separate holding tanks. Three body characteristics were measured: standard length (tip of telson to orbit of eye), and lengths of left and right chelae. The animals were tagged by means of a small plastic "bread bag twist-tie" that was color coded and tied around the tail. It took about 15 s to attach. Following tagging the two animals were placed separately in experimental tanks. Three observations were made before the introduction of the "immigrant" and four observations were made after the introduction. The preintroduction observations were made on the second, third, and seventh days after the animals were placed in their separate experimental tanks. There were three observations per animal, each lasting 3 min. After the preintroduction week a coin was flipped to determine which animal would be the immigrant. The immigrant was designated as the introduced specimen and was moved via a dip net from its tank to the resident's tank. The resident was the animal that was not moved from one experimental tank to another. The postintroduction observations were made on the day of introduction, and the second, third, and seventh days after introduction. The observation performed on the day of introduction was 15 min and designed to monitor agonistic interactions associated with the initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank. All observations were made between 1000 and 1530. Since these animals are nocturnal, movement and behavioral interactions were minimal during the daytime.

A total of 36 animals (18 immigrants, 18 residents) were used. Paired animals were of the same sex. This controlled for the possible confounding effect heterosexual courtship behavior might have on competition for shelter occupancy.

Simultaneous Introduction Experiment

The treatment of the simultaneous introduction experiment differed from the prior resident experiment in four ways: 1) only males were used; 2) the animals were simultaneously introduced into the oblong tanks; 3) two additional body characteristics were measured (body weight and carapace length); and 4) the animals were not separately observed prior to introduction.

Fifteen trials were run employing a total of 15 pairs or 30 animals. Observations were made on the day of simultaneous introduction, and the second, third, and seventh days after introduction. The observation performed on the day of simultaneous introduction was 15 min and designed to monitor agonistic interactions associated with initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank.

Control Experiment

Eleven controls were run to test the effect of handling. Animals were selected, measured, tagged, and placed individually in experimental tanks. One week later the control was netted, held in the air, and reintroduced into the same experimental tank. Observations were made for the week before and the week after netting (mock immigration).

Operational Definitions

Successful: an animal that was in a shelter at the end of the 7-day period following immigration.

Unsuccessful: an animal that was not in a shel-

ter at the end of a 7-day period following immigration.

Push: an aggressive act where one animal pushes one of its chelae against the body of another animal.

Nip: an aggressive act where one animal closes down the tips of its chela on the body part of another animal.

Tête-a-tête: a type of aggressive act characterized by a head to head confrontation with at least one nip or one push. The tête-a-tête appeared to be difficult enough in orientation from the push and the nip to be placed in a separate category. Further observation and analysis might not support this separation.

Shove: an aggressive act where one animal holds both chela forward and parallel while charging into the flanks of another animal.

Bout: an agonistic exchange between two animals where at least one aggressive act occurred. A bout was considered terminated when aggressive acts stopped or one animal moved away and was not chased. Bouts were measured in units of aggressive acts.

Bout length: the number of aggressive acts that occurred during a bout.

Body characteristics: standard length (centimeters), right and left chelae length (centimeters), weight (grams), and carapace length (centimeters).

Body size index: the number of body characteristics in which an animal was larger. It was derived as follows: animal A larger than animal B in standard length and right chela length, then A's body size index is two. In the Prior Resident Experiment three body characteristics were measured, thus the maximum body size index in this experiment was three. In the Simultaneous Introduction Experiment five body characteristics were measured, thus in this experiment the maximum body damage index was five.

Results

Control Experiment

Ten out of 11 animals were in the shelter on every observation period before mock immigration. The remaining animal was in the shelter on one of the three observation periods. The same 10 were in the shelters on all observations following mock immigration, while the same remaining one was never observed in a shelter after immigration. It was concluded that the act of netting had no effect on shelter use.

Prior Resident Experiment

Shelters were occupied on every observation by every animal during the preimmigration week. Following immigration all shelters were occupied on every observation period. On several occasions more than one animal was in a shelter during the first two observation periods following immigration. However, by the end of the week, observation period 4, one animal was in a shelter while the other was usually at the opposite end of the tank. When the data were examined by immigrant versus resident for shelter use over the 7-day period, an interesting change became apparent (Figure 1). On the day of immigration, residents were occupying shelter significantly more often than immigrants (Binomial Test, $P = 0.044$, Siegel 1956). By the second observation period and for the remaining two observations there were no significant differences between residents and immigrants in frequency of shelter use (Binomial Test: day 2 after immigration, $P = 1.0$, day 3, $P = 0.814$; day 7, $P = 0.814$).

Examining the data for the effect of size (Figure 2) revealed that successful animals were significantly larger than their unsuccessful paired

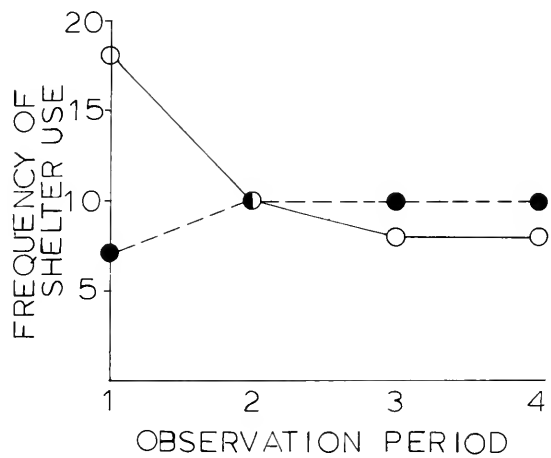

FIGURE 1.—Shelter usage by observation period for 18 pairs of *Macrobrachium rosenbergii*. The data from prior resident experiments are summed for the 18 pairs. During observation period 1, 18 residents (circles) and 7 immigrants (dots) were inside shelters. On observation period 1 there were seven cases of double occupancy; observation period 2, two cases; and observation period 3, none.

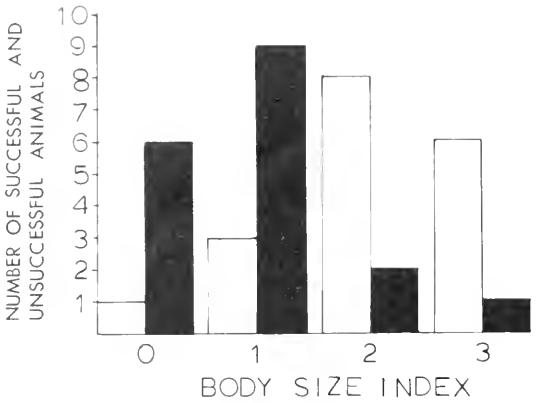

FIGURE 2.—Frequency of relative body size for successful (open bar) and unsuccessful (solid bar) prawns in the prior resident experiment. A body size index of one indicates one *Macrobrachium rosenbergii* was larger than the other in one body trait but smaller in the other two body traits.

partners (Kolmogorov-Smirnov Two Sample Test: D max = 11, n = 18, P = 0.01).

Simultaneous Introduction Experiment

A similar effect of size on shelter use was observed in the simultaneous introduction experiment (Figure 3; $r_s = 0.579, P<0.001$). Once again larger animals used the shelters more often than their smaller partners.

Aggressive behavior was observed only on the day of introduction. The nip and push occurred more often than the shove or tête-a-tête (Figure 4). Generally aggressive interactions were limited to a few (one to three) bouts per 15 min (Figure 5), and these bouts were usually one or two aggressive acts long (Figure 6).

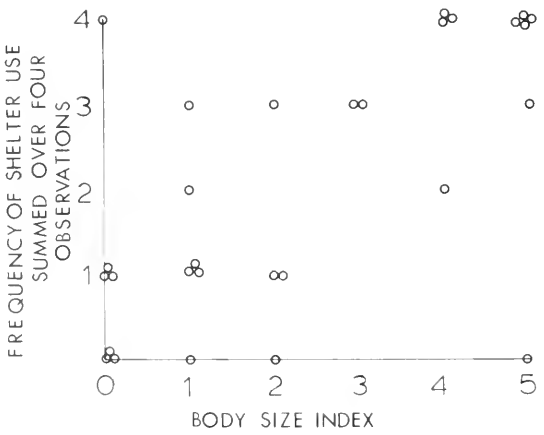

FIGURE 3.—Correlation between frequency of shelter use and body size index for *Macrobrachium rosenbergii*, from the simultaneous introduction experiment. A body size index of one indicates one animal was larger than the other in one body trait but smaller in the other four body traits.

Prior Resident Experiment by Simultaneous Introduction Experiment

A Kolmogorov-Smirnov chi-square approximation (Goodman 1954; Siegel 1956) revealed that animals of the simultaneous introduction experiment were more aggressive on the day of introduction than were animals in the prior resident experiment on the day of immigration (χ^2 = 15.54, $P<0.002$ for number of bouts/animal per 15-min period; χ^2 = 13.877, $P<0.002$ for number of ag-

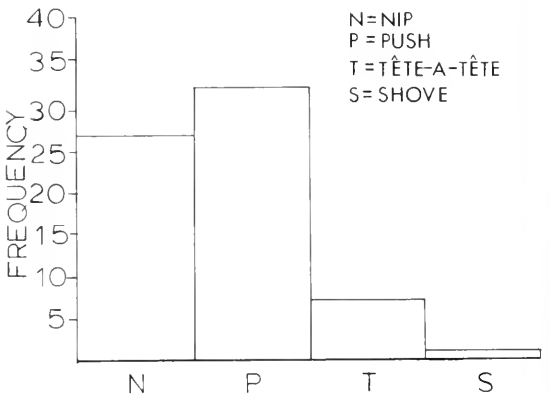

FIGURE 4.—Frequency by type of aggressive acts observed on the first day after introduction for the experiment on simultaneous *Macrobrachium rosenbergii* introduction. Frequency equals the number of aggressive acts by 17 animals.

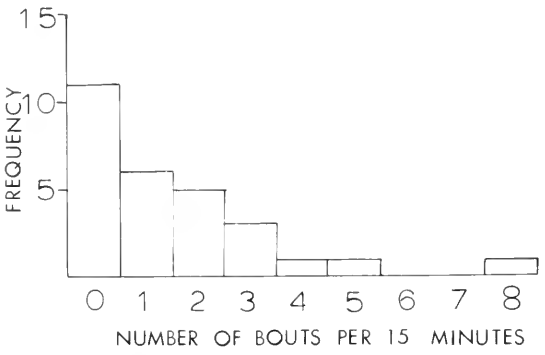

FIGURE 5.—Frequency of number of aggressive bouts per animal during the 15-min period of observation after simultaneous introduction of male *Macrobrachium rosenbergii* (14 pairs).

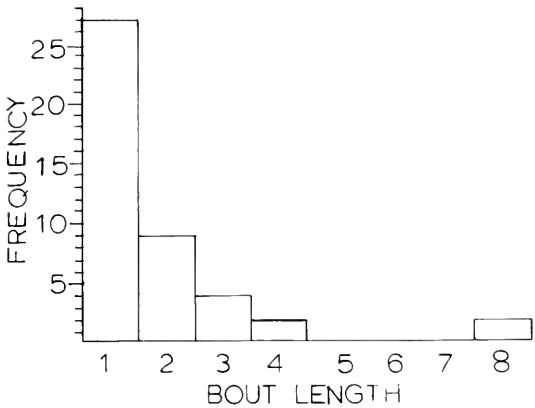

FIGURE 6.—Frequency of bout length (number of aggressive acts per bout per animal) for the simultaneous introduction of 14 pairs of male *Macrobrachium rosenbergii*.

gressive acts/animal per 15-min period). Simultaneous introduction animals exhibited a total of 68 aggressive acts occurring in 43 bouts (n = 28 animals), while the prawns from the prior resident experiment exhibited only five aggressive acts in five bouts (n = 32 animals).

Discussion

The results indicate that when *M. rosenbergii* compete for shelter at least three factors, relative size, prior residence, and length of time contestants are paired, play important roles in determining who occupies a shelter. It has long been recognized that in crustaceans relative size plays a large role in determining dominance (Allee and Douglas 1945; Bovbjerg 1953, 1956, 1960; Lowe 1956). More recent observations have confirmed the size/dominance relationship (Hughes 1966; Crane 1967; Griffin 1968; Hazlett 1968; Dingle and Caldwell 1969; Warner 1970; Rubenstein and Hazlett 1974; Jachowski 1974; Molenock 1976; Sinclair 1977). However, relative size does not appear equally important in all species (Hazlett and Estabrook 1974).

In prawns, relative size strongly influences the outcome of competition. When two prawns encounter one another in an area new to both, the larger animal usually has the advantage. Often these encounters are characterized by a limited series of pushes with one or the other chela. The function of the pushing might be threefold: 1) to test their opponent's weight (rest inertia), 2) to determine the opponent's molt state, and 3) to see if the opponent is capable of pushing back (has chelae). Other crustaceans appear to measure their opponent's physical strength by means of physical interactions involving the chelae (Griffin 1968; Schöne 1968). In *Cambarellus shufeldtii*, claw removal causes dominant animals to drop in rank (Lowe 1956). In *M. rosenbergii* deaths related to agonistic behavior usually occurred near ecdysis and often the first appendages lost during an agonistic encounter were the chelae (Peebles 1977).

Smaller animals have been observed successfully defending shelters from attempted occupation by larger congeners (Bovbjerg 1953; Griffin 1968; Sinclair 1977). This is related to the prior resident phenomenon and it is central to Nobel's (1939) definition of territory. Resident *M. rosenbergii*, regardless of their relative size, successfully retained their shelters. The mechanism the residents employed apparently was not limited to direct physical interaction. Immigrants and residents seldom fought. Generally immigrants were inactive upon placement into a tank housing a resident. The immigrant's aggressive behavior was well below its counterpart in the simultaneous introduction group. Only occasionally (Figure 1) did the immigrant seek out the shelter. This latter behavior is in direct contrast to the control group. A control group animal was usually back in its shelter within 1 min after reintroduction. Possibly an exocrine was an agent of communication between resident and immigrant prawns, since a novel environment did not inhibit exploration in animals of the simultaneous introduction experiment; and animals from the control experiment reintroduced into tanks contaminated with their own exocrines, rapidly entered their shelter.

The advantage conferred upon resident *M. rosenbergii* appears to disappear within a short period of time. The smaller resident can defend its shelter against intrusion for no longer than a few days (Figure 1). Apparently relative size can overcome the prior resident effect if resident and immigrant continue to encounter one another. Similar observations were reported by Lowe (1956). In the case of the *C. shufeldtii*, a dominance hierarchy was established before shelters were introduced. Dominant *C. shufeldtii* displaced subordinates from occupied shelters. In my experiments, *M. rosenbergii* first exhibited territoriality as determined by the presence of the prior resident effect. Territoriality then broke down, due to continued encounters, into simple dominance.

The important point addressed in this paper is not who wins or loses the encounter but which animal gains access to the resource. Investigators whose observations were limited to the first encounter might suggest that residents almost always outcompete intruders for shelter. However, I have shown that in a closed system the prior resident effect breaks down into simple size-related dominance. These results offer a behavioral explanation for the known and recognized bull effect in prawn aquaculture ponds. Larger animals have preferential access to food and shelter, two important resources which are often dispersed in a clumped or patchy fashion.

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PRINCIPAL SPAWNING AREAS AND TIMES OF MARINE FISHES, CAPE SABLE TO CAPE HATTERAS

The purpose of this compendium is to summarize spawning areas and seasons of the more abundant marine fishes of the continental shelf between Cape Sable, N.S., and Cape Hatteras, N.C., as an aid to the identification of fish eggs and larvae and planning and scheduling ichthyoplankton surveys. We have used the term "marine" to encompass fishes which spawn at sea (in contrast to estuarine spawners), although some of the species included spawn in both environments contingent on geographic location (e.g., winter flounder which spawn exclusively in estuaries in the Middle Atlantic Bight and offshore in the Gulf of Maine and Atlantic menhaden which spawn in estuaries along southern New England and in the New York Bight and offshore in the lower Middle Atlantic Bight and in the South Atlantic Bight).

The Gulf of Maine is defined as the oceanic bight bounded by Nantucket Shoals and Cape Cod on the west (long. 70°W) and Cape Sable on the east (long. 65°W) including Georges and Browns Banks and waters out to the 200-m contour (Colton 1964). The Middle Atlantic Bight is the area

inshore of the continental slope bounded by Cape Cod and Nantucket Shoals to the east (long. 70°W) and Cape Hatteras to the south (lat. 35°N). The New York Bight, as defined in the MESA New York Bight Atlas Monograph Series (Bowman and Wunderlich 1977), is the offshore water area in the bend of the Atlantic coastline from Long Island (long. 71°30′W) to New Jersey (lat. 38°30′N). A chart of the Gulf of Maine and Middle Atlantic Bight and the names of places and areas referred to in the spawning summary are given in Figure 1.

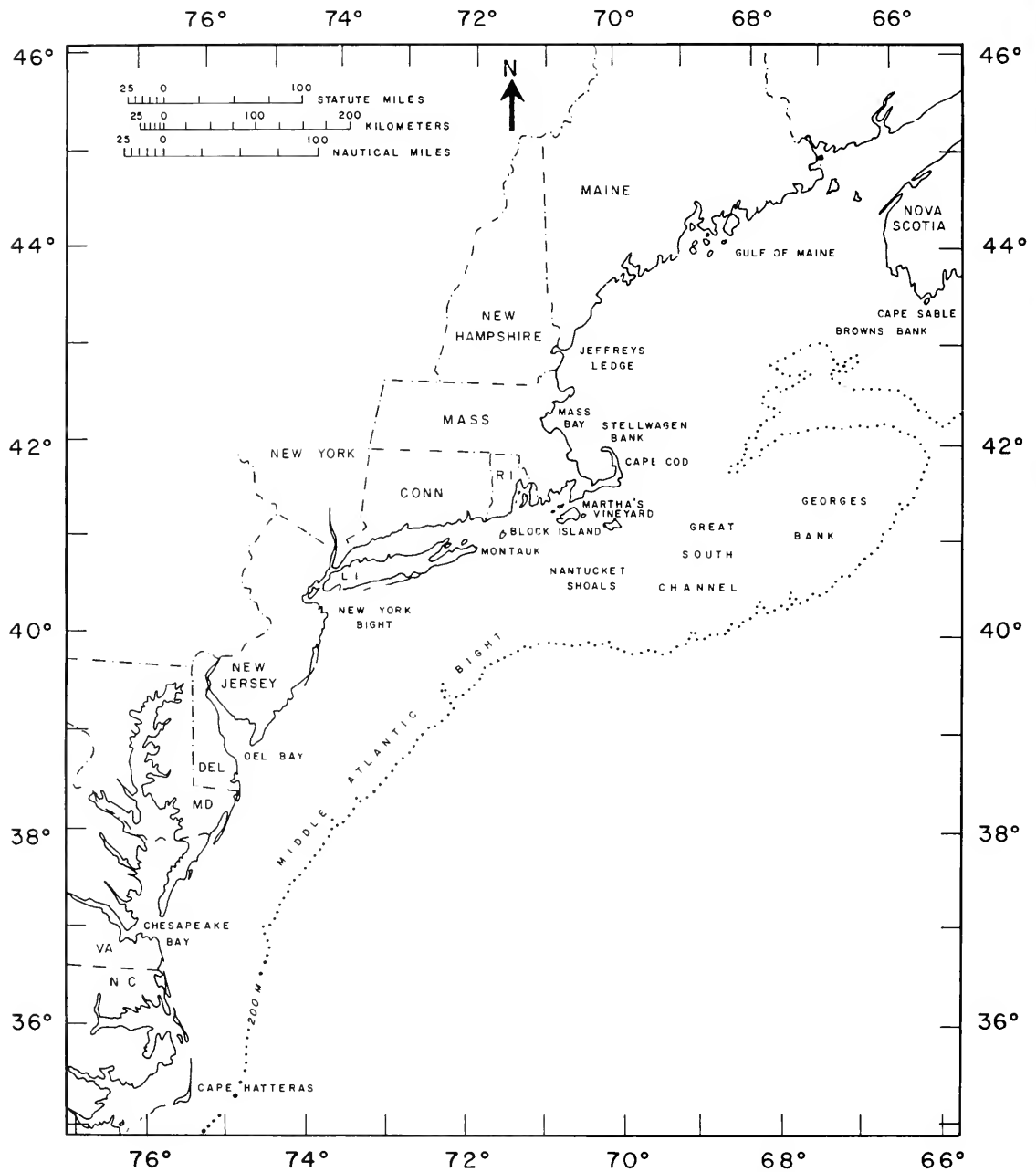


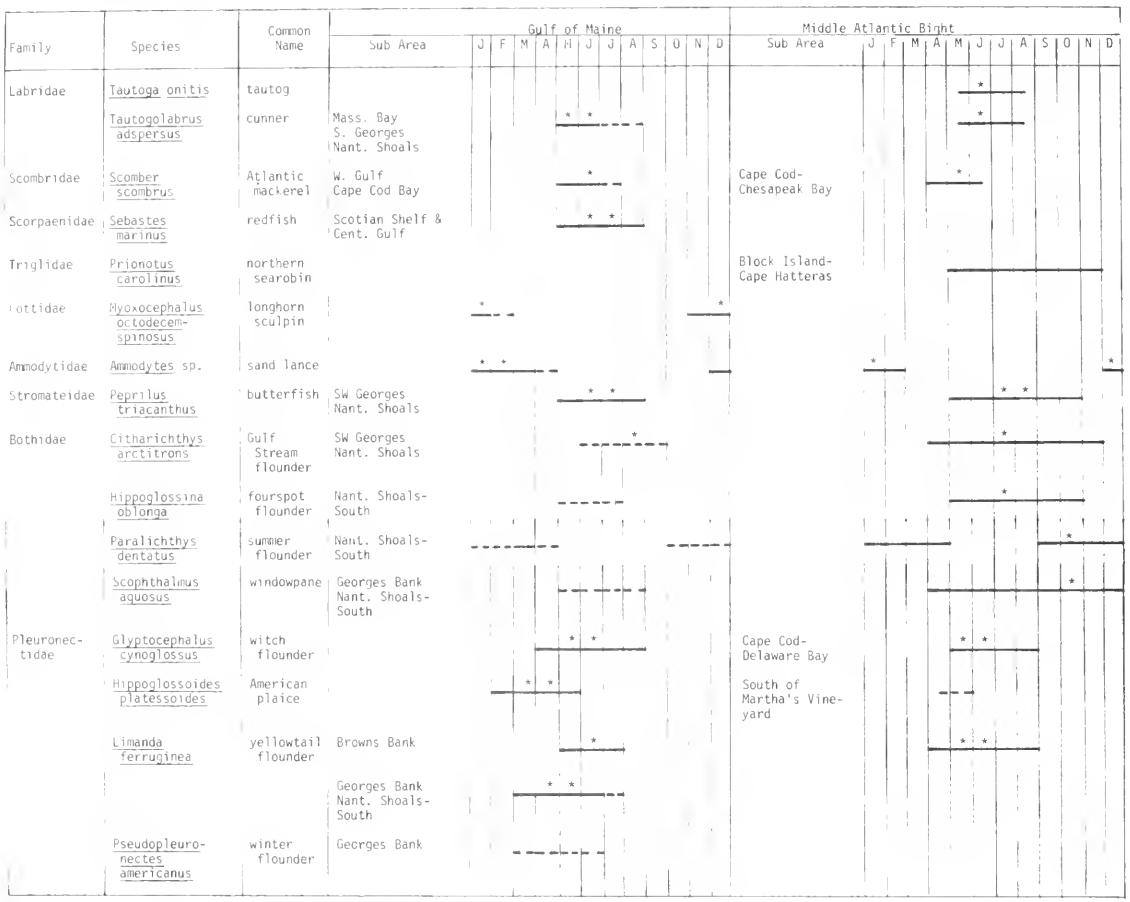
FIGURE 1.—Orientation chart of the Gulf of Maine and Middle Atlantic Bight.

In this summary (Table 1) we have treated the Gulf of Maine and the Middle Atlantic Bight separately for there is an abrupt general division between the biological and physical properties of water east and west of Cape Cod. The boreal waters over most of the Gulf of Maine are well mixed by strong tidal currents, while the circulation of the warmer shelf waters west of Cape Cod is more sluggish, and its chemical and physical properties are less complex (Colton 1964). The offing of Cape Cod also appears to be a definite transition zone (probably thermal) for some northern and southern species of fishes and invertebrates, both pelagic and benthic (Colton 1964). The species composition and abundance of fishes vary markedly between the two regions, with boreal, nonmigratory species dominating the Gulf of Maine and warmwater, migratory species prevailing in the Middle Atlantic Bight. The bulk or total spawning of many species of fishes is restricted to areas east (e.g., haddock, pollock, redfish) or west (e.g., bluefish, menhaden, anchovies) of Nantuck-

TABLE 1.—Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras.

Family	Species	Common Name	Gulf of Maine Sub Area	Middle Atlantic Bight Sub Area
Clupeidae	Brevoortia tyrannus	Atlantic menhaden		
	Clupea harengus harengus	Atlantic herring	Georges Bank	N. of Delaware
			Western Nova Scotia	
			Jeffries Ledge & Stellwagen Bank	
			Nantucket Shoals	
Engraulidae	Anchoa hepsetus	striped anchovy		
	Engraulis eurystole	silver anchovy		
Gadidae	Brosme brosme	cusk		
	Enchelyopus cimbrius	fourbeard rockling		
	Gadus morhua	Atlantic cod	Georges Bank	
			Browns Bank	
			Nantucket Shoals	
	Melanogrammus aeglefinus	haddock	Georges Bank	
			Browns Bank	
			South Channel	
	Merluccius albidus	offshore hake		
	Merluccius bilinearis	silver hake	NE Georges & Cent. Gulf	Nant. Shoals-Virginia
			Southern Georges	
	Pollachius virens	pollock	Mass. Bay Stellwagen South Channel	
	Urophycis chesteri	long finned hake		NY Bight
	Urophycis chuss	red hake	S. Georges Nant. Shoals	
	Urophycis regius	spotted hake		NY Bight-C. Hatteras
	Urophycis tenuis	white hake		Cont. Slope
Pomatomidae	Pomatomus saltatrix	bluefish		
Scianidae	Leiostomus xanthurus	spot		Ches. Bay-Cape Hatteras
	Micropogon undulatus	Atlantic croaker		Ches. Bay-Cape Hatteras
	Cynoscion regalis	weakfish		Ches. Bay-Montauk, LI

TABLE 1.—Continued.



Known spawning season.

Uncertain spawning season.

*Peak spawning.

et Shoals, although there are exceptions to this general rule (notably, yellowtail flounder and silver hake).

The spawning summaries are based primarily on published data collected on Bureau of Commercial Fisheries (now National Marine Fisheries Service) ichthyoplankton surveys of the Gulf of Maine and Middle Atlantic Bight made in the 1950's and 1960's and listed in the References. Published data from earlier studies (e.g., Fish 1929; Walford 1938; Pearson 1941; Sette 1943; Bigelow and Schroeder 1953) and some unpublished information from more recent National Marine Fisheries Service ichthyoplankton surveys have also been utilized. We have not attempted to make the bibliography encyclopedic. However, the papers cited include references to all pertinent spawning summaries. Spawning areas and seasons were determined on a basis of the occurrence of eggs and/or early stage (yolk-sac) larvae. The families are arranged in phyletic sequence (Greenwood et al. 1966) and the species are listed in alphabetical order. Common names follows those recommended by Bailey et al. (1970).

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RECENT SIGHTINGS OF THE BLUE WHALE, *BALENOPTERA MUSCULUS*, IN THE NORTHEASTERN TROPICAL PACIFIC

The blue whale, *Balenoptera musculus*, in the North Pacific, migrates to the Gulf of Alaska and Aleutians in the summer for feeding (Nishiwaki 1966). It is believed to migrate to tropical waters in winter for calving, but sightings of blue whales in lower latitudes are rare (Tomilin 1957). In mid-July 1928, Cruikshank reported seeing ". . . several blue whales . . ." at lat. 11°32'N and long. 91°58'W (Kellogg 1929). A Peruvian fishery reported taking 247 blue whales between December 1925 and March 1926 (Ingebrigtsen 1929). Potentially these were from a North Pacific stock, since the Southern Hemisphere blue whale is most numerous in the Antarctic at this time. Volkov and Moroz (1977) noted an abundance of baleen

whales between lat. 7° and 10°N. Although individual species of baleen whales were not enumerated by Volkov and Moroz, two sightings of blue whales were made on 29 March 1975 and are presented here (Table 1, *Vnushitelnyi* cruise).

Typically blue whales are seen along the Baja California coast in October while migrating southward, and subsequently reappear off Baja California in large numbers in March-June on their northward migration (Rice 1974). The whereabouts of the North Pacific blue whales during the winter months is completely unknown, but this is probably due to the lack of sighting effort. For instance, Japanese whale scouting has been carried out systematically since 1965, but their effort has been restricted to the Pacific waters north of lat. 20°N (Wada 1977).

Two theories have evolved regarding the wintering grounds of the blue whale. Wheeler (1946), suggested that blue whales winter within a limited area of the subtropics. He maintained that whales congregate in large groups in areas not frequented by vessels. A second theory maintains that wintering blue whales disperse between the feeding grounds and the tropics (Harmer 1931; Mackintosh 1942). Presented in this note is a 3-yr record of blue whales sighted in the northeastern tropical Pacific. Reference is made to migration, whale groupings, behavior, and to the oceanographic features of the sighting area. These recent sightings were made by trained observers aboard vessels involved with the National Marine Fisheries Service Tuna/Porpoise Research Program. Sighting information from other experienced observers has also been contributed.

Shipboard identification of rorquals is difficult and this problem was compounded by the fact that most of the sightings mentioned in this paper were incidental to ship's activities. However, the blue whale is easily discerned from other rorquals by the recognition of the following combination of characteristics:

1. Mottled blue-grey coloration. All other rorquals are uniformly steel grey on the dorsal surface.
2. A small dorsal fin of varying shapes located in the posterior third of the body. The dorsal fin of the sei, fin, and brydes whales is larger, falcate shape, and placed farther anterior than the blue whale dorsal fin.
3. A U-shaped rostrum. The rostrum shape of other balenopterids is more pointed.
4. Tall, dense, disperse blows. Generally, the blow of the sei and brydes whales is low and dissipated, while the fin whale has a tall conical-shaped blow.

A total of 11 cruises are discussed in this report, covering the period from January to May for 1971, 1975, 1976, and 1977.[1] The area of effort and sightings of blue whales are reported in Figure 1. The

[1]No blue whale sightings were made in 1977, although two cruises have been included in Figure 1 to complement survey effort.

TABLE 1.—Annotated list of blue whale sightings by National Marine Fisheries Service observers in the northeastern tropical Pacific, January-May 1971-76.

Date	Lat., Long.	No. of whales	Observations	Cruise/Observer
8 Jan. 1971	07°54'N, 095°52'W	1		*Nautilus*/Leatherwood
23 Jan. 1975	01°30'N, 083°04'W	1	Dove for 7 min	*Pan Pacific*/Friedrichsen
3 Feb. 1975	07°29'N, 093°48'W	cow and calf	3 dives, 5.57 min/dive; length: cow 27 m, calf 8-10 m	*Aquarius*/Wade
4 Feb. 1975	07°48'N, 097°40'W	1	Surfaced in middle of tuna school	*Finesterre*/Walker
7 Feb. 1975	07°45'N, 098°21'W	1	5 dives, 10.11 min/dive	*Aquarius*/Wade
7 Feb. 1975	07°47'N, 098°24'W	1	2 dives, 8.19 min/dive	*Aquarius*/Wade
7 Feb. 1975	07°52'N, 098°47'W	2	Small unidentified whale, 10 m, with visible blow, swimming with a large blue whale	*Aquarius*/Wade
7 Feb. 1975	07°47'N, 099°00'W	1	3 dives, 11.39 min/dive, exposed tail fluke on all dives	*Aquarius*/Wade
9 Feb. 1975	08°50'N, 096°04'W	4-6	Paired groups, length estimate: 27 m	*Pan Pacific*/Friedrichsen
10 Feb. 1975	08°33'N, 096°47'W	1		*Pan Pacific*/Friedrichsen
15 Feb. 1975	08°36'N, 096°29'W	1		*Pan Pacific*/Friedrichsen
17 Feb. 1975	08°58'N, 096°54'W	8-10	Mostly pairs dispersed over several square miles; all headed northeast	*Pan Pacific*/Friedrichsen
17 Feb. 1975	08°53'N, 096°36'W	1		*Pan Pacific*/Friedrichsen
29 Mar. 1975	08°55'N, 093°34'W	10-13		*Vnushitelnyi*/Rice
29 Mar. 1975	09°07'N, 093°55'W	6-7		*Vnushitelnyi*/Rice
13 Feb. 1976	09°44'N, 092°25'W	2		*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°31'W	1	Length estimate: 23 m	*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°35'W	4-5	Whales dispersed over 4-5 mi²	*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°52'W	1	Exposed tail flukes prior to sounding	*Cromwell*/Friedrichsen et al.
28 May 1976	10°31'N, 092°45'W	1	Length estimate: 20 m	*Martinac*/Friedrichsen

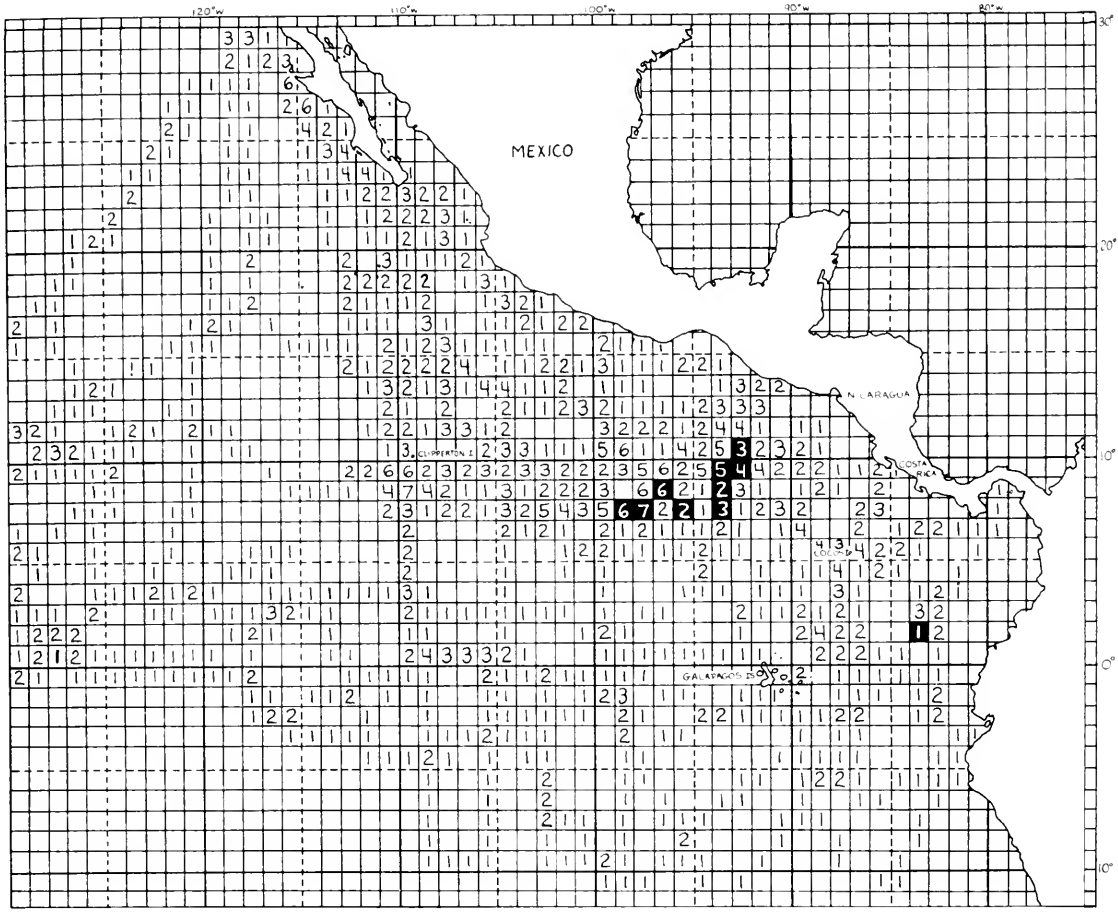

FIGURE 1.—Survey effort for blue whales in the northeastern tropical Pacific over 11 cruises from January to June in 1971, 1975, 1976, and 1977. Each numeral represents the total number of times that vessels entered a 1° block. Darkened blocks indicate blue whale sightings.

fact that blue whales have been sighted in the same general area for three winters indicates that North Pacific blue whales may have a distinct wintering ground to which they migrate each year.

The location of the suggested wintering grounds indicated by the sighting data are lat. 7°29′-10°31′N and long. 95°25′-99°00′W.[2] Only 1 of the 20 blue whale sightings (lat 1°30′N and long. 83°04′W, 23 January 1975, a solitary individual) was outside of these bounds. The equatorial sighting location of this whale may indicate that either it was not from the North Pacific population, or that North Pacific blue whales do not restrict migration to the hypothetical wintering grounds.

[2]Cruikshank's observations, in 1928, were also in this area.

Whale Groupings and Behavior

Blue whales are believed to be found singly or in pairs (Leatherwood et al. 1976). In fact, Nemoto (1964) reported that blue whales observed on the summer feeding grounds were solitary. However, five of the sightings reported here were aggregations of whales dispersed over several square miles. Many of the whales were paired. The multiple sightings on 7 February 1975 and 13 February 1976 appear to be mostly of solitary animals (Table 1). However, on both days, no less than 40 n.mi. separated the first and last whales sighted. Also, four out of the five whales observed on 7 February 1975 were headed in a northeasterly direction. This information may indicate that these apparently solitary whales were part of a large dispersed group.

At least one cow and calf were observed and possibly a second pair (Table 1). This is the first actual record of a blue whale calf in the tropics, although historically it has been believed that blue whales have their calves in the warm tropical waters (Mackintosh 1966:126).[3]

Oceanographic Features

There are several unique oceanographic features which relate to the sighting location of the blue whales. Cromwell (1958) and Wyrtki (1964) discussed the Costa Rican Dome which is located at approximately lat. 9°N, long. 89°W. The dome is apparently a permanent topographic feature (150 km × 300 km) and is formed by the convergence of several major current systems. These currents typically create an area of nutrient transport or upwelling. High standing stocks of zooplankton in the area near the Costa Rican Dome (lat. 7°25′N-10°N) has been reported by several authors (Reid 1962; Blackburn et al. 1970; Holmes[4]). Volkov and Moroz (1977) suggested that the high stable food base of the area creates a habitat suitable for nonmigratory populations of baleen whales. North Pacific blue whales may also use this area for their winter feeding grounds.

In conclusion, the recent sightings of blue whales in the tropics indicates that North Pacific blue whales have a wintering area to which they return each year. Since most of the cruises have occurred largely during the winter months, more information must be collected to determine if whales are found in this area the year round. The high standing stock of zooplankton in this area may indicate that this is a winter feeding area, as well as a calving ground.

Acknowledgments

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[3]The average water temperature for 11 sightings was 26.5°C.

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SEX COMPOSITION, LENGTH-WEIGHT RELATIONSHIP, AND REPRODUCTION OF THE WHITE MARLIN, *TETRAPTURUS ALBIDUS*, IN THE WESTERN NORTH ATLANTIC OCEAN[1]

In the Atlantic, white marlin, *Tetrapturus albidus*, range from lat. 35°S to 45°N with concentrations in the western Atlantic, including the Gulf of Mexico, and the Caribbean Sea (Mather et al. 1975). Tag returns show that some white marlin migrate seasonally from the U.S. Middle Atlantic Bight (the coastal area between Cape Cod and Cape Hatteras) in the summer to the southeastern Caribbean Sea in the winter (Mather et al. 1972). Commercial catches by Japanese longline vessels support the tagging results, but the catches also indicate that a second group of white marlin moves from a wintering area in the southeastern Caribbean to summer grounds in the Gulf of Mexico (Ueyanagi et al. 1970; Mather et al. 1972; Wise and Davis 1973).

A substantial sport fishery exists for white marlin in the Atlantic off North and South America. In the United States, the major sport fisheries occur along the Middle Atlantic States, from New Jersey to North Carolina, off southeast Florida, and along the Gulf Coast States. Important sport fisheries also occur in the Bahamas, off Havana, Cuba, and along the coast of Venezuela (Mather et al. 1972). Another important sport fishery recently developed off eastern Brazil (Anonymous 1976).

The white marlin is also an incidental catch of commercial longline vessels fishing for tuna in the Atlantic and Gulf of Mexico (Mather et al. 1975). The marlin is highly prized as a food item in some countries (Kume and Joseph 1969).

My review of the literature on white marlin shows that there is a need for additional information on sex composition and length-weight relationships. Until recently, no information was available regarding its reproductive potential (Baglin[2]). In this paper I update reproductive and sex ratio data presented by Baglin (see footnote 2) and include length-weight relationships.

Materials and Methods

White marlin from the northern Gulf of Mexico (hereafter referred to as the gulf), the Florida Straits, the western Bahamas, and the Middle Atlantic Bight of the western North Atlantic (hereafter referred to as the Atlantic) were sampled from anglers' catches at sport fishing tournaments and at Pflueger Marine Taxidermy, Inc., Hallandale, Fla. One marlin was collected by longline in the Windward Passage between Cuba and Hispaniola during RV *Oregon* Cruise 66.

Sex data were obtained from 1,128 white marlin captured by anglers in the gulf (1971-77) and from 720 white marlin caught by anglers from the Atlantic (1972-77).

Lengths and weights were obtained from 904 white marlin captured in the gulf (1971-76) and from 489 white marlin captured in the Atlantic (1972-76). Body lengths (straight distance from tip of lower jaw to tips of midcaudal rays) were measured in centimeters (Rivas 1956); weights were recorded to the nearest pound and converted to kilograms.

[1]Contribution No. 78-44M, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, Fla.

[2]Baglin, R. E., Jr. 1977. Maturity, fecundity and sex composition of white marlin (*Tetrapturus albidus*). Collective Volume of Scientific Papers 6(79):408-416. International Commission for the Conservation of Atlantic Tunas, Madrid, Spain.

Ovaries from 186 females caught from 1972 through 1976 were examined. Fresh ovaries were either blotted dry and weighed in grams or stored in 10% Formalin[3] and weighed later. No significant difference was found between the mean weight of fresh and preserved ovaries ($F = 0.0001$; df = 1, 16; $P > 0.75$). The gonosomatic index (GSI), ovary weight as a percentage of total body weight, was used as an indicator of maturity.

Preserved eggs 0.56 mm in diameter and larger were counted when estimating fecundity. Eggs <0.56 mm were less spherical in shape and in an earlier stage of development. The 0.56-mm size was determined by measuring the diameters of 3,912 eggs from mature, partly spent, and spent fish. Small transparent ova were stained with aceto-carmine to facilitate measuring. Egg diameters were measured with an ocular micrometer at 30× magnification and the orientation of egg diameters was assumed to be random. Thin cross sections were taken from the anterior, middle, and posterior parts of one ovary of a mature fish and subdivided into three subsamples, representing the center, midregion, and periphery of the ovary (Otsu and Uchida 1959).

Fecundity was defined as the potential number of mature eggs (yolked ova in the most advanced size mode) that could be spawned during one reproductive season and was estimated using a dry weight method. For six fish in which entire ovaries were saved for fecundity analysis, subsamples consisted of a thin cross section taken from the anterior, middle, and posterior parts of each ovary. The eggs in these subsamples were separated from the ovarian tissue, enumerated, dried, and weighed according to the procedure described by Baglin (see footnote 2). For six other fish, only the ovary weight and a single cross section from the middle of the ovary were taken; these cross sections comprised the subsamples. The eggs were separated, counted, dried, and weighed. A dry/wet weight regression was used to estimate the total dry weight of the eggs in these ovaries, which were not saved. Before the eggs in the subsample were counted, 25 eggs 0.30 mm and larger from the two most advanced modes were randomly selected and measured. Eggs in this second most advanced mode were included to give an indication of the percentage of eggs in both modes because future histological studies may indicate that these smaller eggs undergo further development and are also spawned. Fecundity estimates, rounded to the nearest 0.1 million eggs, were calculated from the relationship: $C = (AD/B) + A$, where A is the number of mature ova in the subsample, B is the weight of the ova in the subsample, C is the number of mature ova, and D is the weight of ova from both ovaries.

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

Results and Discussion

Sex Composition

From 1971 through 1977, sex was determined from 1,128 white marlin from the gulf (Table 1). The deviation from an expected 1:1 sex ratio was significant from May through October. Sampling was inadequate for the remaining months. Females were more prevalent than males for each month studied.

From 1972 through 1977, sex was determined for 720 white marlin from the Atlantic (Table 1). There were 323 sex determinations from the Florida Straits (March through May) and 397 from the Middle Atlantic Bight (June through September). Sampling was inadequate from October through February. No significant difference from an expected 1:1 sex ratio was found for March, May, July, August, and September, but a significant difference was found for April and June. For the months in which the sex ratio was significantly different from the expected 1:1 ratio, females were more prevalent.

deSylva and Davis (1963) found a significant difference from an expected 1:1 sex ratio (60% females) when they combined their data from the Middle Atlantic Bight for the summers of 1959 and 1960. They presented monthly sex composi-

TABLE 1.—Monthly sex ratios for white marlin from the northern Gulf of Mexico (1971-77), Florida Straits and Middle Atlantic Bight (1972-77).

Location	Month	Number of white marlin	Sex ratio (females/males)
Gulf of Mexico	May	21	4.25*
	June	85	4.00*
	July	374	3.16*
	August	444	1.63*
	September	150	1.50*
	October	54	1.84*
Florida Straits	March	103	0.87
	April	172	1.96*
	May	48	1.40
Middle Atlantic Bight	June	55	3.23*
	July	56	1.67
	August	219	0.80
	September	67	0.97

*Significant departure from null hypothesis at 0.05 level (chi-square).

tion data for 1960 only. My analysis of their data shows a significant difference for June and July but no significant difference for August and September. Their findings for June, August, and September agree with those in this study. The extreme difference in sex ratios found in the present study for the gulf (May through October) and for the Florida Straits in April has not been reported previously. The above findings suggest that some white marlin segregate into distinct areal groups according to the predominating sex and that sex ratios may change with season. A similar occurrence has been noted for the blue marlin, *Makaira nigricans* (Kume and Joseph 1969).

Length-Weight Relationship

The average length of females is greater than that of males from both the gulf and the Atlantic (Figure 1). It is also apparent (Figures 2, 3) that the average length of females is greater than that of males from each area for each month studied. This difference may be due to faster growth of females or higher mortality of males and should be considered in future growth studies of the white marlin.

The length-weight relationship by sex was determined for white marlin taken in the gulf from 1971 through 1976 (Figure 4) and in the Atlantic from 1972 through 1976 (Figure 5). Analysis of covariance (Table 2) indicated that length-weight regression coefficients were significantly different between gulf females and males ($F = 16.0$; df = 1, 900; $P<0.001$), gulf males and Atlantic males ($F = 19.2$; df = 1, 514; $P<0.001$), and gulf females and Atlantic females ($F = 10.8$; df = 1, 871; $P<0.001$). The adjusted means were also significantly different between Atlantic females and males ($F = 13.4$; df = 1, 486; $P<0.001$). These findings agree with those of Lenarz and Nakamura (1974), who found a significant difference between sexes in the relationship between weight and eye-fork length for white marlin from the gulf during 1971.

Analysis of covariance was conducted for the length-weight relationship, on a monthly basis, for which sufficient samples were available: gulf females versus Atlantic females in May, June, August, and September, and gulf males versus Atlantic males for June, August, and September. A significant difference in the regression coefficients was found only for the August males ($F = 13.7$; df = 1, 211; $P<0.001$). A significant difference in adjusted means was found for females during June ($F = 9.3$; df = 1, 74; $P<0.005$) and August ($F = 12.0$ df = 1, 286; $P<0.001$), and for males during September ($P = 7.6$; df = 1, 73; $P<0.01$).

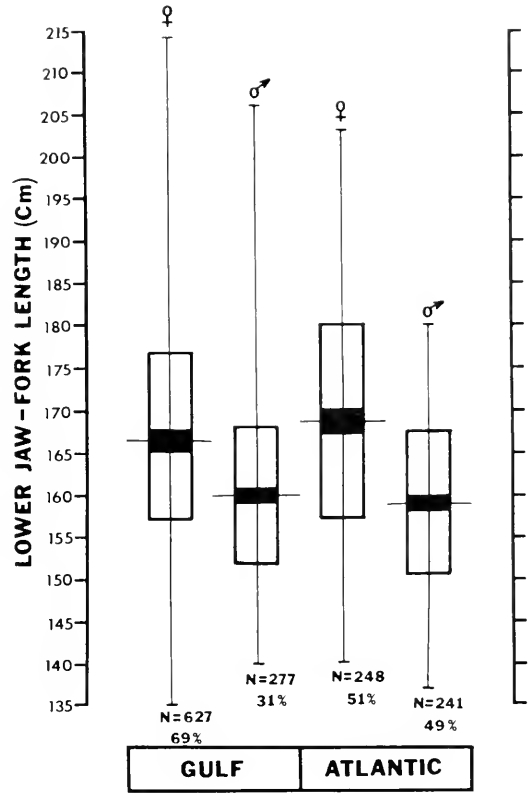

FIGURE 1.—Comparison of length between female and male white marlin collected in the northern Gulf of Mexico (1971 through 1976) and in the Atlantic (1972 through 1976). The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

Differences between length-weight relationships of white marlin from the gulf and the Atlantic suggest the possibility of separate groups inhabiting the two areas. Tag returns, however, showed there is at least some migratory movement from the Middle Atlantic Bight to the gulf. To date, tag return data have not shown white marlin migrations in the reverse direction, although one fish tagged in the gulf was recaptured off Cuba, giving some support to the likelihood that they do migrate in the opposite direction (Chester C. Buchanan, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun.)

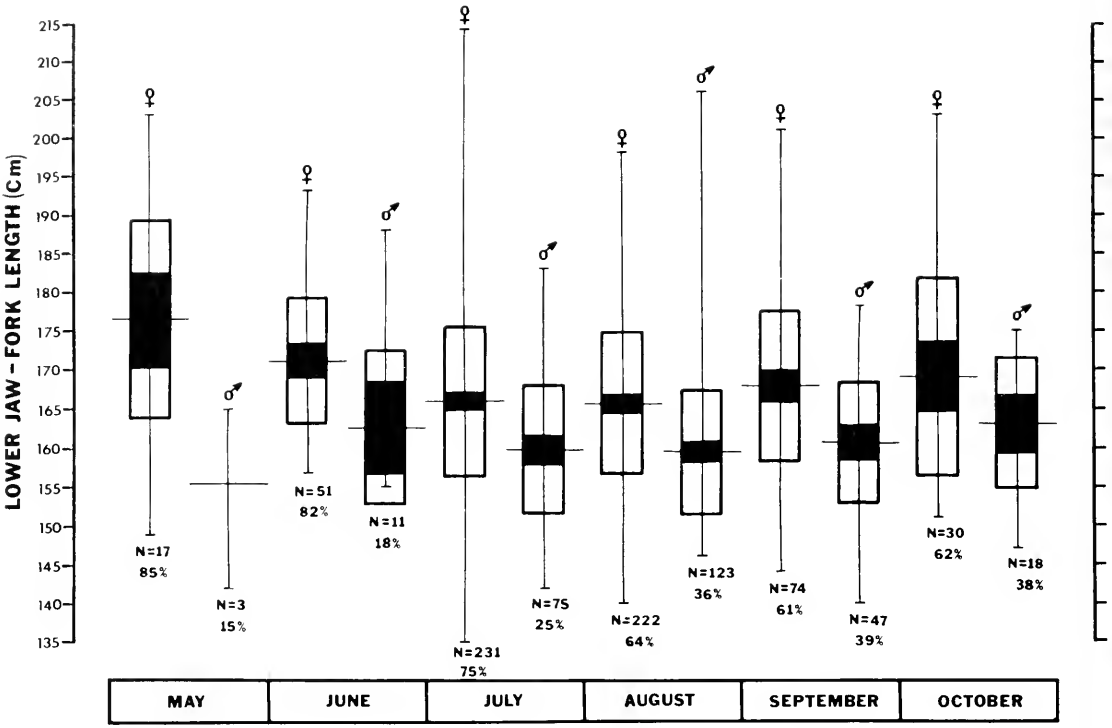

FIGURE 2.—Monthly comparisons of length between female and male white marlin collected in the northern Gulf of Mexico during 1971 through 1976. The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

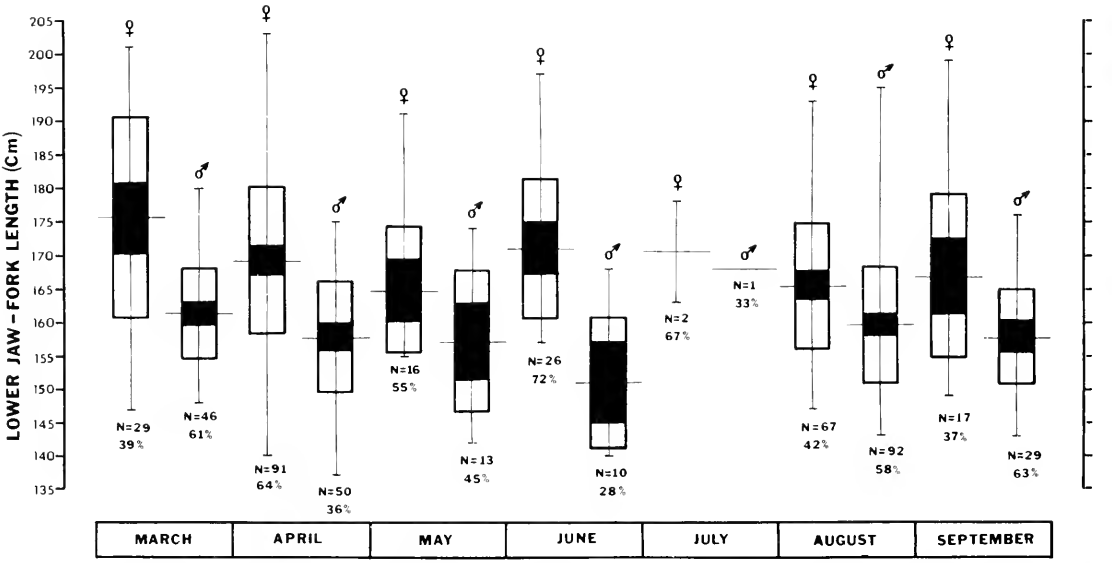

FIGURE 3.—Monthly comparisons of length between female and male white marlin collected in the Atlantic during 1972 through 1976. The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

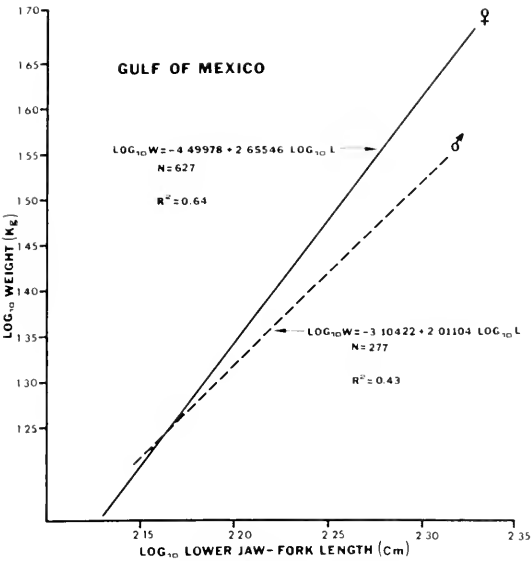

FIGURE 4.—Length-weight relationship (log transformation) for female and male white marlin from the northern Gulf of Mexico.

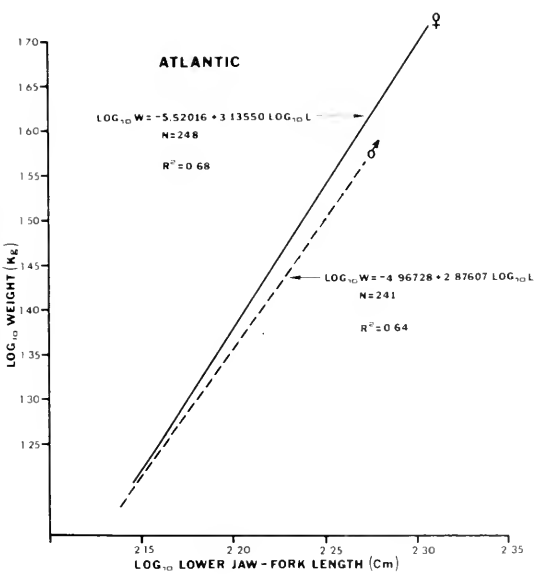

FIGURE 5.—Length-weight relationship (log transformation) for female and male white marlin from the Atlantic.

TABLE 2.—Regression equations, number, sum of squares of x, and mean square calculated for the length-weight relationship ($\log_{10}$ transformations) of white marlin from the northern Gulf of Mexico and the Atlantic.

$Y = \overline{Y} + b(X - \overline{X})$	N	Σx^2	$\frac{\Sigma y^2 - b\Sigma xy}{N-2}$
Gulf and Atlantic females:			
1.41704 + 2.88186(X − 2.22302)	875	0.604832	0.00336706
Gulf and Atlantic males:			
1.34355 + 2.37655(X − 2.20228)	518	0.254956	0.00299720
Gulf females:			
1.39996 + 2.65546(X − 2.22174)	627	0.396458	0.00252756
Gulf males:			
1.32735 + 2.01104(X − 2.20363)	277	0.128593	0.00250737
Atlantic females:			
1.46021 + 3.13550(X − 2.22624)	248	0.204773	0.00377638
Atlantic males:			
1.36217 + 2.87607(X − 2.20073)	241	0.125280	0.00244554
May gulf females:			
1.48714 + 2.60014(X − 2.24572)	17	0.0164014	0.00365206
May Atlantic females:			
1.44276 + 2.96929(X − 2.21669)	16	0.0085322	0.00226977
June gulf females:			
1.44221 + 3.22066(X − 2.23317)	51	0.0210122	0.00162473
June Atlantic females:			
1 40502 + 2.60180(X − 2.23216)	26	0.0163375	0.00323226
June gulf males:			
1.35686 + 3.55091(X − 2.21054)	11	0.00624798	0.00085387
June Atlantic males:			
1.24868 + 3.01101(X − 2.17815)	10	0.00707686	0.00165193
August gulf females:			
1.38976 + 2.72170(X − 2.21831)	222	0 121132	0.00226799
August Atlantic females:			
1.41118 + 2.81615(X − 2.21783)	67	0.0391569	0.00206003
August gulf males:			
1.32575 + 1.93866(X − 2.20207)	123	0.524543	0.00179221
August Atlantic males:			
1.35384 + 2.91546(X − 2.20279)	92	0.0484607	0.00169370
September gulf females:			
1.40689 + 3.01922(X − 2.22399)	74	0.0440863	0.00317564
September Atlantic females:			
1.42732 + 3.10221(X − 2.22137)	17	0.0150308	0.00160237
September gulf males:			
1.32709 + 1.39787(X − 2.20530)	47	0.0199974	0.00220416
September Atlantic males:			
1.34390 + 2.01746(X − 2.19767)	29	0.0105484	0.00144724

Reproduction

A significant difference in egg diameter was found among the anterior, middle, and posterior sections of an ovary from a mature fish ($F = 7.7$; df = 2, 2,676; $P<0.001$). There was no significant difference in mean diameter among the center, midregion, and periphery within each of the three sections. Because some heterogeneity occurred, estimates of fecundity were based, when possible, on eggs from each section of both ovaries. Heterogeneity of egg size within an ovary has also been shown for albacore, *Thunnus alalunga* (Otsu and Uchida 1959), and swordfish, *Xiphias gladius* (Uchiyama and Shomura 1974).

The left ovary ($\overline{X}$ = 25.0 cm, $S_{\overline{X}}$ = 0.732) was significantly longer (F = 35.7; df = 1, 196; $P<0.001$) than the right ovary ($\overline{X}$ = 19.4 cm, $S_{\overline{X}}$ = 0.561). Eldridge and Wares (1974) reported differential growth in the size of ovaries for striped marlin, *Tetrapturus audax*, and for sailfish, *Istiophorus platypterus*. Both were similar to the white marlin in having larger left ovaries.

Well-developed ovaries were present only in 12 white marlin collected during April and May in the Florida Straits. These fish had a GSI of about

6% or greater and were used for estimating fecundity. The mean GSI showed that ovarian weights were lowest during October and increased from November through May (Figure 6). The mean GSI of 2.6 for April and May is lower than the 4.5 mean GSI found by Krumholz (1958) for late April. The GSI of 9.3 (Table 3) agrees with the highest GSI of 9.76 found by Krumholz. The high mean GSI values determined by me for April and May, with the sudden decrease in June, indicated that spawning probably occurred during April and May (Figure 6). Therefore, only one spawning season per year was indicated for the Florida Straits.

White marlin may also spawn in other areas. One fish captured in April 1976 in the Windward Passage had ripe eggs measuring 1.16 mm. Hayasi et al. (1970) found white marlin with mature gonads during April-June in the northern Caribbean. Erdman (1956) found well-developed ovaries in white marlin caught off Puerto Rico in April and found well-formed eggs in a fish taken in June from the same locality.

The smallest fish approaching a ripe condition with large ovaries weighed 26.8 kg (Table 3). Ueyanagi et al. (1970) reported that white marlin reach sexual maturity at 130 cm eye-fork length. Using the conversion equation of Lenarz and Nakamura (1974), 130 cm eye-fork length would be equal to about 20.3 kg.

Frequency distributions of white marlin ovum diameters were made from measurements on 3,912 ova from spent, partly spent, and mature fish (Figure 7). Spent fish caught during May and June contained mostly eggs 0.15 mm in diameter and smaller. Eggs from a partly spent fish caught during June had a frequency mode of about 0.35 mm, with few eggs larger than 0.60 mm. Some of the larger eggs appeared to be undergoing absorption. Jolley (1977), in his histological examination of spent sailfish, found degeneration and absorption of advanced unovulated eggs common. Merrett (1970), studying several species of billfish from the Indian Ocean, suggested that there also may be at least a partial resorption of resting

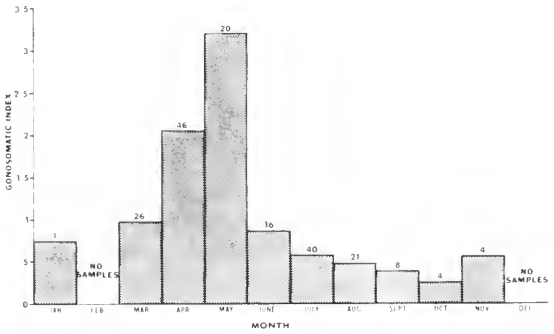

FIGURE 6.—Seasonal variation of mean gonosomatic index in 186 white marlin collected from 1972 to 1976 (number of fish indicated above histograms).

TABLE 3.—Weight, length, and gonadal data for 12 female white marlin from the Florida Straits collected during 1972, 1974, and 1975. The mean and standard error of the mean are given at the bottom of the columns.

Body weight (kg)	Body length (cm)	Ovary wet weight (g)	Gonosomatic index	Estimated number of eggs: .0.55 mm in diameter (millions)	Estimated number of eggs: .0.29 mm in diameter[1] (millions)
26.8	160	[2]1,600	6.0	5.4	10.4
26.8	169	[2]2,050	7.6	4.8	8.0
30.4	168	[2]2,324	7.6	7.0	11.7
30.4	176	[2]1,700	5.6	3.8	7.3
31.3	168	2,908	9.3	10.4	18.6
32.7	166	2,150	6.6	7.1	11.8
32.7	166	2,693	8.2	10.1	16.8
33.6	167	2,161	6.4	7.6	11.9
35.0	169	[2]2,250	6.4	6.5	10.2
35.4	170	[2]2,320	6.6	7.5	14.4
36.3	171	2,488	6.8	10.5	20.2
37.2	179	[2]2,050	5.5	8.1	14.5
32.4	169	2,224	6.9	7.4	13.0
0.98	1.4	107	0.32	0.62	1.16

[1]Estimated using actual percent from 0.30 to 0.55 mm in diameter from 25 eggs measured for each fish.
[2]Entire ovaries available.

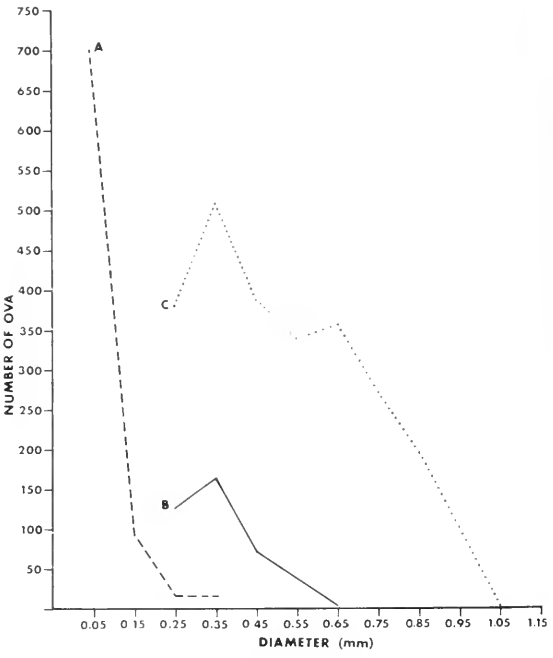

FIGURE 7.—Frequency distribution of white marlin ovum diameters for: A, four spent fish (827 ova) in May and June; B, one partially spent fish (406 ova) in June; C, one mature fish (2,679 ova) in April.

oocytes. I found frequency modes of about 0.35 mm and 0.65 mm in a mature fish caught in April. Only eggs measuring 0.56 mm and larger were included when estimating fecundity. Because there were two frequency modes present in mature fish, an estimate of the number of eggs 0.30 mm in diameter and larger is also presented (Table 3).

Fecundity, based on the number of ova in the most advanced size mode, ranged from 3.8 to 10.5 million eggs ($\bar{X} = 7.4, S_{\bar{X}} = 0.62$) for white marlin weighing 26.8 to 37.2 kg (Table 3). The number of mature ova per gram of body weight ranged from 125 to 332 ($\bar{X} = 227, S_{\bar{X}} = 16.76$). The average number of eggs measuring 0.30 mm in diameter and larger was estimated as 13 million ($S_{\bar{X}} = 1.16$).

Fecundity was based on the number of fully yolked eggs, forming a group distinct from another group of developing eggs. Fecundity would vary depending on whether smaller eggs develop further or are absorbed. If fractional spawning occurs, as reported for sailfish by Jolley (1977), the eggs in the next distinct group should be included in seasonal fecundity estimates.

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RECORDS OF PISCIVORUS LEECHES (HIRUDINEA) FROM THE CENTRAL COLUMBIA RIVER, WASHINGTON STATE

No records of leech infestations on fish of the Columbia River exist in the published literature. As a whole, the freshwater hirudinean fauna of the Pacific Northwest remains a relatively unsurveyed, little known, and neglected biotic group. This is due, in part, to problems in leech identification as well as in obtaining representative collections.

We obtained leeches from the external surface, oral cavity, and gill chambers of fish during a continuing environmental assessment program on the central Columbia River above Richland, Wash. (Benton and Franklin Counties), from 1975 through 1977. This paper identifies four piscivorous species, provides new host and distribution records, and reviews some recent taxonomic changes for the species encountered. Ecological observations are included.

The leeches recorded herein are *Myzobdella lugubris* Leidy 1851, *Piscicola salmositica* Meyer 1946, *Placobdella montifera* Moore 1906, and *Actinobdella inequiannulata* Moore 1901.

Methods and Site Description

Fish were collected at monthly or bimonthly intervals by a variety of gear (gill nets, trammel nets, hoop nets, beach seines, and electroshocker) from January 1975 to December 1977. Over 20,000 fish, representing nearly 40 species, were examined during this period (Gray and Dauble 1977). Leech specimens were preserved in 10% Formalin[1] solution, either when captured or after being examined alive in the laboratory.

Our leech collections were more qualitative than quantitative because leech-fish associations in nature are normally periodic and facultative despite the nutritional requirement of piscivorous leeches for fish blood. Also, piscivorous leeches can readily detach from fish captured by most types of fishing gear, particularly from fish recovered when moribund or dead.

Occurrence of many freshwater leech species can be correlated with characteristic aquatic habitats. Water quality parameters vary seasonally in the central Columbia River, as follows: dissolved oxygen, 8.0-12.0 mg/l; pH, 7.4-8.6; phosphate (as PO_4), 0.03-0.04 mg/l; ammonia-nitrogen, 0.01-0.2 mg/l; hardness (Ca, Mg), 55-75 mg/l; and alkalinity ($CaCO_3$), 50-67 mg/l. Water temperatures range from 1° to 3°C in midwinter to about 21°C in late August and early September. There are no significant quantities of organic and inorganic pollutants (our data). The water carries minimal silt loads.

The central Columbia River in the Hanford Reach where our collections were made (river km 550-629) survives as the last free-flowing section of the main channel above Bonneville Dam. Decades of hydroelectric development have transformed other sections into a consecutive series of river-run reservoirs. River flows in the study area usually range from about 2,000 m^3/s over much of the year to over 12,000 m^3/s during the annual spring spate, when surplus runoff is passed downriver over spillways from reservoirs (Nees and Corley[2]).

Additionally, Hanford flows are now regulated at Priest Rapids Dam in response to daily and weekly power demand peaks, causing water levels in the river to fluctuate widely. This periodically exposes and inundates a rocky or muddy shoreline zone, apparently restricting development of a diverse leech fauna along the river margins. Water levels in Wanapum Reservoir behind Priest Rapids Dam (river km 639) and in Umatilla Reservoir behind McNary Dam (river km 470) are relatively stable, although subject to controlled summer drawdowns. Substantial populations of such common omnivorous leeches as *Erpobdella punctata* (Leidy 1870), *Helobdella stagnalis* (Linnaeus 1758), and *Theromyzon* spp. occur along the

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

[2]Nees, W. L., and J. P. Corley. 1974. Environmental surveillance at Hanford for CY-1973. Unpubl. manuscr., 56 p. R&D Rep., BNWL-1881, Battelle, Pacific Northwest Laboratories, Richland, WA 99352.

margins of these mid-Columbia River reservoirs (our observations).

Results and Discussion

Four leech species were recovered from Columbia River fish (Table 1). About 90% of the specimens were *Myzobdella lugubris*. Two families belonging to the order Rhynchobdella were represented, Glossiphoniidae and Piscicolidae. Members of this order typically possess a small pore on the anterior sucker for a mouth, from which a muscular pharyngeal proboscis can be protruded, and lack biting jaws or denticles. Relatively few glossiphoniids are piscivorous (Klemm 1975). However, the piscicolids characteristically are ectoparasites of fish and feed on fish blood. The muscular proboscis of piscicolids is effective in penetrating epidermal layers of fish wherever scales are reduced or absent, although gills are favored feeding sites.

Myzobdella lugubris

Myzobdella lugubris has not been recorded previously as a common ectoparasite of Columbia River fish. Its distribution and host records are included in previous publications that refer to the genus *Illinobdella* in which *M. lugubris* was formerly placed.

Myzobdella lugubris and *M.* (syn. *Illinobdella*) *moorei* (Meyer and Moore 1954) were until recently believed to be two distinct species. The former was considered characteristic of brackish and marine waters, while the latter was considered characteristic of freshwater. The distinction was primarily ecological since anatomical features of both species were remarkably similar. However, *M. lugubris* and *M. moorei* are now considered to be a single euryhaline species (Sawyer et al. 1975).

Further, it now appears that all members of the related piscicolid genus *Illinobdella* are synonymous with *M. lugubris*. Thus species reported in the literature as *Illinobdella alba*, *I. elongata*, and *I. richardsoni*, as well as *M.* (=*I.*) *moorei*, all preying on fish in North American waters (Meyer 1940, 1946b), are junior synonyms of *M. lugubris*, which holds taxonomic priority. Locality and host records of the ubiquitous *M. lugubris* under these synonyms are given by Hoffman (1967), Klemm (1972a, b, 1977), and Sawyer et al. (1975). Studies on *M. lugubris* infesting the blue crab, *Callinectes sapidus*, and the white catfish, *Ictalurus catus*, in a South Carolina tidal river support this synonymy (Daniels and Sawyer 1975).

Myzobdella lugubris was recovered from a wide size range of adult chiselmouth, *Acrocheilus alutaceus*, and northern squawfish, *Ptychocheilus oregonensis*, in our collections, and less frequently from adult suckers, *Catostomus macrocheilus* and *C. columbianus*. The associations were apparently facultative. *Myzobdella lugubris* occurred primarily in the oral cavity of chiselmouth (Figure 1) and northern squawfish, where they were retained during the struggle of hosts captured in overnight net sets. Leeches were recorded and counted the next day when fish were recovered. Many leeches on the external surfaces of moribund or dead fish may have detached before net recovery. *Myzobdella lugubris* were never found in the mouth of suckers but only in the axila of pelvic or pectoral fins, on fin rays, or in the gill chambers.

Myzobdella lugubris was also a fairly common ectoparasite of brown bullhead, *I. nebulosus*, collected by angling in backwater sloughs of the central Columbia and lower Snake Rivers during the summer. Infestations on bullheads usually consisted of one or two small leeches attached to the pectoral or pelvic fins.

The incidence of *M. lugubris* on adult chiselmouth and northern squawfish (Table 2) shows infestations only during June, July, and August when Columbia River water temperatures ranged from 13° to 21°C. The leeches were primarily sexually mature. Collections from the oral cavity of chiselmouth in October 1975, 1977 and November 1977 contained numerous small, immature leeches that had apparently hatched within the preceding 1 or 2 mo.

TABLE 1.—Piscivorous leeches (Hirudinea) collected in this survey from teleost fishes in the central Columbia River, Washington State.

Species	Host infected
Piscicolidae:	
Myzobdella lugubris	Northern squawfish, *Ptychocheilus oregonensis*
	Chiselmouth, *Acrocheilus alutaceus*
	Brown bullhead, *Ictalurus nebulosus*
	Largescale sucker, *Catostomus macrocheilus*
	Bridgelip sucker, *C. columbianus*
Piscicola salmositica	Chinook salmon, *Oncorhynchus tshawytscha*, fry
	Sucker, *Catostomus* sp., fingerling
Glossiphoniidae:	
Placobdella montifera	Sucker, *Catostomus* sp., fingerling
Actinobdella inequiannulata	Largescale sucker, *C. macrocheilus*

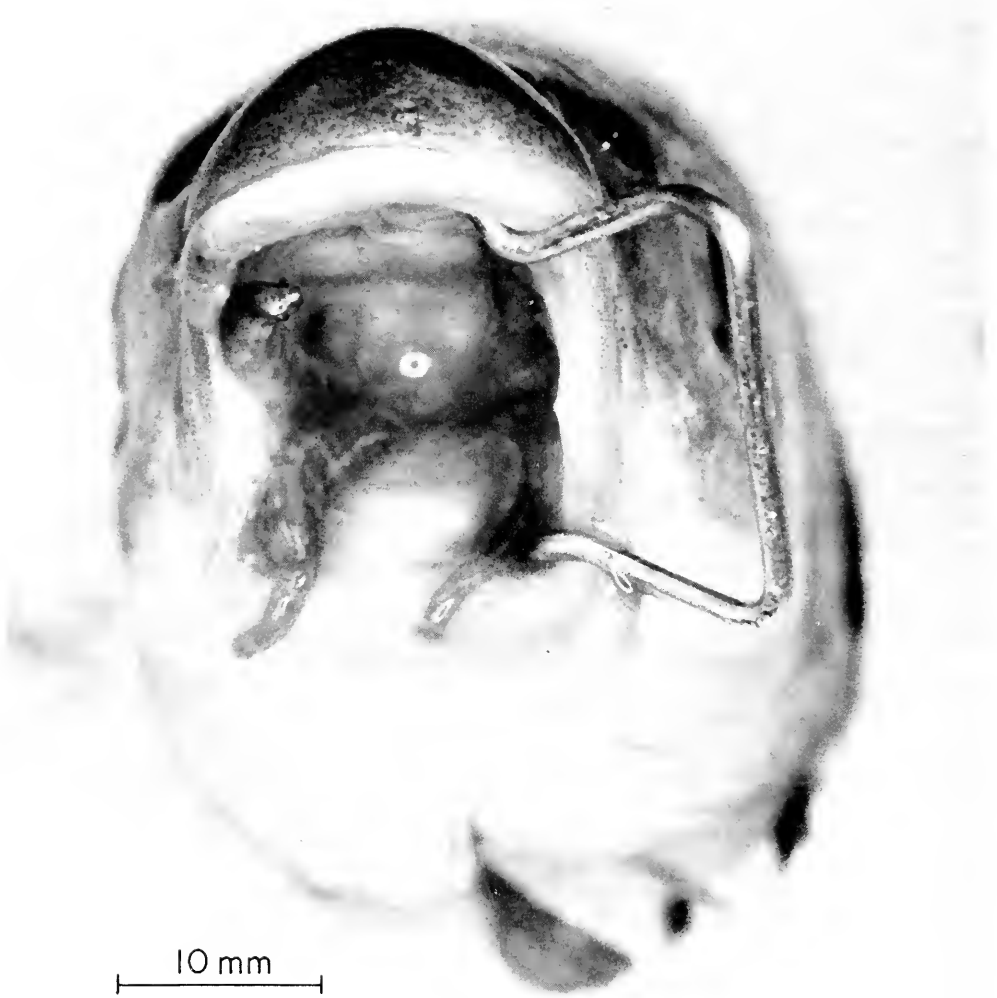

FIGURE 1.—Four sexually mature *Myzobdella lugubris* in the oral cavity of chiselmouth collected in the central Columbia River. The small subterminal mouth of the host is bordered by a cartilaginous upper and lower lip for grazing on sessile algae. The leeches occupy most of the available space in the oral cavity when the mouth is closed.

TABLE 2.—Incidence of infestation of chiselmouth and northern squawfish by the piscicolid leech, *Myzobdella lugubris*, indicated by infestation ratio.[1]

Month	Chiselmouth			Northern squawfish		
	1975	1976	1977	1975	1976	1977
Jan.	0/5	0/4	—	0/5	0/2	0/1
Feb	0/1	—	—	0/3	0/2	0/1
Mar	—	—	—	0/1	—	—
Apr	0/5	0/3	0/4	0/14	0/9	0/7
May	0/22	0/5	0/10	0/34	0/7	0/14
June	0/32	0/16	6/27	0/33	0/3	0/19
July	1/32	8/19	1/12	3/38	0/16	6/25
Aug.	1/19	0/4	19/42	0/13	0/2	0/8
Sept.	0/46	0/9	0/13	0/18	0/15	0/4
Oct	[2]7/37	0/10	[2]3/13	0/23	0/2	0/1
Nov	0/7	0/2	[2]7/9	0/4	—	0/3
Dec.	0/6	0/7	0/2	0/2	—	0/1

[1]Infestation ratio = number of fish infested/number of fish examined
[2]Numerous small leeches, recently hatched, were attached to some hosts.

According to Sawyer et al. (1975), *M. lugubris* is a relatively warm-water species encountered most often at 21°-30°C, occasionally at 16°-20°C, and less often in colder water. They reported that the leech appeared to be injured if the water was suddenly cooled to 10°-15°C in laboratory experiments. Obviously some *M. lugubris* survive over winter at low temperatures, but it must remain inconspicuous due to dormancy in temperate regions of North America. We have never recovered *M. lugubris* during winter in the central Columbia River, either from fish or from benthic samples

designed to quantitatively collect invertebrates.

Large, adult *M. lugubris* from Columbia River fish were characterized by a green background coloration, superficially suggesting that they fed on algal cells ingested by the host. Chiselmouth and suckers commonly feed on sessile, green-colored diatoms from bottom substrates. However, microscopic examination revealed that this coloration was due entirely to pigments in the adult leech's musculature and not to the presence of algae in their digestive tract. *Myzobdella lugubris* fed entirely on fish blood cells and plasma.

Feeding on fish blood is clearly required by *M. lugubris* for growth and reproduction. Copulating *M. lugubris* were noted on fish. But since deposition of a cocoon requires hard substrates, sexually mature leeches must eventually detach, thus freeing fish of infestations. The breeding, growth, and reproductive cycle of piscivorous leeches may account for the periodic infestations of fish so frequently documented in the literature.

In the Columbia River, the cycle in *M. lugubris* is correlated with a seasonal change in water temperatures, with peak activity occurring in late summer and fall.

In tidal estuaries on the east coast of the United States, *M. lugubris* has a life cycle that involves two hosts, a fish and a crustacean. It engorges on fish blood before detaching to deposit cocoons on crabs (Daniels and Sawyer 1975). This indicates possible involvement of a freshwater crustacean in the life cycle of *M. lugubris* in the Columbia River. The only large crustacean available is *Pacifasticus leniusculus*, but extensive collections of this crawfish in previous years by the senior author disclosed no attached leeches. Therefore, stones are probably used as cocoon deposition sites in the Columbia River.

Piscivorous leeches are often vectors of hemoflagellates (genera *Trypanoplasma* and *Trypanosoma*) found in the blood of freshwater and marine fishes (Khaibulaev 1970; Becker 1977). Although we have occasionally detected *Trypanoplasma* in Columbia River fish, we found no hemoflagellates in the digestive tract of over 20 *M. lugubris* taken from various hosts.

We did not examine histopathology of leech attachment and feeding sites in the oral cavity of infested Columbia River fish, although petechiae were evident during the fall on some chiselmouth. Inflammatory conditions and hyperplasia were described previously from a massive infestation of *M. lugubris* (misidentified as *Cystobranchus virginicus*) on white catfish in Virginia (Paperna and Zwerner 1974).

Piscicola salmositica

The salmonid leech, *P. salmositica*, was described from specimens taken, in part, from sea-run steelhead trout, *Salmo gairdneri*, transferred from the Columbia River to Mason Creek, Chelan County, Wash. (Meyer 1946a). The leeches infesting the fish originated either in the Columbia River or from Mason Creek. Thus the salmonid leech has previously been recorded from the upper Columbia River system. This species is usually associated with fall spawning runs of adult salmonid fishes in coastal streams, but it occurs elsewhere in the Pacific Northwest (Becker and Katz 1965a).

We collected several *P. salmositica* at various times from chinook salmon, *Oncorhynchus tshawytscha*, fry and once from a fingerling sucker. Each infestation consisted of a solitary leech attached to the dorsal surface of its host and feeding on blood. All specimens were taken in April and June as water temperatures (10°-14°C) increased and consisted of small leeches that presumably had hatched from cocoons the previous fall or winter. Three specimens contained developing trypanoplasms among their intestinal contents, evidence of prior feeding on infected fish. Therefore, *P. salmositica* is confirmed as a vector transmitting trypanoplasms among various fish in the central Columbia River. The salmonid leech is the only known vector of the piscine hemoflagellate *Trypanoplasma salmositica* (Katz 1951) in the Pacific Northwest (Becker and Katz 1965b).

Piscicola salmositica requires meals of fish blood before detaching to deposit cocoons on bottom substrates (Becker and Katz 1965a). Thus salmonid leeches presumably occur among and infest populations of anadromous chinook salmon that spawn each fall in the central Columbia River near our fish collection sites. However, we have not detected *P. salmositica* on transient adult fall chinook salmon returning from the sea to spawn or from downstream drifting, spawned out salmon carcasses. Neither have we found salmonid leeches on several adult steelhead trout and spring-run chinook salmon examined during the summer at the Ringold Hatchery (Washington State Department of Game) above Richland. On the basis of our observations, *P. salmositica* is not an abundant leech in the central Columbia River.

Placobdella montifera

One immature *P. montifera* was recovered from the dorsal surface of a fingerling sucker in early October 1976. We also collected one adult specimen from beneath shoreline rocks at Umatilla Reservoir during June where it was depositing a cocoon. The species is not a common ectoparasite of fish. It probably occurs mostly along reservoir shorelines where water levels remain relatively stable, rather than along the margins of the free-flowing Columbia River above Richland.

Placobdella montifera has been reported to attack aquatic worms, insect larvae, mussels, frogs, toads, and fish, but the only specific host records are fish (Hoffman 1967; Klemm 1972a, 1975, 1976; Sawyer 1972; and others). This leech, as do most glossiphoniids, broods its cocoon and carries its young. An uncommon but widely distributed species, *P. montifera* is listed as having been reported previously from Washington (Klemm 1972b). Distributional records probably valid include British Columbia, Saskatchewan, Ontario, and the northern states east of the Mississippi River southward to Georgia (Sawyer 1972; Klemm 1977).

Actinobdella inequiannulata

Six *A. inequiannulata* were collected from the axila of the pelvic and pectoral fins of one adult largescale sucker in mid-August 1975. According to Sawyer (1972), this glossiphoniid is known from Illinois, Minnesota, and Ohio; Klemm (1972a, b, 1977) adds Michigan, Pennsylvania, and New York; and Daniels and Freeman (1976) add Ontario. *Actinobdella triannulata* Moore 1924, a name common in earlier literature, is now considered a junior synonym of *A. inequiannulata* (Daniels and Freeman 1976; Klemm 1977).

Daniels and Freeman (1976) provide a redescription of *A. inequiannulata* on basis of specimens collected from two species of suckers (genus *Catostomus*) and preserved material from the U.S. National Museum. The species was earlier considered as free-living with no known hosts (Sawyer 1972; Klemm 1972a). Since its synonym *A. triannulata* displayed a predilection for suckers (Hoffman 1967), the host preference of *A. inequiannulata* is now partially resolved. Little is known of its ecology and life cycle. We did not examine our specimens for ingested fish blood.

The host relationship for glossiphoniids is generally considered to be less obligatory than for piscicolids, and most are omnivorous feeders. Apparently *A. inequiannulata*, *P. montifera*, and *P. pediculata* Hemingway 1908 are the only three American glossiphoniids consistently reported to parasitize fish. Several authors have reported *P. pediculata* from the freshwater drum, *Aplodinotus grunniens*, and Sawyer (1972) has indicated a high degree of host specificity; it has not been reported from the Pacific Northwest, nor would it be expected in this region due to its narrow host preference.

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INDUCED SPAWNING AND LARVAL REARING OF THE YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

The yellowtail flounder, *Limanda ferruginea* (Storer), a commercially important flatfish, occurs in North American continental waters from the north shore of the Gulf of St. Lawrence southward to the lower part of Chesapeake Bay (Bigelow and Schroeder 1953). The yellowtail flounder spawns from March through August where water temperatures over its range vary from about 5° to 12°C (Colton 1972). The eggs are pelagic and lack an oil globule; diameter of the live eggs (range 0.79-1.01 mm) averages 0.88 mm (Colton and Marak 1969).

A program to obtain viable yellowtail eggs through hormone induction, to rear larvae through metamorphosis, and to determine the mechanisms of survival of early life stages under controlled laboratory conditions was undertaken. The successful induction of yellowtail flounder and subsequent rearing of the larvae through metamorphosis marks the first time the early life history of this flatfish has been completed in the laboratory.

Materials and Methods

Adult yellowtail flounder were captured by otter trawling in Block Island Sound in the winters of 1974, 1975, and 1976 and transported to the Narragansett Laboratory in a 380-l live car equipped with an aerator. In the laboratory the fish were held in a 28,000-l aquarium. A continual supply of filtered seawater was pumped to the aquarium from Narragansett Bay.

Individuals presumed to be sexually mature were selected by length. Available length-weight data (Lux 1969) indicated that yellowtail flounder in southern New England waters mature when they attain a length near 35 cm or an age of 3 yr (Lux and Nichy 1969). After acclimating in the laboratory, the fish were segregated by sex, measured and weighed, and tagged with numbered plastic pennants secured through the caudal peduncle. Yellowtail flounder were sexed by holding the white underside to the light and looking through the flesh. The outline of the ovary extending posteriorly from the mass of viscera can readily be seen even in immature females (Royce et al. 1959). Yellowtail flounder are delicate and excitable. To minimize injury, the fish were anesthetized in a solution of tricane methanesulfonate (MS-222[1]) at a concentration of 1:20,000 (Leitritz and Lewis 1976) during each examination.

While the fish were held in captivity, a photoperiod of 11 h of light and 13 h of dark simulated spawning light conditions. Four banks of fluorescent lights (each bank composed of 16 40-W bulbs) were suspended 4 m from the ceiling and mechanically timed. The light banks were sequentially turned on and off in the morning and evening at 15-min intervals to simulate dawn and twilight. Prior to receiving hormones the fish were fed a daily diet of chopped frozen hake, whiting, or squid. During the trials the fish were not fed.

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

The effectiveness of the pituitary preparations was evaluated by monitoring the gonosomatic index (GSI), ovulation, success of egg fertilization, and hatching success. Hormones were prepared on the day of injection, and dosages were established by the weight of each individual fish. A saline solution of isotonic sodium chloride was used as a carrier. All injections were administered (2-cm^3 syringe, 20 gage 3.85-cm needle) intramuscularly into the back below the dorsal fin. Inserting and withdrawing the needle slowly aided in retaining most of the fluid in the flesh. After injection, the flesh of the fish was massaged to diffuse the fluid into the muscles.

Sexually mature fish were hand stripped and the eggs fertilized in a polyethylene pan. Several thousand eggs were collected at each spawning, and the sperm of two males was used to fertilize the eggs from each female. Yellowtail flounder are nonsynchronous spawners (Bigelow and Schroeder 1953), and multiple spawnings occurred among most induced fish. The fecundity of yellowtail flounder increases with age and body length, and an individual female may yield from 350,000 to more than 4,000,000 eggs during the spawning season (Pitt 1971).

The state of ova maturation of the experimental fish was observed at the start and termination of each experiment. Before injecting, a polyethylene cannula was inserted into the oviduct and oocyte samples were orally withdrawn. The oogenesis of oocytes was divided by microscopic observation into three general histological stages:

Stage I - the primary oocyte stage, oocytes contained cytoplasmic vacuoles and measured between 0.1 and 0.25 mm.

Stage II - the yolk globule stage, cytoplasm of oocytes was filled with dense yolk granules and measured up to 0.6 mm.

Stage III - ripe stage, hyaline oocytes present and measured 0.75-1.00 mm in size.

Fertilized eggs were incubated in static, aerated, black-sided aquaria that had been inoculated with the green algae *Dunaliella* sp. A single application of penicillin (25 international units [IU]/ml) and streptomycin (0.02 mg/ml) at the concentration of 50 mg/l was effective in controlling bacterial contamination of the aquaria in almost all cases.

Three series of experiments were undertaken to determine the effectiveness of the hormone injections (Table 1). The first trial was conducted in winter 1975 to determine if induced spawning would occur at low winter water temperatures. The second and third were conducted in the springs of 1976-77 and coincided with the yellowtail flounder's natural spawning season.

Hormone dosage levels of 2, 5, and 10 mg/kg fish and frequency of injecting were dictated by previous successful results obtained with the summer flounder, *Paralichthys dentatus*, (Smigielski 1975a) and winter flounder, *Pseudopleuronectes americanus*, (Smigielski 1975b). After each trial the female fish were killed and reweighed, the ovaries were examined, and gonosomatic indices were recorded. Prior to receiving hormone injections, all the female test fish in the first trial were in Stage I of oocyte oogenesis, and most females prior to the second and third trials were in Stage II. Males were not injected in the second and third trials because they were sexually ripe.

Results and Discussion

First Trial

In the first trial (Table 1), most females in the group receiving 10 daily injections of 2 mg pituitary were refractory with low GSI values (7-13%). One fish hydrated but did not ovulate, and a small number of Stage II ova were found in the ovaries. Hydration is an increase in total body weight. The weight gain is due mostly to water intake and is reflected by higher GSI values as most of the water appears to go into the gonads. Excessive hydration is manifested by grossly bloated fish which in some instances can hydrate to the point of death without ovulating.

TABLE 1.—Hormone dosages, water temperatures, and number of yellowtail flounder in each trial.

	Trial 1 - January 1975 Water temperatures, 3°-6°C (Mean 5.1°C)			Trial 2 - April 1976 Water temperatures, 7°-10°C (Mean 9.2°C)			Trial 3 - April 1977 Water temperatures, 8.5°-12.5°C (Mean 10.1°C)		
Daily carp pituitary dosages	Number of females	Number of males	Uninjected controls	Number of females	Number of males	Sham injected controls	Number of females	Number of males	Sham injected controls
2.0 mg/kg fish	6	4	3	8	0	4	9	0	4
5.0 mg/kg fish	6	4	3	8	0	4			
10.0 mg/kg fish	6	4	3	7	0	4			

In the group of females receiving 10 daily injections of 5 mg, three fish were refractory with low GSI values (10-15%), and three hydrated but did not ovulate. Two of the latter fish contained a small number of Stage II ova; the other developed a cloacal plug of membranous tissue and Stage I ova.

In the group receiving 10 daily injections of 10 mg, all were refractory with low GSI values (9-11%), except for one fish that hydrated but did not ovulate. A membranous plug developed in the cloaca of this fish, and it was bloated. A very small number of Stage II ova were found in the ovaries. There was no indication of sexual ripening in the uninjected control fish, and their GSI values were low (10-13%). Copious semen was obtained from the males injected at all three dosages; however, fertilization was not attempted. It was reasoned from the first trial that low GSI values (7-15%) of females coupled with low water temperatures (3°-6°C, mean 5.1°C) that were less than optimum inhibited the effectiveness of the hormones, for although some fish hydrated, they did not ovulate.

Second Trial

The results obtained from the second trial were variable (Table 2). All but one fish receiving injections of 2 mg hydrated and ovulated. Two fish died during the trial; one, after yielding spawn on two occasions, developed a membranous plug and became grossly bloated.

In the group receiving injections of 5 mg, two fish ovulated but the eggs obtained were not fertile. Three other fish developed plugs and hydrated to the point of death. Injections were discontinued at the first sign of abnormal hydration, but the fish continued to imbibe water.

In the group that received 10 mg, five fish experienced excessive hydration manifestated by bloating, plug formation, and, in two instances, death. The membranous plugs were identical to those that developed in the test group that received hormone dosages of 5 mg. The controls had four fish with signs of hydration but no Stage III ova were found in their ovaries.

Third Trial

The results of the third trial paralleled those of the second trial at a dosage of 2 mg. Seven of the experimental females hydrated normally and ovulated (Table 3). Fertilization and hatching of these eggs were satisfactory and the larvae were normal. The remaining two fish died during the trial, and their ovaries had a small number of Stage III ova. The control fish neither hydrated nor ovulated; GSI values were fairly high, but Stage III ova were absent.

The anomalous hydration with bloating and formation of membranous plugs during hormonal induction is not unique. Clemens and Grant (1964) injected female goldfish, *Carassius auratus*, with carp pituitary and observed that the gonadal water content increased, apparently in association with ovulation. The hormone regulating the hydration process appeared to be a gonadotropin.

Shehadeh and Ellis (1970) reported the formation of plugs in the cloaca in striped mullet, *Mugil cephalus*, treated with a combination of salmon pituitary and Synahorin. Sinha (1971) studied the gonadal hydration response of *Puntis gonionotus* using the second fraction of molecular seived carp pituitary extract and suggested that the second fraction is involved in osmoregulation, since an injection of an additional amount enhances the rate of water transport resulting in maturation.

Hirose and Ishida (1974) studied the effects of Cortisol and human chorionic gonadotropin (HCG) in ayu, *Plecoglossus altivelis*, and reported that the water content of the ovary from hormone-treated fish increased by 6%. Smigielski (1975b) reported a similar response in winter flounder injected with pregnant mare serum (PMS) and HCG. Hirose (1976) demonstrated that gonadotropin-treated ayu imbided a greater quantity of water than control ayu. He suggested that gonadotropin may act on the sodium and potassium system or permeability of the egg membrane.

Hydration is a normal and necessary prelude to maturation and ovulation. The cases of abnormal hydration experienced with yellowtail flounder may be attributed to an adverse reaction to hormone dosage. Most of the test fish that hydrated abnormally and became bloated had an increase in body weight of more than 10%. The increase in body weight appeared to be a result of the fish imbibing an excess amount of water. An excessive amount of introduced hormone may upset the water transport or sodium potassium systems, resulting in more water bing imbibed.

In conclusion, it appears that water temperatures higher than 6°C and GSI values approaching 20% coupled with carp pituitary injections approximating 2 mg/kg of fish is an effective combi-

TABLE 2.—Effects of carp pituitary on yellowtail flounder receiving daily injections. All fish were exposed to 11L:13D photoperiod and water temperatures of 8.5°-12.5°C (Mean 10.1°C). Symbols: + = did, 0 = did not hydrate or ovulate.

Dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% initial wt)	GSI (% final wt)	Effect: Hydrated	Effect: Ovulated	Date of spawning 1976	Fertilization (%)	Hatch (%)
2.0 mg/kg fish	8	348	396	+6.94	19.7	+[1]	0			
	7	340	392	−1.84	5.6	+	+	Apr. 6	80	70
								Apr. 7	70	75
	4	353	421	−3.30	5.1	+	+	Apr. 6	75	55
								Apr. 7	70	60
								Apr. 8	80	70
								Apr. 9	90	75
								Apr. 11	70	60
	1	435	817	−0.96	4.3	+	+	Apr. 4	75	80
								Apr. 5	80	75
								Apr. 6	70	60
								Apr. 7	70	50
								Apr. 9	75	75
	6	280	263	−0.49	7.0	+	+	Apr. 5	80	75
								Apr. 7	75	70
								Apr. 8	80	70
	4	350	381	+1.12	8.4	+	+	Apr. 8	80	60
								Apr. 9	80	50
								Apr. 11	70	80
	6	450	882	+9.54	24.0	+	+[2]	Apr. 1	80	75
								Apr. 3	75	70
	6	387	721	+0.98	11.2	+	+	Apr. 5	80	80
								Apr. 6	75	65
Controls		420	667	+2.12	18.6	0	0			
		392	611	+2.63	19.6	+	0			
		361	409	+1.09	10.5	0	0			
		381	562	+0.44	9.8	0	0			
5.0 mg/kg fish	5	401	683	+2.11	18.6	+	+[3]			
	6	501	1,489	+9.62	29.5	+[2]	0			
	4	307	566	+11.69	26.1	+[2]	0			
	5	435	1,131	+13.17	24.9	+[2]	0			
	10	348	762	−0.19	4.6	0	0			
	5	351	491	+8.47	30.8	+[4]	+[3]			
	10	336	418	+0.96	11.0	0	0			
Controls		361	521	+2.92	19.3	+	0			
		392	587	+2.87	19.5	+	0			
		406	702	+2.19	15.1	0	0			
		339	367	+1.87	12.9	0	0			
10 mg/kg fish	5	467	1,259	+11.15	28.6	+[4]	0			
	4	346	593	+13.57	27.6	+[2]	0			
	5	352	463	+15.11	29.6	+[4]	+[3]			
	5	433	1,245	+10.76	25.3	+[4]	0			
	7	341	485	+14.06	29.1	+[2]	0			
	10	360	501	+1.16	12.6	0	0			
	10	348	437	+1.84	14.2	0	0			
Controls		343	428	+1.23	15.1	0	0			
		389	672	+2.63	17.9	+	0			
		430	891	+4.78	19.3	+	0			
		369	551	+1.63	14.3	0	0			

[1]Died, ~ 10% Stage III ova in ovaries, not fertilized.
[2]Plug formed, fish became bloated and hydrated to point of death
[3]Stage III ova in ovaries, not fertilized
[4]Plug formed, fish became bloated

nation for inducing spawning of yellowtail flounder.

Larval Rearing

Fertilized yellowtail flounder embryos were incubated in 64-l, rectangular, black-sided, static, well-aerated aquaria at a density of approximately 80 embryos/l. The incubating and rearing temperature was 10°C and the salinity 32‰. Banks of 40-W timed fluorescent lights suspended 1 m over the aquaria simulated a day and night regimen of 15 h light and 9 h dark (15L:9D). The aquaria were inoculated with green algae (*Dunaliella* sp.) which may have aided in the removal of metabolic waste products produced by the larvae. The algae also served to sustain the zooplankton introduced as food. A single application of penicillin (25 IU/ml) and streptomycin (0.02 mg/ml) was effective in controlling bacterial contamination in almost all cases.

At 10°C, hatching occurred 6-7 days after fertilization. Yolk absorption occurred 4-5 days after hatching, which coincided with first feeding. The larvae averaged 2.75 mm long upon hatching and possessed a completely formed gut. The eyes were

TABLE 3.—Effects of carp pituitary on yellowtail flounder receiving daily injections. All fish were exposed to 11L:13D photoperiod and water temperatures of 8.5°-12.5°C (Mean 10.1°C). Symbols: + = did, 0 = did not hydrate or ovulate.

Dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% initial wt)	GSI (% final wt)	Effect		Date of spawning 1977	Fertilization (%)	Hatch (%)
						Hydrated	Ovulated			
2.0 mg/kg fish	3	391	552	+0.56	4.6	+	+	Apr. 12	75	80
	3	453	898	+9.13	21.2	+[1]	0			
	2	474	1,298	+4.70	6.9	+	+	Apr. 12	80	70
								Apr. 14	80	75
	4	424	878	+7.16	20.8	+[1]	0			
	5	412	733	+2.04	5.3	+	+	Apr. 16	50	60
								Apr. 17	60	40
								Apr. 18	60	45
	5	364	486	+0.97	10.7	+	+	Apr. 17	60	55
								Apr. 18	70	65
	6	396	598	+1.62	8.8	+	+	Apr. 17	70	60
								Apr. 18	70	55
	5	405	694	+2.79	7.7	+	+	Apr. 16	85	60
	3	437	945	+3.17	9.3	+	+	Apr. 14	70	80
Controls		392	601	+2.16	18.0	0	0			
		446	891	+2.79	18.9	0	0			
		409	667	+1.92	16.7	0	0			
		359	472	+2.19	18.4	0	0			

[1]Died. Stage III ova in ovaries

pigmented at 1 day and the mouth was functional at 1-3 days after hatching. No abnormalities were observed in hormone-induced larvae.

Twenty larvae were sampled weekly (Table 4). The specific growth rates for the 63-day period from first feeding averaged 9.97%/day for dry weight (micrograms) and 2.75% standard length (millimeters). The first fish metamorphosed 54 days after hatching at 17.00 mm standard length. By the 63d day after hatching, all the larvae had completed metamorphosis, and average length was 17.40 mm.

Wild copepod nauplii were collected daily from a nearby estuary and fed to the larvae after being sieved to obtain the proper particle size. Larvae of the yellowtail flounder required small food organisms (<100μm in largest dimension) to initiate feeding. The most difficult aspect of rearing the larvae was the problem of obtaining enough food organisms in the size range required. Larval mortality was high for the first 2 wk of feeding, possibly caused by starvation. However, yellowtail flounder larvae are able to survive for considerable periods of days without exogenous food. Some larvae were maintained at 8°C and fed successfully and survived after being deprived of food for 10 days after hatching (Smigielski unpubl. data). As the larvae increased in size through metamorphosis, larger food organisms such as adult copepods, the rotifer *Branchionus plicatilis*, and the brine shrimp, *Artemia* sp., were offered.

TABLE 4.—Size of yellowtail flounder larvae reared artificially at 10°C from hatching to metamorphosis. Average sizes of 20 larvae are followed by standard deviation.

Days after first feeding	Mean length (mm)	Mean dry weight (μg)
1	3.08±0.20	16.2±4.3
7	3.39±0.25	19.8±4.3
14	5.16±0.47	56.0±20.1
21	5.92±0.79	89.9±57.4
27	6.82±0.51	126.5±34.0
34	6.68±0.89	161.5±66.4
41	8.95±1.03	608.6±340.2
48	10.53±4.38	1,133.3±1,267.8
55	14.73±3.98	5,576.6±2,694.1
63	17.40±2.33	8,635.9±3,058.4

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TRACE METAL CONTAMINATION OF THE ROCK SCALLOP, *HINNITES GIGANTEUS*, NEAR A LARGE SOUTHERN CALIFORNIA MUNICIPAL OUTFALL[1]

Los Angeles County's submarine discharge of municipal wastewater from the Joint Water Pollution Control Plant (JWPCP) off Palos Verdes Peninsula is the single largest anthropogenic source of trace metals to the marine ecosystem off southern California. The 1974 annual mass emission rates of chromium, copper, and zinc via this discharge (4.8×10^{11} l/yr, which underwent primary treatment only) were about 400, 300, and 850 t, respectively; these were approximately 10 times the corresponding inputs measured in 1971-72 surface runoff from southern California (Young et al. 1973). As a result, bottom sediments around this submarine outfall system are highly contaminated by a number of trace metals (Galloway 1972; Young et al. 1975). Here we report abnormal levels of seven metals in three tissues of the filter-feeding rock scallop, *Hinnites giganteus*,[2] that was collected in the discharge zone and thus had been exposed to suspended wastewater particulates. (The adductor muscle of this bivalve mollusc is considered to be a delicacy, and scallops near the discharge are sought by sport divers.)

Procedures

During 1974, divers collected eight scallops within the size range generally consumed (10 to 25 cm in diameter) from depths of about 20 m at three stations in the discharge zone between Whites Point and Point Vicente: these stations were <1 km off Palos Verdes Peninsula. Six scallops in the same size range also were taken from control stations at similar depths off Santa Catalina and Santa Barbara Islands (Figure 1). To check our 1974 results, during 1976 eight specimens within this size range were again collected from this region in the discharge zone. However, we were not able to obtain additional island samples; therefore, five specimens were collected from each of two coastal stations located approximately 50 km to the north and south of Palos Verdes Peninsula. The samples were frozen in plastic bags after collection. Later, digestive gland, gonad, and adductor muscle tissues were excised from each specimen before it was fully thawed, using a new carbon steel scalpel and a cleaned Teflon[3] sheet; the tissues were placed in cleaned polyethylene vials. Care was taken to avoid contaminating the gonadal or muscle tissue samples with sediments or juices from the digestive glands.

Following dissection, each sample (1 to 2 g wet weight) was digested in 10 ml of a 1:1 nitric acid

[1]Contribution No. 85 of the Southern California Coastal Water Research Project.

[2]Formerly *Hinnites multirugosus* (Roth and Coan 1978).

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

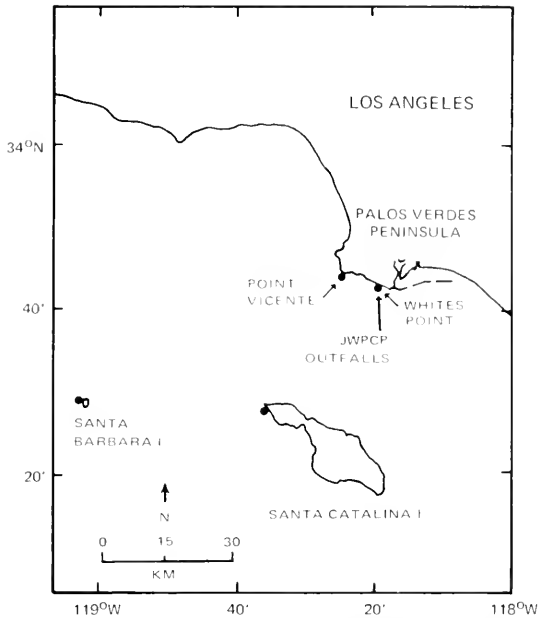

FIGURE 1.—Outfall and island control sites off Los Angeles, Calif., for collection of rock scallops.

solution (ultrahigh-purity reagent grade) until the remaining volume was about 3 ml. This procedure was repeated once, and the final residue was filtered through an acid-washed Whatman No. 40 filter. The filtrate was then diluted to an appropriate volume, and the treated sample was analyzed by atomic absorption spectrometry. Silver, chromium, copper, nickel, and lead were measured by injecting 2.5 μl of sample into a graphite furnace; cadmium and zinc levels were determined by aspirating the sample into an air-acetylene flame.

Process blanks were analyzed with all samples. Typical blank corrections were <10% of the gross concentrations observed, except for chromium, nickel, and zinc in adductor muscle, where the blank corrections were 15-20% of the gross concentrations. To test digestion efficiency, residues collected after filtration were redigested following the same procedure employed initially but using only 5 ml of 1:1 nitric acid solution; levels measured in the residue generally were <5% of the concentrations found in the first digestion. In addition, using this procedure on Standard Reference Material No. 1571 (orchard leaves) we have obtained values for our target metals which are within the ranges reported by the National Bureau of Standards (NBS); in all cases our results agreed within ±20% of the NBS values.

Results and Discussion

A comparison of the 1974 and 1976 results indicated that, for each of the seven metals studied, there were no significant differences between levels in the Palos Verdes scallops collected during the 2 yr. Therefore, the data from these 16 specimens have been combined to obtain an estimate of metal concentrations in scallops around the JWPCP submarine outfalls (Table 1). However, distinctly higher levels of silver, chromium, and copper were measured in the specimens from the other two coastal stations, compared with those in the scallops from the island control sites. Alexander and Young (1976) also observed elevated concentrations of these three metals in digestive glands of the intertidal mussel *Mytilus californianus* collected within 100 km of Los Angeles, indicating the widespread influence of municipal wastewater discharges on distributions of silver, chromium, and copper in the nearshore marine ecosystem of southern California. Therefore, we have used only the data from the six island specimens to estimate natural concentrations of the target trace metals in the three scallop tissues investigated (Table 1). For each metal we have calculated a "contamination factor," defined as the

TABLE 1.—Trace metal concentrations (mg/wet kg) in tissues of rock scallops collected during 1974-76 from the Palos Verdes outfall zone (16 specimens) and from island control stations (6 specimens). Single and double asterisks indicate experimental results are significantly different from control results at $P<0.05$ and $P<0.01$, respectively.[1]

	Digestive gland		Gonad		Adductor muscle	
Metal	Outfall	Control	Outfall	Control	Outfall	Control
Silver:						
Mean	2.0**	0.31	0.21**	0.018	0.016	0.010
±SE	0.34	0.068	0.071	0.008	0.004	0.003
Cadmium:						
Mean	430	550	5.0	5.5	0.92**	0.34
±SE	76	61	1.4	2.3	0.070	0.027
Chromium:						
Mean	42**	2.2	8.8**	0.39	0.33**	0.050
±SE	5.7	0.48	3.0	0.049	0.038	0.025
Copper:						
Mean	210**	65	3.7*	2.3	0.32*	0.16
±SE	25	16	0.52	0.49	0.058	0.042
Nickel:						
Mean	1.1	1.5	0.36	0.26	0.14	0.12
±SE	0.13	0.11	0.12	0.10	0.034	0.050
Lead:						
Mean	9.3	4.4	0.08	<0.06	0.05	0.03
±SE	1.8	1.4	—	—	—	—
Zinc:						
Mean	120	100	38*	20	22	22
±SE	10	17	3.9	7.2	1.7	0.69

[1]Determined by the nonparametric 2-sided Mann-Whitney *U* Test.

ratio of the mean concentrations for the outfall and control samples (Table 2).

It seems clear from these data that rock scallops living inshore of the JWPCP discharge accumulate trace metals at above-normal levels. Application of the 2-sided Mann-Whitney *U* Test (Tate and Clelland 1957), a nonparametric test which assumes neither normality nor homogeneity of variance, indicated that, in 10 of the 19 comparisons, the experimental (JWPCP) results are significantly different from those of the controls (Table 1). In all 10 of these cases the experimental means are higher.

In our past studies with molluscan bioindicators, we have generally used digestive gland concentrations to locate possible metal contamination because concentrations are usually higher in this tissue than in the gonad or adductor muscle (Alexander and Young 1976; Eganhouse and Young 1976). However, these values may not be representative of the degree to which metals are actually incorporated into the body tissues because the digestive gland sample may contain ingested particulates contaminated by metals that are not biologically available. Therefore, the gonad and muscle contamination ratios found in this study are of special interest. In 7 of the 12 comparisons, the experimental results were found to be significantly higher than those of the controls (Table 2). For five of the six metals measurable (lead was undetectable in these tissues), at least one of the two contamination ratios is essentially ≥ 2. In addition, we found the mean concentration (± 1 SE) of total mercury in adductor muscle of three Palos Verdes scallops to be 0.059 ± 0.005 mg/wet kg. This value is more than twice the mean concentration measured in three island specimens (0.027 ± 0.008 mg/wet kg). However, it should be noted that mercury levels in the Palos Verdes specimens were still an order of magnitude below the U.S. Food and Drug Administration action level of 0.5 mg/wet kg in seafood intended for interstate commerce.

TABLE 2.—Contamination factors[1] for seven metals in three tissues of rock scallops from the Palos Verdes outfall zone and island control stations. Factors indicate experimental to control ratios for mean concentrations (Table 1).

Metal	Digestive gland	Gonad	Adductor muscle
Silver	6.5**	12**	1.6
Cadmium	0.78	0.91	2.7**
Chromium	19**	23**	6.6**
Copper	3.2**	1.6*	2.0*
Nickel	0.73	1.4	1.2
Lead	2.1	—	—
Zinc	1.2	1.9*	1.0

[1]Single and double asterisks indicate significant differences between experimental and control results at $P<0.05$ and $P<0.01$, respectively.

As shown in Table 1, the mean concentration of lead in the digestive gland of the outfall scallops was 9.3 mg/wet kg, approximately 100 and 200 times the upper limit concentrations measured in the gonadal and muscle tissues, respectively. These results indicate that elevated concentrations of other metals measured in the gonad and muscle tissues were not caused by contamination from the digestive gland during dissection. Thus, rock scallops exposed to municipal discharges do appear to be capable of physiologically incorporating at least six potentially toxic trace metals in their gonadal or muscle tissue to levels at least twice normal concentrations.

The mean values for cadmium in the digestive gland and gonads of the Palos Verdes specimens were somewhat lower than those for the island controls (Table 1); the respective outfall-to-control ratios were 0.80 and 0.92. We have made similar observations in previous studies of metals in flatfish taken by trawl from the two areas (de Goeij et al. 1974; McDermott, Alexander, Young, and Mearns 1976). Liver tissue from Dover sole, *Microstomus pacificus*, collected during 1971-72 and known by their high DDT levels and high incidence of fin erosion disease to have inhabited the highly contaminated sediments, were shown by neutron activation analysis to have significantly lower concentrations of cadmium than did the livers of island control specimens; the outfall-to-control ratio was 0.33 (de Goeij et al. 1974). Analyses of subsequent collections (1972-73) using a different laboratory and analytical technique (arc emission spectroscopy) confirmed this observation, yielding an outfall-to-control ratio of 0.59 (McDermott, Alexander, Young, and Mearns 1976). In addition, analyses by atomic absorption spectroscopy recently conducted in our laboratory revealed depressed cadmium concentrations in livers of diseased flatfish collected during 1976 and 1977 off Palos Verdes Peninsula and in Seattle's Duwamish River Estuary (two regions highly contaminated by chlorinated hydrocarbons); relative to control levels, the corresponding concentration ratios were 0.60 and 0.30, respectively.[4] Further, analyses of digestive glands of intertidal mussels we collected at the base of the

[4]Sherwood, M. J. 1977. Fin erosion disease and liver chemistry: Los Angeles and Seattle. *In* Coastal water research project annual report, p. 213-219. South. Calif. Coastal Water Res. Proj., El Segundo. NTIS PB274463/AS.

Palos Verdes outfalls and at island control stations during 1971 yielded[5] an outfall-to-control ratio for cadmium of 0.81.

The relatively low cadmium levels often found in some tissues or organisms living around the Palos Verdes outfalls may be related to the high levels of chlorinated hydrocarbons that have accumulated there from past wastewater discharges. Concentrations of total DDT and total PCB in mussels, sediments, and flatfish from the region are 100 to 1,000 times those measured in samples from island control areas (Young et al. 1976: McDermott, Young, and Heesen 1976). Recently, Nimmo and Bahner (1976) reported that exposure of a penaeid shrimp to methoxychlor (a chlorinated pesticide somewhat similar to DDT and PCB) appeared to depress concentrations of cadmium in this organism. It is possible that animals off Palos Verdes are showing a similar effect.

Conclusions

The data presented here indicate that the submarine injection of primary-treated municipal wastewater can lead to distinct trace metal contamination of filter-feeding rock scallops within a few kilometers of the discharge. Mean values for silver, cadmium, chromium, copper, mercury, and zinc in gonadal and or muscle tissue of specimens collected near the Los Angeles County outfalls ranged from approximately 2 to 23 times the corresponding means for control specimens. These elevations do not appear to be artifacts caused by contamination from particulates in the digestive gland, but rather to result from actual physiological uptake of the metals. Although the results of this study point to a potential problem from waste metals discharged via municipal outfalls, we do not yet know the degree to which such elevated metals affect the rock scallop or its predators.

Acknowledgments

We thank Douglas Hotchkiss and the captain and crew of the Los Angeles County Sanitation District research vessel for collecting the scallop specimens used in this study. We also thank Project associates Deirdre McDermott-Ehrlich, Patrick Hershelman, Michael Moore, and Edward Motola for their assistance.

[5]Southern California Coastal Water Research Project. 1973. The ecology of the Southern California Bight: Implications for water quality management. South. Calif. Coastal Water Res. Proj., El Segundo, TR 104, 531 p. NTIS PB274462 AS.

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INDEX

Fishery Bulletin Vol. 76, No. 1-4

ERRATA

Fishery Bulletin, Vol. 76, No. 3

Leis, Jeffrey M., "Systematics and zoogeography of the porcupinefishes (*Diodon*, Diodontidae, Tetraodontiformes), with comments on egg and larval development," p. 535-567.

1) Page 545, the photo is mirror image of a photo of *Diodon holocanthus* by J. E. Randall.

2) Page 555, the photo is mirror image of a photo of *Diodon hystrix* by J. E. Randall.

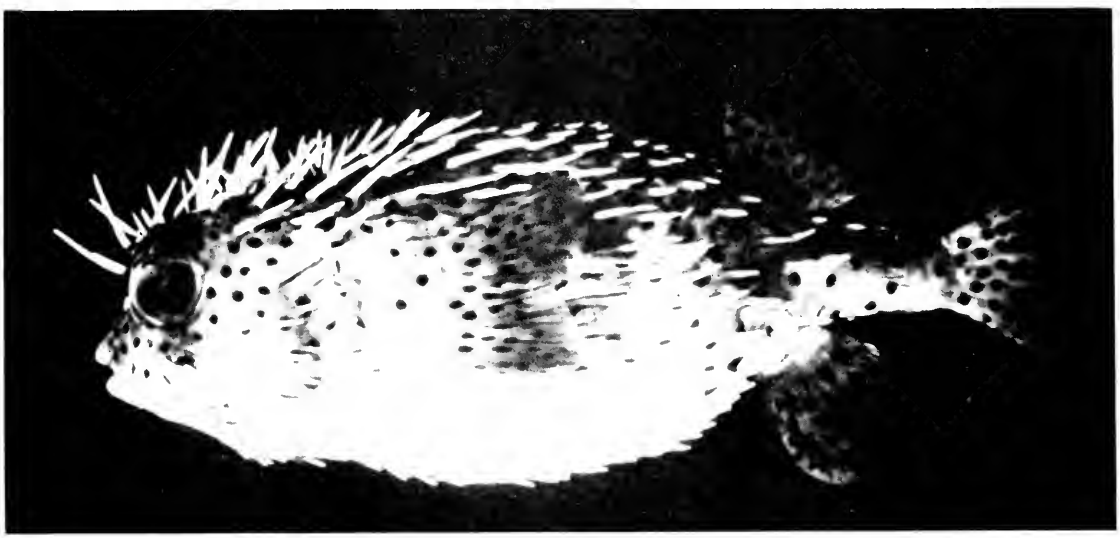

FIGURE 9.—*Diodon hystrix*, 273 mm SL, Oahu, Hawaiian Islands (BPBM 11656). Photo by J. E. Randall.

545

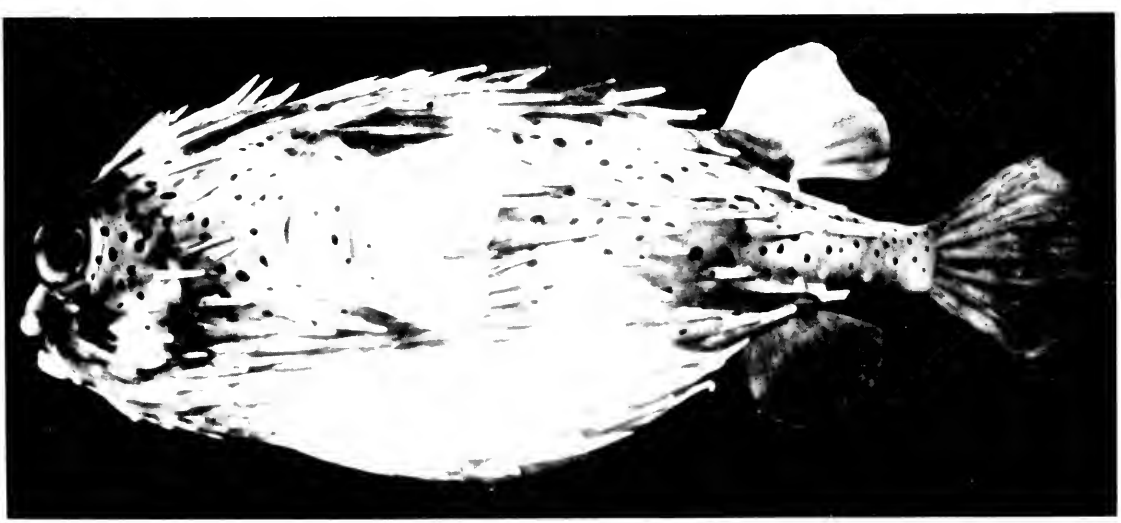

FIGURE 17.—*Diodon holocanthus*, 195 mm SL, Wolmar, Mauritius (BPBM 20255). Photo by J. E. Randall.

555

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Contents–continued

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